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1 **New Siluro-Devonian anomalocystitids (Echinodermata,**
2 **Stylophora) from Bolivia and Canada, and a reevaluation of**
3 **skeletal homologies in mitrates**

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14 **Abstract**– Two new mitrate stylophorans are described from the upper part of the Santa Rosa
15 Formation (Lochkovian) in the Central Subandean Zone of Bolivia and from the Jupiter
16 Formation (Cybèle Member, late Llandovery) of Anticosti Island (Canada). Both stylophorans
17 are identified as allanicytidiine anomalocystitids. The new Bolivian mitrate, *Perikefalea*
18 *racheboeufi* gen. and sp. nov. is characterized by a strongly reduced number of plates (five)
19 on its upper thecal surface and a strong spike on its posterior median marginal. The
20 morphology of *P. racheboeufi* suggests relatively strong affinities with *Occultocystis*, from
21 the Lower Devonian Talacasto Formation of Argentina. Although incompletely preserved, the
22 Anticosti mitrate, *Perikefalea? cybeleae* sp. nov., represents the first stylophoran described in
23 the Silurian of North America and the first report of post-Ordovician Allanicytidiinae outside
24 of (peri) Gondwanan regions. Skeletal homologies in mitrates (marginals, infracentrals,
25 posterior spines, adorals, supracentrals) are reevaluated, so as to describe the plate pattern of

Perikefalea. This revision was prompted by new fossil evidence from the Furongian–Tremadocian interval suggesting that (1) mitrates derive from '*Phyllocystis*' *jingxiensis*-like cornutes with wide marginals, a posteriorly open marginal frame (loss of M₅ and M'₅), a zygial plate in central position, and confluent, sutured M₃ and G; (2) anomalocystitids derive from *Mitrocystites*-like mitrocystitidans by modification of two marginals (digital and glossal) into posterior spines. Two distinct terminologies are tentatively proposed for supracentrals in Allanicystidiinae and Anomalocystitinae, because the highly standardized plate patterns of their Siluro-Devonian representatives were possibly acquired independently in the two clades.

Keywords: Anticosti, Bolivia, Canada, Devonian, Echinodermata, Malvinokaffric Realm, Silurian, Stylophora

INTRODUCTION

Stylophorans are an extinct clade of single-armed, vagile, benthic echinoderms, which flourished on soft substrates from the Wuliuan (Miaolingian, middle Cambrian) to the Bashkirian (Lower Pennsylvanian, Carboniferous) (Ubaghs, 1967a; Kolata et al., 1991; Zamora et al., 2013a; Lefebvre et al., 2019). In the late Guzhangian–late Tremadocian interval immediately preceding the major diversification of crinoids, stylophorans were a major component of worldwide echinoderm communities (Sumrall et al., 1997; Guensburg and Sprinkle, 2000; Lefebvre and Fatka, 2003; Lefebvre et al., 2013). All main stylophoran clades, including anomalocystitid mitrates, appeared and diversified during this late Cambrian–Early Ordovician interval (Lefebvre, 2007a; Lefebvre et al., 2013; Zamora et al., 2013b). In Middle Ordovician times, the paleobiogeographic distribution of stylophorans was limited to high-latitude (peri-) Gondwanan areas and relatively deep settings of Avalonia

(Jefferies, 1987; Lefebvre and Fatka, 2003; Lefebvre, 2007a; Botting et al., 2013). However, during the Late Ordovician, they spread to Baltica and Laurentia (Mohawkian invasion), where some clades (anomalocystitids, peltocystids) eventually diversified into shallower and warmer environmental conditions (Caster, 1952; Kolata and Guensburg, 1979; Kolata and Jollie, 1982; Parsley, 1982, 1991; Lefebvre, 2007a, 2007b; Lefebvre et al., 2013). Conversely, stylophorans almost disappeared from most high-latitude (peri-) Gondwanan regions during the late Katian Boda Event, with the onset of more temperate environmental conditions and the invasion of echinoderm faunas from lower latitudes (Lefebvre, 2007a, 2007b; Lefebvre et al., 2013).

Stylophorans were severely affected by the Hirnantian mass extinction, with only four clades reported from younger deposits (Lefebvre, 2007a). Although they are sometimes locally abundant (e.g. *Placocystites forbesianus*, in the Dudley Limestone of Britain; *Rhenocystis latipedunculata*, in the Hunsrück Slate of Germany; Jefferies and Lewis, 1978; Ruta and Bartels, 1998), post-Ordovician stylophorans are generally extremely rare, and their fossil record particularly sparse. For example, peltocystidans, which are one of the most abundant and widespread clades of Ordovician stylophorans, are only known from three younger occurrences: '*Mitrocystites*' *styloideus* (Emsian, Germany; Dehm, 1934; Lefebvre, 2007a), yet undescribed Middle Devonian forms (Eifelian–Givetian, Germany; Haude, 1983) and *Jaekelocarpus oklahomaensis* (Bashkirian, USA; Kolata et al., 1991). Similarly, the paleobiogeographic distribution of Siluro-Devonian mitrocystitidans (Anomalocystitidae and Paranacystidae) is poorly known and suffers from a strong sampling bias. For example, paranacystids were long considered as typical members of the Early–Middle Devonian high-latitude Malvinokaffric faunas (e.g. Derstler, 1979; Haude, 1995; Ruta, 1997a; Penn-Clarke, 2019; but see Boucot and Rachebœuf, 1993). This interpretation is based on a very small

number of occurrences from Argentina (*Yachalicystis triangularis*; Haude, 1995), Brazil (*Paranacystis petrii*; Caster, 1954a; Caster and Eaton, 1956), and South Africa (*P. simoneae*; Ruta, 1997a; Reid et al., 2015). However, the reinterpretation of the Middle Devonian genus *Dalejocystis* (Czech Republic, Germany; Prokop, 1963; Haude, 1983) as a paranacystid, as well as the discovery of several new occurrences in the Wenlock of Sweden (Reich et al., 2008), the Ludlow of Australia (Ruta and Jell, 1999b), the Lochkovian of Australia and Bolivia (Ruta and Jell, 1999b; Lefebvre and Rachebœuf, 2007) and the Givetian of France (Lefebvre, 1999, 2000a) suggest a more complex and widespread distribution of paranacystids.

In the two main clades of anomalocystitids (Allanicystidiinae and Anomalocystitinae), the evolutionary transition from Late Ordovician to younger taxa, as well as their Siluro-Devonian paleobiogeographic distribution are similarly poorly understood. Post-Ordovician anomalocystitines were traditionally considered as a 'boreal' group, restricted to low-latitude regions of the 'Old World' and 'North Eastern Americas' faunal realms *sensu* Boucot (1988) (see e.g. Gill and Caster, 1960; Derstler, 1979; Parsley, 1991; Ruta, 1997b; Ruta and Bartels, 1998). This interpretation relied on the very low number of Siluro-Devonian anomalocystitine taxa described between the late 1850s and the late 1990s: *Anomalocystites cornutus* Hall, 1859 (Lower Devonian, North America; Parsley, 1991), *Placocystites forbesianus* de Koninck, 1869 (Wenlock, Britain; Jefferies and Lewis, 1978), *Rhenocystis latipedunculata* Dehm, 1932 (Emsian, Germany; Ruta and Bartels, 1998), and *Victoriacystis wilkinsi* Gill and Caster, 1960 (Ludlow, Australia; Ruta, 1997b; Ruta and Jell, 1999d). However, the reinterpretation of *Mongolocarpos minzhini* (Ludlow, Mongolia; Rozhnov, 1990) as a probable anomalocystitine (Ruta, 1999a), as well as new discoveries in regions (Bolivia, South Africa) belonging to the Devonian Malvinokaffric faunal realm (see Ruta and Theron,

1997; Lefebvre and Rachebœuf, 2007) suggest a more cosmopolitan distribution for Siluro-Devonian Anomalocystitinae.

The second clade of post-Ordovician anomalocystitids, Allanicystidiinae, has been long considered as an 'austral' group of stylophorans, restricted to (peri-) Gondwanan regions belonging either to the eastern part of the Old World faunal realm (Australia, New Zealand) or to the higher latitude Malvinokaffric Realm (Argentina, Brazil, South Africa) (see Caster, 1954b, 1983; Ubaghs, 1967a; Philip, 1981; Parsley, 1991; Haude, 1995; Ruta, 1997b; Ruta and Theron, 1997; Ruta and Jell, 1999e; Lefebvre and Rachebœuf, 2007; Jell, 2013; Penn-Clarke, 2019; Scheffler et al., 2019; but see Boucot and Rachebœuf, 1993). In this context, the two mitrates described here from the late Llandovery of Anticosti Island (Canada) and the Lochkovian of Bolivia are particularly important. The Canadian occurrence represents both the first stylophoran described in Silurian deposits from North America and also the first report of post-Ordovician Allanicystidiinae outside of (peri) Gondwanan regions. The Anticosti mitrate is here tentatively assigned to a new genus of allanicystidiines, described from better-preserved and more complete material from Bolivia. The morphology of the Bolivian stylophoran suggests stronger affinities with *Occultocystis* (Lower Devonian; Argentina) than with the widespread coeval genus *Placocystella* (late Llandovery–early Givetian; Australia, Brazil, New-Zealand, South Africa).

Consequently, the main objective of this paper is to describe the morphology of the two new allanicystidiines from Bolivia and Canada. However, so as to compare them properly with other mitrates, a reevaluation of the two main models of plate homologies elaborated by Ruta (1999a) for supracentrals, and Lefebvre (2001) for adorals and marginals, is a necessary pre-

requisite. Many new data, including previously unrecorded plate patterns, have been accumulated since these two models were proposed, twenty years ago.

GEOLOGICAL SETTING

Anticosti Island, Canada

Anticosti Island is in the Gulf of St. Lawrence and part of Québec, Canada (Fig. 1). The section on Anticosti Island is a nearly complete Katian (Ordovician) through Llandovery (Silurian) stratigraphic section (Fig. 1c), and the most complete section known in shelly facies. A long history of stratigraphic and paleontological studies has clarified the geology of Anticosti Island (see e.g. Richardson, 1857; Schuchert and Twenhofel, 1910; Twenhofel, 1928; Bolton, 1961; Cocks and Copper, 1981; Petryk, 1981; Long and Copper, 1987; Barnes, 1988; Copper, 1989, 2001; Jin and Copper, 2008; Desrochers et al., 2008, 2010; Copper et al., 2013). Recent investigations have identified the position of the Ordovician-Silurian boundary and, significant to this study, revised the east-west correlation of Aeronian-Telychian stratigraphy based on a combination of biostratigraphy and sequence stratigraphy (Fig. 2; Copper et al., 2013).

The new mitrate is from the Cybèle Member of the Jupiter Formation (Telychian; Fig. 2) in eastern Anticosti Island (Fig. 1c). It was collected by the junior author in 2001 from a long, low outcrop along the western bank of the Box River, approximately 700 m north of the Dauphiné-Bell Road (N 49° 08' 53.5" W 62° 21' 13.6"). Fossils are relatively abundant in the lithographic limestones of the Cybèle Member. Assemblages are dominated by trilobites,

brachiopods and endemic crinoids, associated to ostracods, tentaculitids, and rare rhenopyrgid edrioasteroids (Ausich and Copper, 2010; Ewin et al., 2020).

Bolivia

During Devonian times, most of Bolivia was part of an intracratonic basin on the western margin of Gondwana (Isaacson and Díaz-Martínez, 1995; Di Pasquo and Noetinger, 2008). About 50 km northeast of Sucre (Fig. 3), the classical section of Presto-El Peral exposes the three lowermost units of the Devonian succession in the Eastern Cordillera area (Fig. 4): the Santa Rosa, Icla and Huamampampa formations (Rachebœuf et al., 1993; Gaillard and Rachebœuf, 2006). The Santa Rosa Formation (Lochokovian) is a thick siliciclastic unit consisting mostly of fluvio-deltaic and coastal deposits, yielding abundant land plant remains, associated to rare marine palynomorphs and low diversity trace fossils (Rachebœuf et al., 1993; Gaillard and Rachebœuf, 2006; Di Pasquo and Noetinger, 2008). However, abundant trace fossils (*Palaeophycus* association) and a relatively diverse, fully marine assemblage occur in the finer-grained sandstones and siltstones of the uppermost part of the Santa Rosa Formation (Rachebœuf et al., 1993; Gaillard and Rachebœuf, 2006). These levels have yielded abundant brachiopods (e.g. *Australostrophia* sp., *Derbyina* sp., *Proboscidina arcei*, *Scaphiocoelia boliviensis*), associated with asterozoans, bivalves (*Nuculites* sp., *Modiolopsis* sp.), crinoid ossicles, gastropods, trilobites and disarticulated vertebrate remains (Rachebœuf et al., 1993; Gaillard and Rachebœuf, 2006; Janvier and Maisey, 2010). Both trace fossils and brachiopods are suggestive of low intertidal environmental conditions (Gaillard and Rachebœuf, 2006). In the early 2000s, fully-articulated remains of two different stylophoran taxa were found by Patrick Rachebœuf in these levels (Gaillard and Rachebœuf, 2006; Lefebvre and Rachebœuf, 2007): a *Paranacystis*-like mitrocystitid, and the new, herein

described, allanicytidiine mitrate. In the same area, the upper part of the overlying Icla Formation yielded remains of a third, yet undescribed, *Placocystites*-like anomalocystine mitrate (Lefebvre and Rachebœuf, 2007). Recent palynological data suggest a Pragian to Emsian age for the shales and siltstones of the Icla Formation (Fig. 4; Troth, 2006; Troth et al., 2011).

MATERIAL AND METHODS

The material described in this paper is registered in the collections of the Museo de Historia Natural Alcide d'Orbigny, Cochabamba, Bolivia (MHNC) and in the collections of the Geological Survey of Canada, Ottawa, Canada (GSC). Additional specimens illustrated here for comparison purposes are deposited in the paleontological collections of Géosciences Rennes, Rennes 1 University, France (IGR) and Lyon 1 University, Villeurbanne, France (UCBL-FSL).

All five Bolivian specimens are preserved as empty moulds (part and counterpart) in relatively coarse sandstones. Latex casts were made, so as to reveal their original, three-dimensional, external aspect. The single specimen from Anticosti is preserved in calcite. Its original morphology is thus immediately accessible, and does not require any casting. All specimens were coated with ammonium chloride (NH₄Cl) to enhance contrast for both drawing and photographic purposes. Specimens were observed with a Zeiss SteREO Discovery V8 stereomicroscope binocular, and drawn using a camera-lucida mounted on the same stereomicroscope, at Lyon 1 University. Photographs were made with a Canon 5DSR camera mounted with a MP-E 65mm macro lens.

The Anticosti specimen is preserved in lower aspect, in close association with a pluricolumnal of *Eomyelodactylus* with attached rhizoids. In all Siluro-Devonian anomalocystitids, the lower surface of the theca is composed of the same number of skeletal elements: two centrals (anomalocystid and zygial plates) and eleven marginals. Consequently, sub-familial assignment and generic identification relies largely on the plate pattern of the opposite, upper thecal surface (see below). So as to reveal the aspect of its diagnostic upper side, which is inserted in the rock, the Anticosti specimen was examined with a vtomex laboratory X-ray computed tomograph (GE Phoenix | X-Ray GmbH) equipped with a 160 kV nano-focus tube, a tungsten transmitting target, and a 1920×1536 pixel Varian detector, at the Mateis Laboratory, INSA de Lyon. Unfortunately, contrast between the calcite specimen and the surrounding carbonate matrix was too low to visualize any structure hidden in the rock. Ewin et al. (2020) reported a similar, unsuccessful CT-scan experiment made on a specimen of rhenopyrgid edrioasteroid from the same lithostratigraphic unit (Cybèle Member).

THECAL PLATE TERMINOLOGY AND HOMOLOGIES

All stylophorans share the same basic body plan, with a single articulated feeding arm (aulacophore) inserted into a polyplated, flattened test (theca), which housed most internal organs (Fig. 5; Ubaghs, 1967a; Chauvel, 1981; Parsley, 1991; Haude, 1995; Ruta, 1999b; David et al., 2000; Lefebvre et al., 2019). The lower side of the theca is generally flat to slightly concave, whereas its upper surface is moderately to highly convex. The two opposite thecal surfaces have distinct plate patterns.

The lower side (Fig. 5b) is characterized by a frame of thick skeletal elements (marginals), which also forms the lateral walls of the test. In various stylophoran clades, some of these marginals can bear long flattened posterior spikes or be modified into posterior spines (Kirk, 1911; Ubaghs, 1967a; Lefebvre, 2001). The number of marginal plates is constant throughout ontogeny, but their respective proportions can be variable (Ubaghs, 1967a). In all stylophorans, an asymmetrical internal structure (the zygial crest or septum) is consistently borne by two plates (forming together the zygial bar or strut), and extends from left of the aulacophore insertion (anteriorly) to right of the anal opening (posteriorly). The marginal frame and the zygial strut delimit two polyplated surfaces: the left and right infracentral areas (Ubaghs, 1967a, 1981; Lefebvre 2001). Both areas are present in most stylophorans, but the right one is frequently lost, independently in various derived taxa (e.g. *Anomalocystitidae*, *Chinianocarpus*, *Kirkocystidae*, *Lyriscarpus*). The number and shape of infracentral elements are generally highly variable in stylophorans (e.g. *Aspidocarpus*, *Cothurnocystis*), but they tend to become constant, independently, in various mitrate taxa (e.g. *Anomalocystitidae*, *Mitrocystella*, *Paranacystidae*, *Peltocystis*).

The upper thecal surface (Fig. 5a) is characterized by two or three skeletal elements (adorals) forming an anterior bridge framing, with the two underlying anterior marginals, the insertion of the aulacophore into the theca (Ubaghs, 1967a, 1981; Lefebvre et al., 1998). Adorals can form a narrow, delicate adaulacophoral arch (e.g. *Ceratocystis*, *Cothurnocystis*) or they can extend posteriorly to form part (e.g. *Lagynocystis*, *Mitrocystites*), most (*Paranacystis*, *Peltocystis*) and even all of the upper thecal surface (*Jaekelocarpus*, *Kirkocystidae*) (Ubaghs, 1967a; Lefebvre, 2001). Their number and relative proportions remain apparently constant during ontogeny. Posteriorly to adorals, the upper side of the theca consists of a large, polyplated integumentary surface (supracentral area). Supracentrals are

generally numerous and unorganized, forming a flexible pavement of tessellate (e.g. *Chinianocarpos*, *Phyllocystis*) and/or imbricate elements (e.g. *Eumitrocystella*, *Lagynocystis*). In derived mitrocystitidan mitrates (anomalocystitids and paranacystids), supracentral areas consist of a reduced and constant number of elements (Caster, 1952; Ubaghs, 1967a; Parsley, 1991; Ruta, 1999a).

Along with some aulacophore-related features, the morphology and number of major skeletal elements (adorals and marginals) are used as primary key characters for the systematics of stylophorans (Ubaghs, 1967a; Lefebvre, 2001). In derived mitrocystitidans, the identification also relies largely on the number, morphology and position of both infracentrals and supracentrals (Caster, 1952; Ubaghs, 1967a; Parsley, 1991; Ruta, 1999a). Unsurprisingly, various plate nomenclatures have been proposed for stylophorans (e.g. Bather, 1913; Jaekel, 1918; Gislen, 1930; Dehm, 1932; Caster, 1952; Ubaghs, 1963; Jefferies, 1968; Jefferies and Prokop, 1972; Philip, 1981; Ruta and Theron, 1997; Ruta and Bartels, 1998; Lefebvre and Vizcaïno, 1999; Ruta, 1999a; Lefebvre, 2000b, 2001). Most of them, however, are either simply descriptive and do not imply any homology (e.g. Jaekel, 1918; Ubaghs, 1963; Jefferies, 1968) and/or can be applied only to a limited group of taxa but not to the whole class Stylophora (e.g. Bather, 1913; Dehm, 1932; Caster, 1952; Philip, 1981; Ruta, 1999a).

In this paper, we largely follow the plate terminology proposed by Lefebvre and Vizcaïno (1999) for cornutes, and extended to mitrates by Lefebvre (2000b, 2001, 2003a). This model implies class-level homologies between major skeletal elements (adorals, marginals), based on their morphology, position, and associated internal structures (Lefebvre et al., 1998; Lefebvre, 2000c, 2001). A similar and complementary plate terminology was elaborated by Ruta (1997b, 1999a) to identify homologies in skeletal elements (adorals, supracentrals)

forming the upper thecal surface of anomalocystitid mitrates (see also Ruta and Theron, 1997; Ruta and Bartels, 1998). These two models are here critically reevaluated and modified, so as to take into account the abundant new data accumulated in the last twenty years and, in particular, those obtained from the late Guzhangian–late Tremadocian time interval (e.g. Sumrall et al., 1997, 2009; Ubaghs, 1998; Smith and Jell, 1999; Sumrall and Sprinkle, 1999; Marti Mus, 2002; Lee et al., 2005; Ware and Lefebvre, 2007; Han and Chen, 2008; Noailles and Lefebvre, 2012; Chen and Han, 2013; Zamora et al., 2013b; Lefebvre et al., 2016; Rozhnov and Parsley, 2017; Peng et al., in press).

In the late Cambrian–Early Ordovician interval, stylophorans underwent a major diversification, characterized by a dramatic increase in morphological disparity (Lefebvre et al., 2006) and the emergence of all main post-Cambrian clades (e.g. Amygdalothecidae, Chauvelicystidae, Cothurnocystidae, Hanusiidae, Lagynocystida, Mitrocystitida, Peltocystida, Scotiaecystidae; Lefebvre and Fatka, 2003; Lefebvre, 2007a).

Marginals and infracentrals

All anomalocystitid mitrates are characterized by a marginal frame made of 11 massive skeletal elements, which can be considered as homologous at the family level (e.g. Dehm, 1932; Caster, 1952, 1954b, 1983; Gill and Caster, 1960; Ubaghs, 1967a, 1979; Jefferies and Lewis, 1978; Philip, 1981; Craske and Jefferies, 1989; Parsley, 1991; Haude, 1995; Ruta, 1997b, 1999a; Ruta and Theron, 1997; Ruta and Bartels, 1998; Ruta and Jell, 1999a, 1999c, 1999d, 1999e; Lefebvre, 2000b, 2001; Jell, 2013; McDermott and Paul, 2017; Scheffler et al., 2019). In all described anomalocystitids, these marginals enclose a large, septum-bearing central plate and a left infracentral area consisting of one ('anomalocystid plate' of Siluro-Devonian taxa) or two elements (Mid-Late Ordovician forms). The right infracentral area is

absent. Most taxa (with the single exception of *Barrandeocarpus*) have two posterior movable spines, which have been often interpreted as modified marginals (Kirk, 1911; Ubaghs, 1967a; Jefferies and Lewis, 1978; Parsley, 1991; Lefebvre, 2000b, 2001; but see Jefferies, 1984; Ruta, 1999a).

Most of these anomalocystitid skeletal elements (marginals, centrals, spines) can be readily identified in other mitrocystitidans (Jefferies and Lewis, 1978; Craske and Jefferies, 1989; Parsley, 1991; Ruta and Theron, 1997), and more tentatively, at class-level (Lefebvre, 2000b, 2001). The model of stylophoran plate homologies proposed by Lefebvre and Vizcaïno (1999) and Lefebvre (2000b, 2001) interprets *Lobocarpus vizcainoi* as a basal mitrate, and considers that mitrates derive from a *Ceratocystis*-like ancestor (Fig. 6a), with large marginals and small infracentral areas. The application of this model to anomalocystitids suggests that: (1) their left series of marginals corresponds to M'₁, M'₂, M'₃, and M'₄; (2) their right marginals can be identified as M₁, M₂, M₃, and M₄; (3) their two posterior spines are homologous to the digital (D) and the glossal (G); (4) their large central septum-bearing element is the zygial plate (Z); and (5) their three posterior plates correspond to M'₅ (on the left) and to two additional platelets of infracentral origin, inserted successively between M₄ and M'₅ (right element PP₁), and between PP₁ and M'₅ (median element PP₂).

All putative mitrate-like features of the Furongian stylophoran *Lobocarpus* (e.g. wide marginals, reduced infracentral areas; Fig. 7a) are plesiomorphic, as they occur in *Ceratocystis* (Fig. 6a), which is almost universally considered as the most basal representative of the class (Ubaghs, 1967b; Jefferies, 1969; Derstler, 1979; Cripps, 1991; Parsley, 1997; Lefebvre and Vizcaïno, 1999; Marti Mus 2002; Ruta, 2003; Lefebvre, 2005; Rahman et al., 2010). Moreover, *Lobocarpus* lacks all apomorphies defining the mitrates: in particular, it

retains small, narrow adorals, and its distal aulacophore is made of unornamented (smooth) ossicles with undifferentiated, flat interbrachial articulations (Ubaghs, 1998). In marked contrast, abundant remains of definitive mitrates have been discovered recently in late Guzhangian to Furongian deposits of Korea (Lefebvre, 2007a) and South China (Chen et al., 2013; Zamora et al., 2013b; Zhu et al., 2016; Peng et al., in press).

'Nanocarpus' guoleensis; from the Furongian Guole Biota of South China, was initially described as an amygdalothecid cornute (Chen and Han, 2013). This identification mostly relied on its thecal outlines, a posteriorly open marginal frame (no M_5 - M'_5 bar), the presence of large infracentral areas, a zygal plate in central (not marginal) position, and spikes on the lower surface of brachials. However, its upper surface has two extremely wide adorals (see e.g. Zamora et al., 2013b, fig. 2E). Moreover, well-differentiated interbrachial articulations are present on aulacophore ossicles, allowing the arm to be preserved in recurved position (see e.g. Chen and Han, 2013, figs 2.1-2), which is a typical post-mortem posture of mitrates (Dehm, 1932; Parsley, 1988; Lefebvre, 2003b). All these characters (large adorals, strongly ornamented ossicles with interbrachial articulations) unambiguously support the identification of *'N. guoleensis* as a mitrate, with strong morphological similarities to late Tremadocian taxa such as *Chinianocarpus* (Fig. 7b) and/or *Vizcainocarpus* (Fig. 5). The occurrence of other, similar-looking undescribed stylophorans in the late Guzhangian of South China (Peng et al., in press) and the Furongian of Korea (Lefebvre, 2007a) suggests that early mitrates were morphologically closer to *Vizcainocarpus* (Fig. 5), with large infracentral areas, and a relatively narrow, posteriorly open marginal frame, than to a heavily-plated, *Lobocarpus*-like form (Fig. 7a).

In both China and Korea, Cambrian early mitrates are associated to abundant remains of cornute stylophorans with relatively rounded thecal outlines, superficially looking like those of *Phyllocystis*: e.g. cornute gen. and sp. indet. A (Lee et al., 2005), '*Phyllocystis*' *jingxiensis* (Han and Chen, 2008), and cothurnocystid gen. and sp. indet. (Peng et al. in press, fig. 4A). Very similar-looking forms occur in the Furongian of France (Fig. 8; Ubaghs, 1998, fig. 4), Spain (S. Zamora, pers. comm., Feb. 2016), and the late Tremadocian of Morocco (Lefebvre et al., 2013, fig. 14.17B). All these stylophorans can thus be described as '*P.*' *jingxiensis*-like taxa, with a boot-shaped theca, relatively wide marginals with a flat peripheral flange, large infracentral areas, small adorals, smooth interbrachial articulations, unornamented aulacophore ossicles, and commonly, typical respiratory structures (e.g. cothurnopores) in the right anterior corner of the supracentral area. Their morphology is thus relatively close to that of *Flabelllicarpus rushtoni* (Fig. 6c) from the late Tremadocian of Britain (Marti Mus, 2002). They also share with both *Persiacarpus* from the late Guzhangian–early Furongian of Iran (Rozhnov and Parsley, 2017) and *Ponticulocarpus* (Fig. 6b) from the Spence Shale (Wulian) of Utah (Sumrall and Sprinkle, 1999) the possession of particularly enlarged glossal and spinal blades, forming two wide posterior processes. However, '*P.*' *jingxiensis*-like taxa (Fig. 8) differ from *Persiacarpus* and *Ponticulocarpus* by their posteriorly open marginal frame (loss of the M₅-M'₅ bar on the lower surface). They also differ from *Flabelllicarpus* (Fig. 6c), *Persiacarpus* and *Ponticulocarpus* (Fig. 6b) by their particularly expanded and adjoining glossal and spinal processes. As a consequence of the posterior M'₃ (spinal) - G (glossal) contact, the zygial plate (Z) no longer contributes to the marginal frame but occurs in a central position (Fig. 8). This previously unrecorded plate pattern could explain the origin of central zygial elements in both amygdalothecids (e.g. *Amygdalotheca*, *Nanocarpus*) and early mitrates (e.g. '*Nanocarpus*' *guoleensis*, *Ovocarpus*, *Vizcainocarpus*).

The new abundant stylophoran material recently collected in various late Ghuzangian and Furongian localities worldwide suggests that the earliest known mitrates (with a central Z, large infracentral areas, and a posteriorly open marginal frame) were morphologically much closer to Cambrian '*P.*' *jingxiensis*-like cornutes (Fig. 8), than to *Lobocarpus*-like, heavily-plated stylophorans (Fig. 7a). Consequently, this new evidence questions the possibility that mitrates originated as early as the late Miaolingian from '*P.*' *jingxiensis*-like taxa. If this interpretation is correct, then this would imply that (monophyletic) mitrates derive from paraphyletic, 'cornute-grade' stylophorans (Jefferies, 1968, 1969; Jefferies and Prokop, 1972; Derstler, 1979; Cripps, 1991; Ubaghs, 1991; Parsley, 1991, 1997; Ruta, 2003; but see Gill and Caster, 1960; Ubaghs, 1967a; Lefebvre and Vizcaino, 1999; Lefebvre, 2001, 2005).

The 'cornute-grade' origin of mitrates implies that their plate homologies have to be reconsidered. This scenario confirms the identification of the left series of marginals as M'₁, M'₂, M'₃ and M'₄, as well as the homology of the posterior zygal plate in all mitrates, whatever its position: central (e.g. anomalocystitids, *Ovocarpus*, *Vizcainocarpus*; Figs 5, 9) or marginal (e.g. *Chinianocarpos*, *Peltocystis*; Fig. 7b-c) (Lefebvre et al., 1998; Lefebvre, 2000b, 2000c, 2001; Lefebvre and Gutiérrez-Marco, 2003). However, comparison with '*Phyllocystis*' *jingxiensis*-like stylophorans (Fig. 8) suggests that the right series of marginal elements in *Vizcainocarpus*-like mitrates (including anomalocystitids) should be identified as M₁, M₂, M₃ and M₄, rather than as M₁, M₂, M₃ and M₄ (Figs 5, 7c, 9a). Similarly, the posterior skeletal element inserted between D and G (e.g. *Chinianocarpos*, *Ovocarpus*; Figs 7b, 9a) cannot represent M'₅, as suggested by Lefebvre (2000b, 2001), because this plate is absent in '*P.*' *jingxiensis*-like stylophorans (Fig. 8) and all known Cambrian mitrates (e.g. '*Nanocarpus*' *guoleensis*). This skeletal element more likely corresponds to an infracentral plate, inserted between D and G, and thus closing posteriorly the marginal frame (Figs 7b, 9a). This

397 additional posterior element, which is an apomorphy of mitrocystitidan mitrates, is here
398 designated M₆.

399
400 A similar phenomenon with successive insertions of infracentral elements (PP₁ and PP₂)
401 into the posterior margin of mitrocystitidans was proposed by Lefebvre (2000a, 2001, 2003a)
402 to explain the regular increase of their number of marginals from 11 (*Ovocarpus*), to 12
403 (*Aspidocarpus*), and 13 (*Mitrocystites*) (see also Parsley, 1991; Lefebvre and Gutiérrez-
404 Marco, 2003). This model of homologies suggests that the two posterior plates of
405 *Aspidocarpus*-like taxa correspond to M₆ (on the left) and PP₁ (on the right). This
406 identification relies mostly on the growth series of *A. bohemicus* illustrated by Ubaghs (1979,
407 fig. 2a-e), which suggests that the smallest observed individual has one less marginal (i.e. 11
408 instead of 12), and that the additional element was inserted in between the glossal and M₆
409 (Lefebvre, 2000b, 2001, 2003a; Lefebvre and Gutiérrez-Marco, 2003). However, the
410 reexamination of Ubaghs' original material of *A. bohemicus* (Fig. 9b) in the Museum für
411 Naturkunde, Berlin (B. Lefebvre, pers. obs., Nov. 2008) and in particular of the smallest
412 specimen (MB.Ca.114) figured by Ubaghs (1979, fig. 2b) shows that the number of marginals
413 is constant at all growth stages and equal to 12. Consequently, the growth series of *A.*
414 *bohemicus* does not have any evidence of insertion of a posterior element during the
415 ontogeny.

416
417 Comparison with the plate patterns of *Ovocarpus*-like mitrocystitidans (with 11 marginals;
418 Fig. 9a) suggests that the two posterior plates of *Aspidocarpus* (Fig. 9b) more likely represent
419 M₆ (on the right) and an element from the left infracentral area, incorporated into the marginal
420 frame between M₆ and D. This new interpretation relies on the similar morphologies (with a
421 strongly rounded posterior edge) and contacts with neighbouring plates (G and Z) of M₆ in

both *Aspidocarpus* and *Ovocarpus*. Moreover, it seems unlikely that the right posterior plate of *Aspidocarpus* is the newly added element, because this marginal is not in contact with any of the two polyplated infracentral surfaces: its origin would be unclear (see Lefebvre, 2000b, p. 897). Conversely, it makes more sense to identify the left posterior plate as the newly added element, because it is in direct contact with the left infracentral area. So as to avoid any confusion with the identification proposed by Lefebvre (2000b, 2001, 2003a), the second additional marginal of mitrocystitidan mitrates is here named M₇ (Fig. 9b).

In *Mitrocystites* (Fig. 9c) and other mitrocystitidans with three posterior marginals (e.g. Anomalocystitidae), the right element very likely corresponds to M₆, because it shows the same morphology (with a rounded posterior edge) and contacts (with both G and Z) as in *Ovocarpus* and *Aspidocarpus*. The identification of the two other posterior plates is more problematic. They are both anteriorly in contact with the left infracentral area, so that any of them can correspond to a plate of infracentral origin inserted into the marginal frame. A first possibility is to consider the skeletal element in median position as an additional plate (PP₂), inserted between M₆ (on the right) and M₇ (on the left) (Lefebvre, 2000b, 2001, 2003a). Alternatively, the right posterior plate could be an additional element inserted between M₇ (on the right) and D (on the left). There are no definitive clues to decipher between these two scenarios. However, two lines of indirect evidence suggest that the second interpretation is more likely (Fig. 9c). First, the teratological specimen of *Mitrocystites* figured by Lefebvre (2003a, fig. 3D) shows that its right and median posterior plates are both anteriorly in contact with Z, which is similar to the situation in *Aspidocarpus*, and could support their identification as M₆ and M₇, respectively. Moreover, in several anomalocystitids, including yet undescribed specimens from the Letná Formation (Sandbian) of Czech Republic (B. Lefebvre, pers. obs.), *Protocystidium elliotiae* (see Ruta and Jell, 1999a), and the two herein

described new allanicytidiines (see below), their median posterior marginal has a strong spike, which is very similar in morphology to the one borne by M_7 in *Aspidocarpus bohemicus* (Fig. 9b). For these reasons, the median posterior marginal of *Mitrocystites* and anomalocystitids is here tentatively identified as M_7 (Fig. 9c). Consequently, the left posterior plate of these mitrates is interpreted as an infracentral element inserted between M_7 (on the right) and the digital (on the left). So as to avoid any confusion with plate homologies suggested by Lefebvre (2000b, 2001, 2003a), the left posterior plate is here designated M'_6 (Fig. 9c). If this interpretation is correct, it would imply that infracentrals (M_6 , then M_7 , and finally M'_6) have been repeatedly inserted into the marginal frame, along the right margin of the digital. This region could represent an area of weakness and/or of reduced mechanical constraints, which might result from the loss of the M_5 - M'_5 bar, which forms the posterior frame of the left infracentral area in other stylophorans (plesiomorphic condition; e.g. *Araucicystis*, *Cothurnocystis*, *Ponticulocarpus*, *Protocystites*; Fig. 6b).

The nature, origin, and homology of the two posterior spines of anomalocystitid mitrates have been long debated (see e.g. Haeckel, 1896; Kirk, 1911; Caster, 1952; Ubaghs, 1967a; Jefferies and Lewis, 1978; Jefferies, 1984; Parsley, 1991; Ruta, 1999a; Lefebvre 2000b, 2001). Lefebvre (2000b, 2001) suggested that these two spines are homologous to the digital and glossal of cornutes: D and G would have the possibility to be either incorporated in the thecal frame as regular marginals (e.g. *Milonicystis*, *Mitrocystites*) or articulated to it and modified as movable spines (e.g. anomalocystitids, *Cothurnocystis*). In this context, the recent discovery of abundant remains of the earliest, yet undescribed anomalocystitid mitrate in the middle Floian of Morocco (Fig. 10) is particularly informative (Lefebvre, 2007a; Noailles and Lefebvre, 2012; Lefebvre et al., 2013, 2016). Its morphology is a mixture of characters typical of anomalocystitids (e.g. possession of two posterior spines) and

plesiomorphic features widespread in early mitrocystitidans but generally lost in younger anomalocystitids (e.g. lateripores, two polyplated infracentral surfaces, and a supracentral area consisting exclusively of imbricate elements). This new anomalocystitid (Fig. 10) is morphologically very close to *Aspidocarpus* (Fig. 9b) and *Mitrocystites* (Fig. 9c). Detailed comparison of the plate patterns of these three mitrates strongly supports the view that Early Ordovician anomalocystitids (with 11 marginals and 2 spines) originated from a *Mitrocystites*-like form (with 13 marginals), by the modification of two postero-lateral marginals (D and G) into articulated spines. The new Moroccan mitrate (Fig. 10) thus confirms the homology of posterior spines in all stylophorans (Lefebvre, 2000b, 2001, 2005).

As in *Aspidocarpus* (Fig. 9b), the left infracentral area of the new Moroccan mitrate is made of numerous, unorganized platelets (Fig. 10). This observation implies that similar-looking plate patterns consisting of a reduced number of infracentral elements (1 to 3) were acquired independently from irregular, polyplated surfaces in younger anomalocystitids (e.g. *Ateleocystites*, *Barrandeocarpus*, *Diamphidiocystis*, *Enoploura*; Fig. 11) and in *Mitrocystites* (Fig. 9c) and related forms (e.g. *Eumitrocystella*, *Mitrocystella*, *Paranacystidae*). Consequently, although they are frequently considered as homologous (e.g. Jefferies and Lewis, 1978; Craske and Jefferies, 1989; Parsley, 1991, 1997; Ruta and Theron, 1997; Ruta, 1999a; Lefebvre, 2000b), the two posterior infracentrals occurring in anomalocystitids (Fig. 11a-b) and other mitrocystitidans (Fig. 9c) are more likely the result of convergent evolution (reduction of the number of infracentrals) in the two lineages. The terminology introduced by Ruta (1999a) for the two infracentrals in anomalocystitids is retained here, with A for the anterior element, and B for the posterior one (Fig. 11). These letters are convenient, because A is almost universally identified as the 'anomalocystid' plate (e.g. Caster, 1952, 1983; Ubaghs, 1967a, 1979; Philip, 1981; Parsley, 1991; Haude, 1995; Ruta and Bartels, 1998;

Ruta, 1999a; Jell, 2013; Scheffler et al., 2019), and the name 'barrandeocarpid plate' is suggested here for the B element. In *Mitrocystites* (Fig. 9c) and related mitrocystitidans, the distinct terminology (with I'₁, I'₂ and I'₃) introduced by Lefebvre (2003a) should be maintained, so as to avoid any confusion with anomalocystitid infracentrals.

Adorals

In anomalocystitids, the anterior margin of the upper thecal surface is invariably consisting of two large skeletal elements, universally considered as homologous at family level (e.g. Dehm, 1932; Caster, 1952, 1954b, 1983; Gill and Caster, 1960; Ubaghs, 1967a, 1979; Jefferies and Lewis, 1978; Kolata and Guensburg, 1979; Philip, 1981; Kolata and Jollie, 1982; Jefferies, 1984; Craske and Jefferies, 1989; Rozhnov, 1990; Parsley, 1991, 1997; Haude, 1995; Ruta, 1997b, 1999a; Ruta and Theron, 1997; Ruta and Bartels, 1998; Ruta and Jell, 1999a, 1999c, 1999d, 1999e; Lefebvre, 2000b, 2001; Jell, 2013; McDermott and Paul, 2017; Scheffler et al., 2019). These two (left and right) elements can be confidently identified as homologous to the left and right adorals (A'₁ and A₁) of other mitrates (Fig. 12b-c), based on the presence of the same internal structures (co-opercula) on their lower (inner) side (see e.g. Chauvel, 1941, 1981; Ubaghs, 1967a, 1979; Jefferies and Lewis, 1978; Kolata and Jollie, 1982; Parsley, 1991, 1997; Lefebvre, 2000b, 2001, 2005). Class-level homology of A₁ and A'₁ (Fig. 12) relies on similarities in position (framing the aulacophore insertion on the anterior edge of the upper thecal side), comparable contacts with the same two underlying marginals (M'₁ and M₁), and also the occurrence of the hydropore on A₁ in most cornutes (e.g. *Cothurnocystis*, *Phyllocystis*) and basal mitrocystitidans (e.g. *Chinianocarpus*, *Mitrocystites*, *Ovocarpus*, *Vizcainocarpus*; Fig. 5a) (Ubaghs, 1967a, 1981, 1994; Parsley, 1991, 1997; Lefebvre, 2000b, 2000c, 2001; Lefebvre and Gutiérrez-Marco, 2003).

522

523 In the Anomalocystitidae, a third, large anterior skeletal element is present and located
524 either posteriorly to A'_1 and A_1 (in most Anomalocystitinae, e.g. *Ateleocystites*,
525 *Barrandeocarpus*, *Placocystites*) or inserted in between the two adorals and part of the
526 anterior margin of the upper surface (in most Allanicystidiinae, e.g. *Enoploura*, *Placocystella*,
527 *Protocystidium*). Comparison with basal mitrocystitidans indicates that a similar, relatively
528 large median anterior plate is present in most taxa (e.g. *Aspidocarpus*, *Chinianocarpus*,
529 *Mitrocystites*) and is consistently located posteriorly to the two adorals (Ubaghs, 1967a, 1979,
530 1994; Lefebvre, 2000b, 2001). In stylophorans, the plesiomorphic condition for the plating of
531 the anterior margin of the upper surface is illustrated by *Ceratocystis* (Fig. 12a) and many
532 cothurnocystid-like taxa (e.g. *Chauvelicystis*, *Flabelllicarpus*, *Phyllocystis*, *Ponticulocarpus*),
533 all characterized by three adoral plates (A'_1 , A_0 , and A_1) that together form an arch above the
534 aulacophore insertion (Ubaghs, 1967a, 1967b, 1970, 1981; Jefferies and Prokop, 1972;
535 Cripps, 1991; Lefebvre and Vizcaïno, 1999; Sumrall and Sprinkle, 1999; Marti Mus, 2002).
536 This plesiomorphic condition with three adorals questions the identification of the median
537 anterior plate of anomalocystitids: this skeletal element has been interpreted either as
538 homologous to the median adoral (A_0) of basal stylophorans (e.g. Kolata and Jollie, 1982;
539 Parsley, 1991; Haude, 1995; Lefebvre, 2000b, 2001, 2005) or as a distinct plate of
540 supracentral origin, inserted in between A'_1 and A_1 (e.g. Dehm, 1932; Kolata and Guensburg,
541 1979; Ubaghs, 1979).

542

543 Deciphering the homology of the median anterior plate of anomalocystitids and A_0 is a
544 particularly difficult issue, because the median adoral has no characteristic internal features,
545 and this plate was frequently lost, independently, in most stylophoran lineages, as for example
546 in Amygdalothecidae (e.g. *Amygdalotheca*, *Nanocarpus*), in derived Chauvelicystidae (e.g.

547 *Ampelocarpus*, *Lyricocarpus*), in derived Cothurnocystidae (e.g. *Cothurnocystis*,
548 *Procothurnocystis*), in Hanusiidae (e.g. *Galliaecystis*, *Hanusia*), and in Scotiaecystidae (e.g.
549 *Bohemiaecystis*, *Scotiaecystis*) (see e.g. Ubaghs, 1967a, 1970, 1991, 1994; Cripps, 1991;
550 Woods and Jefferies, 1992; Lefebvre and Vizcaïno, 1999; Marti Mus, 2002). Examination of
551 Cambrian '*Phyllocystis*' *jingxiensis*-like stylophorans suggests that A₀ was probably present in
552 '*P.*' *jingxiensis* (see Han and Chen, 2008), but absent in unassigned Furongian cornutes. from
553 France (see Ubaghs, 1998, fig. 4.3) and Korea (see Lee et al., 2005, figs. 3.3, 4.2). The
554 situation in the earliest known, late Guzhangian–late Tremadocian mitrates is similarly
555 contrasted. Lagynocystids (Furongian–Upper Ordovician; Fig. 12b) are a small clade of
556 morphologically extremely conservative mitrates, characterized by the possession of three
557 large adorals (Ubaghs, 1967a, 1991; Jefferies, 1973; Lefebvre et al., 2010; Zhu et al., 2016;
558 Rozhnov et al., 2019). In contrast, the aulacophore insertions of '*Nanocarpus*' *guoleensis* (late
559 Guzhangian–Furongian, China) and *Peltocystis cornuta* (late Tremadocian; Fig. 12c) are both
560 framed by only two large adorals (Ubaghs, 1970; Lefebvre and Botting, 2007; Chen et al.,
561 2013). Consequently, the wide expansion of the two lateral adorals in early mitrocystitidans
562 and peltocystidans questions the possible loss of the small, median adoral in these forms.

563

564 In *Peltocystis* (Fig. 12c), a large skeletal element is consistently present posteriorly to A'₁
565 and A₁. This plate is morphologically indistinct from the surrounding imbricate supracentrals,
566 and also extremely variable in size and shape from one individual to another (see Ubaghs,
567 1967a, 1970; Lefebvre and Botting, 2007). These observations suggest that the large median
568 plate in contact with A'₁ and A₁ in *Peltocystis* is probably of supracentral origin, which
569 implies that A₀ is very likely lost in peltocystidans (see Ubaghs, 1967a, 1970; Lefebvre, 2001;
570 Lefebvre and Botting, 2007). In *Chinianocarpos* and various other Ordovician
571 mitrocystitidans (e.g. *Aspidocarpus*, *Mitrocystites*, new Floian anomalocystitid; Fig. 13a), a

single large skeletal element is also consistently present posteriorly to A'₁ and A₁. Contrary to the situation in *Peltocystis*, the size and shape of this median plate are relatively similar from one individual to another (see Ubaghs, 1967a, 1970, 1979; Cripps, 1990). Although it cannot be excluded that this skeletal element in close contact with A'₁ and A₁ corresponds to A₀, it is equally possible that it is a distinct plate of supracentral origin. The future descriptions of the Cambrian earliest mitrates will certainly help elucidating the identification of this skeletal element, which will be herein designated as 'A₀?' in mitrocystitidans (Figs. 13–16), so as to express the uncertainties about its homology with the median adoral of other stylophorans.

Supracentrals

All anomalocystitids have similar plate patterns for their lower thecal surface, with consistently the same 14 homologous skeletal elements: four marginals on the left (M'₁, M'₂, M'₃, M'₄), four ones on the right (M₁, M₂, M_c, M₃), a central zygale (Z), three posterior plates (M'₆, M'₇, M'₈), and two posterior spines (D and G) (see above; Fig. 11). In all taxa, but the new Floian anomalocystitid from Morocco, the right infracentral area is absent, and the left one consists of A (Siluro-Devonian forms; Fig. 11c), or A and B (Mid-Late Ordovician taxa; Fig. 11a-b) (see above). Consequently, the systematics of anomalocystitids mostly relies on the plate pattern of their upper thecal surface, and in particular on the number, extent and arrangement of their supracentrals (e.g. Dehm, 1932; Gill and Caster, 1960; Parsley, 1991; Ruta and Theron, 1997; Ruta and Bartels, 1998; Ruta, 1999a; Lefebvre, 2001; McDermott and Paul, 2017). Contrary to the situation in most other stylophorans, anomalocystitid supracentrals are frequently arranged into regular transverse rows, each made of a limited and fixed number of relatively large plates. Various terminologies have been introduced to identify supracentrals in Allanicystidiinae (e.g. Caster, 1952, 1954b; Philip, 1981),

Anomalocystitinae (e.g. Dehm, 1932; Gill and Caster, 1960) or in both groups (e.g. Jefferies and Lewis, 1978; Parsley, 1991). However, the most comprehensive models of plate homologies for the upper thecal surface of anomalocystitids were produced successively by Ruta and Theron (1997), Ruta and Bartels (1998) and Ruta (1999a) (see also Ruta, 1997b; Ruta and Jell, 1999a, 1999c, 1999d, 1999e; Jell, 2013; McDermott and Paul, 2017).

The terminology elaborated by Ruta (1999a) considers that the supracentrals of all anomalocystitids can be identified from a comparison with the plate pattern of *Bokkeveldia oosthuizeni* (see Ruta, 1997b; Ruta and Theron, 1997; Ruta and Bartels, 1998). The choice of *Bokkeveldia* as a reference was justified by the number of transverse supracentral rows (i.e. four, posteriorly to adorals), which is equal (e.g. *Victoriacystis*), but generally higher than in most other anomalocystitids (e.g. *Enoploura*, *Occultocystis*, *Placocystella*, *Placocystites*). This model considers that the possession of four regular rows of tessellate supracentrals is the plesiomorphic condition in anomalocystitids, which implies that taxa with three rows have lost one (e.g. *Enoploura*, *Placocystites*). This model also largely relies on the parsimonious assumption that standardization of the upper thecal surface occurred only once in anomalocystitids (Ruta, 1999a).

Posteriorly to adorals, the upper surface of the two earliest known anomalocystitids, i.e. the above-mentioned undescribed form from the middle Floian of Morocco (Fig. 13a; Noailles and Lefebvre, 2012) and *Diamphidiocystis* sp. from the late Darriwilian of France (Fig. 13b; Chauvel, 1981; Lefebvre, 1999, 2000a), consists of numerous imbricate supracentrals forming an irregular, polyplated pavement. Such an unorganized arrangement with imbricate elements (at least in the posterior part of the supracentral area) very likely represents the plesiomorphic condition in anomalocystitids (Lefebvre, 1999). The same plate pattern occurs in various

other Ordovician mitrates (e.g. *Eumitrocystella*, *Lagynocystis*, *Peltocystis*, *Promitrocystites*; Fig. 12b-c) (Ubaghs, 1967a).

The subfamily Diamphidiocystinae represents a small, highly-distinctive clade of Ordovician anomalocystitids characterized by a markedly sinistrally flexed theca (Kolata and Guensburg, 1979; Chauvel, 1981; Lefebvre, 1999, 2000a, 2001, 2003b; Ruta, 1999a). Contrary to the situation in the Darriwilian form from western France (Fig. 13b), the plate pattern of *D. drepanon* (Katian, Illinois) is characterized by a regular pavement made of few, particularly large, tessellate plates (Kolata and Guensburg, 1979). This observation suggests that the regular arrangement of tessellate supracentrals in *D. drepanon* derives from an originally unorganized pavement of imbricate elements (Darriwilian *Diamphidiocystis*). This example implies that comparable plate patterns with few, tessellate supracentrals can be acquired, independently, in various anomalocystitid lineages and, thus, questions the possibility of identifying plate homologies in the two main other clades of the family.

Allanicytidiinae (Fig. 14) are defined by the possession of a distinctive ploughshare-like stylocone with transverse blades (Ubaghs, 1967a; Caster, 1983; Haude, 1995; Lefebvre, 1999, 2001; Ruta, 1999a; Ruta and Jell, 1999a; Jell, 2013; Scheffler et al., 2017). Contrary to the situation in most other mitrocystitidans, $A_0?$ is also generally inserted between A'_1 and A_1 , and framing the aulacophore insertion (e.g. *Enoploura*, *Protocytidium*, *Placocystella*; Fig. 14a-b). In the earliest known representatives of the subfamily Allanicytidiinae (*Enoploura* spp., late Sandbian–Katian of North America), the supracentral area has an almost bilaterally symmetrical plate pattern (Fig. 14a), characterized by a fixed number of tessellate elements (11), organized into three incomplete rows (Caster, 1952; Parsley, 1982, 1991). The plate pattern of *Enoploura* can be readily compared with those of all younger allanicytidiines, and a

well-defined set of homologies can be established at sub-family level (see discussions in Haude, 1995; Ruta and Theron, 1997; Ruta, 1999a; Ruta and Jell, 1999a; Lefebvre, 2001; Jell, 2013; Scheffler et al., 2017). For example, the reduced number of supracentrals (nine) in *Protocytidium elliotiae* (Hirnantian, Australia; Fig. 14b) most likely results from the loss of two posterior supracentrals (Ruta and Jell, 1999a). Similarly, the plate patterns of *Occultocystis* (Lower Devonian, Argentina; Fig. 14c) and *Placocystella* spp. (late Llandovery–early Givetian; Australia, Brazil, New Zealand, South Africa) can be both interpreted as resulting from further drastic reductions of the number of supracentrals from nine elements (*Protocytidium*) to five and six, respectively (Haude, 1995; Ruta and Theron, 1997; Ruta, 1999a; Ruta and Jell, 1999a; Lefebvre, 2001; Jell, 2013; Scheffler et al., 2017).

Anomalocystitinae (Figs 15b-c, 16) are characterized by the possession of a highly distinctive supracentral element with rounded to elliptical outlines: the placocystid plate (P). The spineless genus *Barrandeocarpus* (with an obvious plate P on its upper thecal surface; Fig. 15b) is thus interpreted here as an anomalocystitine mitrate, in which both D and G have been secondarily lost (Lefebvre, 1999; Lefebvre and Gutiérrez-Marco, 2003; McDermott and Paul, 2017; but see Ubaghs, 1979; Craske and Jefferies, 1989; Ruta, 1997c, 1999a). Anomalocystitines also retain many plesiomorphic mitrocystitidan features, such as longitudinally compressed styloid blades and, in most taxa, a median anterior plate A_0 ? located posteriorly to A'_1 and A_1 and, thus, not in contact with the aulacophore insertion (Figs. 15b-c, 16a; Lefebvre, 1999). The earliest known representatives of this subfamily, *Barrandeocarpus jaekeli* (Sandbian, Czech Republic; Fig. 15b), *B.* sp. (Sandbian, UK), *Ateleocystites* spp. (early Katian, Canada and USA; Fig. 15c) and *A? lansae* (late Katian, UK) are all characterized by two anterior, relatively regular rows of supracentrals, each made of a fixed number of elements (Ubaghs, 1979; Kolata and Jollie, 1982; Parsley, 1991; Ruta,

1997c; McDermott and Paul, 2017). In both *Ateleocystites* and *Barrandeocarpus*, the most anterior transverse row of supracentrals always comprises five plates, including P in central position, whereas the next, more posterior row is made of four elements (Fig. 15b-c). However, in some specimens of *A. huxleyi* (and possibly also in some individuals of *B. jaekeli*), a fifth plate can be sometimes more or less deeply inserted posteriorly and in between the two large median supracentrals of the second row (Kolata and Jollie, 1982; Parsley, 1991). In the two genera *Ateleocystites* (Fig. 15c) and *Barrandeocarpus* (Fig. 15b), the posterior part of the supracentral area mostly consists of imbricate, irregularly arranged elements in variable number (Ubaghs, 1979; Kolata and Jollie, 1982; McDermott and Paul, 2017). In this respect, the very nice reconstructions of both *A. guttenbergensis* and *B. jaekeli* provided by Kolata and Jollie (1982, fig. 3) and Ubaghs (1979, fig. 5), respectively, are partly misleading, because they suggest the existence of a more or less regular arrangement for posterior supracentrals, which is not the case. As stated by Kolata and Jollie (1982, p. 640), the total number of supracentrals varies between 20 and 25 in *Ateleocystites* (i.e. between 11 and 16 in the posterior, imbricate region; see also McDermott and Paul, 2017, p. 7).

The imbricate nature of posterior supracentrals in all known Ordovician anomalocystitines (*Ateleocystites*, *Barrandeocarpus*; Fig. 15b-c) suggests that regularization of their upper thecal surface into regular rows of tessellate elements occurred very likely through different processes and later than in coeval Late Ordovician allanicytidiines (*Enoploura*, *Protocytidium*; Fig. 14a-b). However, the comparison of the two anterior rows of supracentrals in Ordovician anomalocystitines and allanicytidiines shows several similarities, which could suggest a shared common original pattern of organization into regular rows of tessellate plates. A new terminology is thus tentatively proposed here, so as to facilitate the

comparison of supracentral plate patterns in early allanicytidiines and anomalocystitines, and also to help identifying putatively homologous skeletal elements.

Similarly to Dehm's terminology (1932), the new system relies primarily on the organization of the upper thecal surface into regular transverse rows of tessellate plates (Figs. 14-15). Within a given row, each plate is assigned a number indicating its position away from the midline, in the same way this is already done for identifying marginals and adorals (see e.g. Lefebvre and Vizcaïno, 1999; Lefebvre, 2001). In all anomalocystitids, the most anterior row (row A) consists of three homologous plates: A'₁ (on the left), A₀? (in median position), and A₁ (on the right). In Ordovician anomalocystitines, the next row (here designated as row B) contains five plates, which are from left to right: B'₂, B'₁, P (placocystid plate, in median position), B₁ and B₂ (Fig. 15b-c). Similarly, the second row of supracentrals (row C) typically contains four elements in both *Ateleocystites* and *Barrandeocarpus*, with from left to right: C'₂, C'₁, C₁ and C₂ (Fig. 15b-c).

Comparison of plate patterns in Ordovician allanicytidiines (Fig. 14a-b) and anomalocystitines (Fig. 15b-c), suggests that supracentrals C'₁ and C₁ in *Ateleocystites* and *Barrandeocarpus* are very likely homologous to the pair of similarly shaped, wide median supracentrals anteriorly in contact with A₀? in both *Enoploura* and *Protocytidium*. Comparison with the situation in Ordovician anomalocystitines indicates that the lateral element in contact with both A'₁ and C'₁ in *Enoploura* and *Protocytidium* can be identified as B'₂ (same position and same contacts with surrounding plates). Similarly, on the right side of allanicytidiine thecae, B₂ corresponds to the supracentral in contact with both A₁ and C₁ (Fig. 14a-b). These identifications imply that, in *Enoploura* (Fig. 14a) and *Protocytidium* (Fig. 14b), the first row of supracentrals consists of only two plates (B'₂ and B₂), instead of five in

Ordovician anomalocystitines (Fig. 15b-c). In both *Enoploura* (Fig. 14a) and *Protocystidium* (Fig. 14b), the absence (loss?) of B'₁, P and B₁ coincides with (and possibly results from) the strong posterior expansion of A₀?. Comparison with *Ateleocystites* (Fig. 15c) and *Barrandeocarpus* (Fig. 15b) suggests that the two allanicytidiine lateral supracentrals in contact with B'₂ and C'₁, on the one hand, and B₂ and C₁, and on the other hand, can be reasonably identified as C'₂ and C₂, respectively (Fig. 14a-b).

In this context, the morphology of the problematic anomalocystitid *Willmanocystis denticulatus* (early Katian, North America), which is here interpreted as a possible sister-taxon of allanicytidiines (see Kolata and Jollie, 1982; Lefebvre, 1999; but see Parsley, 1991; Ruta, 1999a), is of particular interest. *Willmanocystis* (Fig. 15a) lacks the distinctive ploughshare stylocone of Allanicytidiinae, but it shares with *Enoploura* (Fig. 14a) and *Protocystidium* (Fig. 14b) the possession of an anterior plate A₀? framing the aulacophore insertion, a supracentral area entirely made of tessellate elements organized into regular rows, and the absence of the placocystid plate. In *Willmanocystis* (Fig. 15a), supracentrals are numerous (at least 17, more likely 18) and arranged into four transverse rows (Kolata and Jollie, 1982). Comparison with coeval allanicytidiines and anomalocystitines suggests that its first row of supracentrals probably consists of B'₂, B'₁, B₁ and B₂, thus supporting the view that the two median elements (B'₁ and B₁) were probably lost in *Enoploura* (Fig. 14a) and *Protocystidium* (Fig. 14b). In *Willmanocystis* (Fig. 15a), the next supracentral row is made of five elements, which is unlike the situation in Late Ordovician allanicytidiines and anomalocystitines. The occasional occurrence of a fifth median element (C₀?) inserted in between C'₁ and C₁ in some specimens of *Ateleocystites huxleyi* (Kolata and Jollie, 1982; Parsley, 1991) and possibly *A? lansae* (McDermott and Paul, 2017) questions the possibility that the five-plated row of *Willmanocystis* represents the plesimorphic condition for row C in

both allanicytidiines and anomalocystitines. Alternatively, this five-plated row might be an autapomorphy of *W. denticulatus* (row absent or lost in e.g. *Enoploura* and *Ateleocystites*), and the next, four-plated row could then be equivalent to row C of Late Ordovician allanicytidiines and anomalocystitines. In *Willmanocystis* (Fig. 15a), the posterior, regularly arranged row of five tessellate supracentrals has no obvious equivalent in the morphology of coeval anomalocystitines, but it is very likely homologous to the similarly positioned row of *Enoploura* (Fig. 14a), which is also made of five small plates along the anal opening. The upper surface of *Willmanocystis* (Fig. 15a) suggests that the arrangement on the upper thecal surface of *Enoploura* (Fig. 14a) results from a drastic reduction in the number of plates (from 18 to 11) and the probable loss of one row of supracentrals (either the second or the third one, by comparison with *W. denticulatus*; see discussion above). For this reason, the third, posterior supracentral row of *Enoploura* is here designated E (Fig. 14a), and its five plates, E₂, E₁, E₀, E₁, and E₂ (from left to right). Finally, the plate pattern of the upper thecal surface of *Willmanocystis* (Fig. 15a) has some troubling similarities with those of much younger, Early Devonian anomalocystitines (e.g. *Anomalocystites* and, mostly, *Bokkeveldia*; Fig. 16b). At this stage, it remains difficult to decipher if these similarities in plating are the result of fortuitous convergence or of iterative evolution, possibly due to heterochronic processes.

In marked contrast with *Ateleocystites* (Fig. 15c) and *Barrandeocarpus* (Fig. 15b), the upper thecal surface of Siluro-Devonian Anomalocystitidae (Fig. 16) is entirely made of tessellate plates with, posteriorly to adorals, three (*Placocystites*, new undescribed form from Bolivia; Llandovery–Pragian), four (*Bokkeveldia*, *Mongolocarpos*, *Rhenocystis*, *Victoriacystis*; Ludlow–Emsian), and even five rows (*Anomalocystites*; Lower Devonian) of regularly arranged supracentrals in fixed number (Dehm, 1932; Gill and Caster, 1960; Ubaghs, 1967a; Jefferies and Lewis, 1978; Rozhnov, 1990; Parsley, 1991; Ruta, 1997b,

1999a; Ruta and Theron, 1997; Ruta and Bartels, 1998; Ruta and Jell, 1999c, 1999d; Lefebvre and Rachebœuf, 2007; Parsley and Sumrall, 2007). Plate patterns of Siluro-Devonian anomalocystitines (Fig. 16) can be easily compared to each other, and a set of robust homologies was proposed by Ruta (1999a; see also Ruta, 1997b; Ruta and Theron, 1997; Ruta and Bartels, 1998). However, the numerical terminology for supracentrals elaborated by Ruta (1999a), which is based on *Bokkeveldia*, with four rows of plates, posteriorly to adorals (Fig. 16b), cannot be applied to taxa such as *Anomalocystites*, with one more row of supracentrals (Fig. 16c; see Parsley, 1991; Ruta 1999a, fig. 9A).

A major issue with Anomalocystitinae lies in the difficulty of comparing the plate patterns of Siluro-Devonian taxa (Fig. 16) with those, very different, of earlier forms (Fig. 15b-c) and, thus, to identify skeletal homologies at subfamily level. In all Anomalocystitinae, row A consists of the same three plates (A'_1 , A_0 ? and A_1), and the most anterior row of supracentrals is always made of five skeletal elements, with the highly distinctive placocystid plate in median position (Figs. 15b-c, 16). This implies that the five anterior supracentrals of Siluro-Devonian anomalocystitines can be readily identified as B'_2 , B'_1 , P, B_1 and B_2 . In marked contrast, in the absence of morphologically intermediate forms between Late Ordovician taxa (*Ateleocystites*, *Barrandeocarpus*; but see discussion above about *Willmanocystis*) and younger anomalocystitines, identifying plate homologies posteriorly to row B is almost impossible at present. For example, the current fossil record of Anomalocystitinae provides no clues to decipher if row C of *Ateleocystites* (Fig. 15c) is lost in Siluro-Devonian taxa (Fig. 16) or equivalent to their second or even their third row of supracentrals. Similarly, it is at present impossible to identify which row(s) of tessellate supracentrals in Siluro-Devonian forms are potentially equivalent to the posterior imbricate area of earlier forms. For this reason, a separate nomenclature (with Roman numerals) is provisionally proposed here for the

four posterior rows of Siluro-Devonian anomalocystitines (Fig. 16). This terminology, which implies row and plate homologies, is kept voluntarily distinct from the above-described nomenclature suggested for Allanicystidiinae and early Anomalocystitinae, because available fossil evidence suggests that the highly standardized plate patterns of their Siluro-Devonian representatives were possibly acquired independently in the two lineages.

The highest total number of transverse rows (six) is present on the upper thecal surface of *Anomalocystites* (Fig. 16c; see Ubaghs, 1967a; Parsley, 1991; Ruta, 1999a). Its two anterior-most rows are homologous to rows A and B in other anomalocystitids (see above). Although it was not shown on Parsley's reconstruction (1991, fig. 5) of *A. cornutus*, the placocystid plate is clearly present in median position, within row B (see e.g. Parsley, 1991, pl. 1 figs 4, 14; Ruta, 1999a). The next four rows are designated III, IV, V and VI (Fig. 16c). Row and plate homologies in all other Siluro-Devonian anomalocystitines (Fig. 16a-b) can be deduced from a comparison with the upper surface of *Anomalocystites* (Fig. 16c). Although their fossil record remains relatively sparse, post-Ordovician anomalocystitines seem to show a more or less regular increase of their number of supracentrals through time, and correlatively of their number of transverse rows (Gill and Caster, 1960; but see Ruta and Bartels, 1998): four-rowed taxa (Fig. 16a) occur in the late Llandovery (A, B, III, and VI; e.g. *Placocystites forbesianus*), whereas five-rowed ones (Fig. 16b) are not documented before the Ludlow (A, B, III, V, and VI; e.g. *Mongolocarpos minzhini*, *Victoriacystis wilkinsi*) and six-rowed forms (Fig. 16c) are only known from the Early Devonian (A, B, III, IV, V, and VI; *Anomalocystites cornutus*). More data are probably necessary to decipher whether this apparent increase in the number of plates and rows in post-Ordovician anomalocystitines represents an actual trend, or if it simply results from a strong sampling bias.

821 SYSTEMATIC PALEONTOLOGY

822

823 PHYLUM ECHINODERMATA BRUGUIERE, 1791 (*ex* KLEIN, 1734)

824

825 CLASS STYLOPHORA GILL & CASTER, 1960

826

827 Order Mitrata Jaekel, 1918

828

829 Suborder Mitrocystitida Caster, 1952

830

831 **Family Anomalocystitidae Bassler, 1938**

832

833 Diagnosis. A family of mitrocystitidan mitrates with asymmetrical to symmetrical theca;
834 lower thecal surface comprising 11 marginals, a large plate Z in central position, and a left
835 infracentral area; digital and glossal modified into posterior spines or secondarily lost; anus
836 opening through a slit or a rake-like anal pyramid with numerous spike-shaped platelets;
837 supracentrals imbricate and/or regularly arranged into transverse rows of tessellate elements;
838 right adoral orifice absent; median element A_0 ? posterior to or inserted between A'_1 and A_1 ;
839 skeletal sculpture more or less extensive on one or both thecal surfaces, consisting of straight
840 to sinuous cuesta-shaped ribs and/or discontinuous scale-like riblets and/or pustules.

841

842 Remarks. Following Lefebvre (1999, 2000b), anomalocystitids are here considered as a
843 clade within mitrocystitidan mitrates. The diagnosis of Anomalocystitidae has been modified
844 here so as to accomodate their wide morphological disparity and their yet undescribed earliest
845 representative from the middle Floian of Morocco (Figs 10, 13a; Lefebvre, 2007a; Noailles

and Lefebvre, 2012; Lefebvre et al., 2013, 2016). Three main subdivisions are here identified within anomalocystitids, based on the literature, previous phylogenetic analyses and, mostly, plate homologies: Allanicystidiinae, Anomalocystitinae and Diamphidiocystinae (see above; e.g. Ubaghs, 1967a; Kolata and Guensburg, 1979; Kolata and Jollie, 1982; Parsley, 1991, 1997; Ruta, 1999a, 2003; Lefebvre, 2000b, 2001, 2005). The subfamily Allanicystidiinae (Figs 11, 14) includes all taxa possessing a ploughshare-shaped stylocone with transverse blades (see below). Anomalocystitines (Figs 15b-c, 16) are defined by the presence of the placocystid plate on their upper thecal surface (see above; *Anomalocystites*, *Ateleocystites*, *Barrandeocarpus*, *Bokkeveldia*, *Mongolocarpos*, *Placocystites*, *Rhenocystis*, *Victoriacystis*). Finally, the subfamily Diamphidiocystinae (Fig. 13b) corresponds to a small clade of anomalocystitids with a markedly asymmetrical, sinistrally flexed theca (*Diamphidiocystis*).

Three Late Ordovician anomalocystitids from North America are not assigned to any subfamily. *Willmanocystis denticulatus* (Fig. 15a) is a possible sister-taxon of Allanicystidiinae (see discussion above; Kolata and Jollie, 1982). The upper thecal surface of *Kopfcystis kirkfieldi* suggests probable affinities with Anomalocystitinae; the single known specimen of *Kopfcystis* could even represent a poorly preserved individual of *Ateleocystites*. Similarly, the morphology of the type and only specimen of *Kierocystis inserta* is extremely poorly known. This genus was defined on the erroneous identification of two tectals (elements of the proximal aulacophore) as a pair of small, additional anterior thecal plates (PSI in Parsley, 1991; but see Ruta, 1999a). The plate pattern of its upper thecal surface is anteriorly poorly preserved, so that it is difficult to identify whether one single large median element $A_0?$ is present (thus suggesting affinities with *Enoploura* and allanicystidiines), or if this area rather corresponds to four plates (see Ruta, 1999a), with a small $A_0?$, B'_1 , B_1 and possibly, P (in this case, *Kierocystis* would be a badly preserved specimen of *Ateleocystites*).

871

872 **Subfamily Allanicystidiinae Caster and Gill, *in* Ubaghs, 1967a**

873

874 Diagnosis. A subfamily of anomalocystitid mitrates with a nearly bilaterally symmetrical
875 theca and two posterior spines (D and G); no right infracentral area; left infracentral area
876 consisting of one or two elements; anus opening through a slit; supracentral area made
877 exclusively of few tessellate plates arranged into two or three transverse rows; no placocystid
878 plate; skeletal sculpture, when present, consisting of discontinuous scale-like riblets and/or
879 pustules; robust ploughshare stylocone with two large transverse blades; proximal ossicles
880 markedly spinose.

881

882 Remarks. The diagnosis of the subfamily is emended here, so as to accommodate all
883 genera previously assigned to Allanicystidiinae (*Enoploura*, *Occultocystis*, *Placocystella*,
884 *Protocystidium*; see Haude, 1995; Ruta and Jell, 1999a), and the two new taxa described
885 herein. As already suggested by Lefebvre (2001), *Allanicystidium* Caster and Gill *in* Ubaghs,
886 1967a, *Australocystis* Caster, 1954b, *Notocarpos* Philip, 1981 and *Tasmanicystidium* Caster,
887 1983 are here considered junior synonyms of *Placocystella* Rennie, 1936 (see Lefebvre and
888 Rachebœuf, 2007; Scheffler et al, 2019; but see Jell, 2013). This synonymy is justified by the
889 possession of similarly built thecae, made entirely of the same homologous plates (adorals,
890 marginals and supracentrals). In stylophorans, generic identification relies primarily on the
891 nature and number of their thecal plates. Differences in the shape and/or relative proportions
892 of skeletal elements (i.e. the shorter anterior extent of anomalocystid plate in *P. garratti*; Fig.
893 11c) are considered as useful characters to discriminate species within a same genus.

894

Reexamination by the senior author of the original specimen of anomalocystitid mentioned by Lindström (1888) in the Wenlock of Sweden (see also Regnell, 1945, 1960) indicates that it consists of a partially preserved right adoral (A_1), some plates of the proximal aulacophore, and an almost complete lower thecal surface. Such remains are generally considered as uninformative for the identification of Siluro-Devonian anomalocystitids (see above). However, Lindström's mitrate has an extensive thecal sculpture consisting of short, discontinuous scale-like riblets on A_1 and numerous pustules on its marginals. This ornamentation suggests allanicytidiine rather than anomalocystitine affinities.

Genus *Perikefalea* Lefebvre et Ausich, gen. nov.

New genus of allanicytidiine anomalocystitids: Lefebvre and Rachebœuf, 2007, p. 241.

New genus of Allanicytidiinae: Scheffler et al., 2019, p. 228.

Etymology. From the Greek *Περικεφαλαία*, helmet, referring to the shape of the theca (with its highly distinctive posterior median spike), which is similar in the aspect to a Corinthian (hoplite) helmet.

Type species. *Perikefalea racheboeufi* sp. nov. Lefebvre and Ausich.

Diagnosis. A genus of allanicytidiine mitrate with a long posterior spike on M_7 ; left infracentral area made of one plate (A); upper thecal surface consisting of five extensive skeletal elements; A_0 ? diamond-shaped, posteriorly inserted to A'_1 and A_1 , not in contact with aulacophore insertion; posterior half of upper thecal surface formed by two supracentrals (C'_1 and C_1).

920

921 Species composition. Besides the type species, *P. racheboeufi*, another anomalocystitid is
922 also tentatively assigned to *Perikefalea*: *P.? cybeleae* sp. nov. Lefebvre and Ausich (late
923 Llandoverly, Anticosti Island, Canada).

924

925 Comparison. The morphology of *Perikefalea* unambiguously supports its assignment to
926 anomalocystitids (two posterior spines) and, more precisely, to allanicytidiines (ploughshare
927 stylocone with transverse blades). The plating of its upper thecal surface differs from those of
928 most other allanicytidiines in (1) the posterior position of $A_0?$, which is not in contact with
929 the aulacophore insertion; and (2) the occurrence of only two supracentrals, instead of eleven
930 (*Enoploura*; Fig. 14a), nine (*Protocytidium*; Fig. 14b) or six (*Placocystella*). The morphology
931 of *Perikefalea* suggests closer affinities with *Occultocystis koeneni* (Fig. 14c; Lower
932 Devonian, Argentina; Haude, 1995). In both taxa, two pairs of lateral supracentrals are lost
933 (B'_2 - B_2 , and C'_2 - C_2) and $A_0?$, occupies a central position, without any contact with the
934 aulacophore insertion. However, *Perikefalea* differs from *Occultocystis* by its lower number
935 of supracentrals (two instead of five), resulting from the loss of the three posterior elements
936 (E'_1 , E_0 and E_1). The posterior M_7 spike of *Perikefalea* has no equivalent in
937 Anomalocystitidae. A similar M_7 spike occurs in *Aspidocarpus bohemicus* (Fig. 9b; Sandbian,
938 Czech Republic; Ubaghs, 1979). However, the two taxa are not closely related: *Perikefalea* is
939 a highly derived anomalocystitid, whereas *A. bohemicus* is a relatively basal mitrocystitidan
940 retaining many plesiomorphic features (e.g. lateripores, digital and glossal incorporated into
941 the marginal frame, two polyplated infracentral areas, polyplated, unorganized supracentral
942 surface). The five-plated upper thecal surface of *Perikefalea* also shares superficial
943 similarities with the plate pattern of some paranacystids (e.g. *Adoketocarpus*, *Paranacystis*;
944 Caster, 1954a; Ubaghs, 1967a; Ruta and Jell, 1999b). Paranacystids are a clade of spineless

mitrocystitidans characterized by a leftward directed anal opening, and a strong expansion of M_6 , which is modified into a large posterior marginal process (Lefebvre, 1999, 2000b; Lefebvre and Rachebœuf, 2007). Consequently, the similar-looking upper thecal surfaces of paranacystids and *Perikefalea* were acquired independently, through convergent, drastic reductions of their numbers of supracentrals.

***Perikefalea racheboeufi* Lefebvre et Ausich, sp. nov.**

Figs 17–21

Etymology. The species is named after Patrick Rachebœuf, who collected all the study material from Bolivia and contributed for many years to paleontological and stratigraphic investigations in the Devonian of Bolivia.

Holotype. MHNC 13354, part and counterpart of an almost complete individual preserved in fine sandstones, and preserving lower and upper thecal surfaces, articulated posterior spines, proximal aulacophore rings, and stylocone (Fig. 17). Uppermost part of the Santa Rosa Formation (Lochkovian, Lower Devonian), Presto-El Peral section, 50 km NE of Sucre, Bolivia.

Diagnosis. A species of *Perikefalea* with a wide, blunt posterior M_7 spike, and reticulate thecal plates with no obvious thecal sculpture.

Description. Relatively broad, almost bilaterally symmetrical theca, with gently curved lateral margins (Fig. 20b-c). Lower thecal surface drop-shaped, with deep, concave, semi-

970 circular, anterior notch at aulacophore insertion (Fig. 18a-b), and narrow posterior margin
971 with two concave lateral sides separated by a wide, median, spout-like blunt expansion
972 formed by M_7 (Figs 17a-b, 18a-b, 19a). Lower thecal surface almost flat, except crescent-
973 shaped raised anterior lip borne by M'_1 and M_1 around aulacophore insertion (Fig. 18a-b), and
974 downward recurved edges of lateral marginals forming two low skate-like flanges on the left
975 (along M'_2 , M'_3 and M'_4) and on the right (along M_2 , M_c and M_3) (Figs 17a-b, 18a-b). Upper
976 thecal surface gently convex, with almost elliptical outlines, and a wide, concave, V-shaped,
977 shallow notch at aulacophore insertion (Figs 17c-d, 18c-d).

978

979 Lower thecal surface consisting of 15 skeletal elements (Figs 20-21): 11 marginals, two
980 plates in central position, and two posterior spines. Anterior marginals M'_1 and M_1 broad,
981 moderately elongate, subequal in size, entirely forming gently curved anterior edge of lower
982 thecal surface interrupted by deep median notch for aulacophore insertion (Figs 17a-b, 18a-b).
983 Relatively high, vertical, symmetrical aulacophore apophyses borne by anterior walls of M_1
984 and M'_1 , posteriorly to appendage insertion (Fig. 20a). Putative apophyses horns not clearly
985 visible. Next marginals, M'_2 (on the left) and M_2 (on the right), large, fan-shaped, delimited by
986 very short adaxial sutures along Z , two longer, strongly diverging, almost straight contacts
987 with neighbouring marginals, and long, gently curved abaxial edges (Figs 17a-b, 18a-b). Next
988 pair of marginals, M'_3 (on the left) and M_c (on the right), quadrangular, moderately elongate,
989 slightly shorter than more anterior marginals, with moderately curved abaxial edges and
990 straight sutures along Z (Figs 17a-b, 18a-b, 19a). Next two lateral marginals, M'_4 (on the left)
991 and M_3 (on the right) unequal in size, with slightly different outlines (Figs 17a-b, 18a-b, 19a).
992 M'_4 and M_3 with similar long, almost straight abaxial edges, and very short posterior margin,
993 corresponding to sockets for spine articulation. M_3 pentagonal, wider than M'_4 , largely in
994 contact with M_c , Z and M_6 along straight sutures. M'_4 with very short suture along Z , concave

adaxial margin along anomalocystitid plate A, and relatively short, straight contact with M'₆. Lateral posterior plates M'₆ (on the left) and M₆ (on the right) subequal in size, similarly shaped, elongate, narrow, quadrangular elements, slightly wider posteriorly than anteriorly (Figs 17a-b, 18a-b, 19a). M'₆ in contact with M₇ (adaxially), Z (anteriorly), and both A and M'₄ (abaxially). M₆ sutured to M₃ (abaxially), Z (anteriorly) and M₇ (adaxially). Median posterior marginal M₇, particularly elongate, subpentagonal, with short anterior margin in contact with Z, long, posteriorly diverging, gently concave sutures along M'₆ (on the left) and M₆ (on the right), and two long marginal edges converging posteriorly towards a blunt, rounded tip (Figs 17a-b, 18a-b, 19a). Posterior part of M₇ thus forming wide, protruding spike-shaped expansion of marginal frame. Zygale plate particularly large, subhexagonal, occupying most of central part of lower thecal surface, in contact with anomalocystid plate and all marginals (Figs 17a-b, 20b). Anomalocystitid plate small central subtrapezoidal skeletal element in close contact with M'₄ (abaxially), and also sutured to both Z (adaxially) and M'₆ (posteriorly) (Figs 17a-b, 18a-b, 19a). Posterior spines, D (digital, on the left) and G (glossal, on the right), elongate, rod-shaped, moderately decreasing in width antero-posteriorly, with rounded proximal ball for articulation with marginal frame, and distal blunt extremity (Figs 17a-b, 19a). Digital almost straight, but glossal possibly weakly curved (Figs 17a-b, 20b).

Bilaterally symmetrical upper thecal surface (Fig. 20c) entirely made of five large, gently domed plates: two adorals (A'₁ and A₁), one median element (A₀?), and two supracentrals (C'₁, C₁). Lateral adorals, A'₁ (on the left) and A₁ (on the right), wide, particularly elongate, forming together most of anterior half of upper thecal surface (Figs 17c-d, 18c-d). A'₁ and A₁ with relatively short, straight anterior margins forming wide, shallow, V-shaped, concave notch above aulacophore insertion. Abaxial margins of lateral adorals particularly elongate,

convex, regularly curved, closely sutured to lateral walls of underlying marginals (M'_1 - M_1 , M'_2 - M_2 and anterior half of M'_3 - M_c). Adaxial margins of A'_1 and A_1 anteriorly sutured to each other along thecal longitudinal midline, and posteriorly diverging abaxially along A_0 ?. Each lateral adoral posteriorly in contact with one supracentral along short, straight, transverse suture. A_0 ? large, elongate, diamond- to fan-shaped skeletal element in central position, sutured to all other plates of upper thecal surface (Figs 17c-d, 18c-d). Maximum width of A_0 ? at contact between adorals and supracentrals. Maximum length of A_0 ? along longitudinal midline. Anterior margins of A_0 ?, long, sinous and converging anteriorly to triple junction with A'_1 and A_1 along thecal longitudinal midline. Posterior margins of A_0 ?, much shorter, gently convex, similarly converging posteriorly to triple junction with C'_1 (on the left) and C_1 (on the right) along longitudinal midline. Supracentrals C'_1 and C_1 almost as extensive as adorals, particularly elongate, sub-triangular to fan-shaped, forming together most of posterior half of upper thecal surface (Figs 17c-d, 18c-d). Long, straight, adaxial suture between C'_1 and C_1 along thecal longitudinal midline. Each supracentral anteriorly in contact with A_0 ? and one lateral adoral. Abaxial margins of C'_1 and C_1 particularly long, convex, regularly flexed, laterally in contact with underlying marginals (posterior half of M'_3 - M_c , M'_4 - M_3), but forming posteriorly a large vault expanding beyond M'_6 and M_6 , up to distal extremity of M_7 spike (Fig. 19a).

Internal thecal features (e.g. infundibulum, septum, scutulae and associated co-opercula) not observed (all specimens fully articulated, no internal moulds, no isolated plates). Anal opening slit-like, narrow, in transversely elongate space roofed by C'_1 - C_1 vault, and floored by distal margin of posterior marginals (M'_6 , M_7 , M_6). Internal thecal cavity anteriorly in contact with lumen of proximal aulacophore through narrow, transversely elongate

passageway between high aulacophore apophyses borne by M'_1 and M_1 (below) and low vault provided by A'_1 and A_1 (above) (Fig. 20a).

Proximal aulacophore relatively short, cylindrical, consisting of four telescopic, bilaterally symmetrical, transverse rings, each made of four plates (Fig. 17): two tectals (above), and two inferolaterals (below). Left and right series of tectals in contact along longitudinal midline (Fig. 17c-d). Left and right series of inferolaterals similarly sutured along longitudinal midline (Fig. 17a-b). Inferolaterals and tectals contributing equally to height of lateral walls of proximal rings (Fig. 19b). Each ring comprising a slightly narrower, depressed proximal neck, and a slightly wider, raised distal lip. No intercalated integumentary platelets observed in between successive rings. Stylocone ploughshare-shaped, with two transverse, oblique blades. Anterior (distal) stylocone blade much more extensive and wider than posterior (proximal) one (Figs 17a-b, 19b). Upper surface of stylocone and more distal brachials not observed. In best preserved aulacophore (Fig. 19b), anterior portion of arm, consisting of more than 20 high, clearly spinose brachials and associated cover plates. Fine details of arm plates obscured by preservation in coarse siliciclastic deposits.

Measurements. Thecal length (TL) is measured between the anterior-most extremity of anterior marginals (M'_1 , M_1) and the posterior tip of the M_7 spike. Thecal width (TW) is estimated perpendicularly to TL, where width is maximum (i.e. along the M'_2 - M_3 and M_2 - M_3 sutures). Spine length (SpL) and width (SpW) are measured along and across, respectively, posterior spines. Maximum width of the stylocone (StylW) is estimated along its anterior (distal) transverse blade. MHNC 13354 (holotype): TL: 8.5 mm, TW: 5.4 mm, SpL: 3.3 mm, SpW: 0.6 mm, StylW: 2.6 mm; MHNC 13355: TL: 8.5 mm, TW: 6.2 mm; MHNC 13356:

TW: 6.2 mm, SpW: 0.6 mm. In the holotype, TW is probably underestimated, because left marginals are slightly shifted adaxially.

Remarks. The occurrence of a new allanicytidiine mitrate in the Lochkovian of Bolivia was originally reported by Lefebvre and Rachebœuf (2007), and later mentioned by Scheffler et al. (2019). Although specimens occur in relatively coarse siliciclastic deposits, the absence of any obvious external skeletal sculpture is probably original in *P. racheboeufi*. Minute details can be preserved, as evidenced by the relatively loose, porous stereom microstructure, which is visible on most thecal plates and that is similar to the 'punctate' morphology described in some Ordovician allanicytidiines (e.g. *Enoploura punctata*; Bassler, 1932; Parsley, 1991). The absence of ornamentation in *P. racheboeufi* is possibly related to an epibenthic, vagile, mode of life, comparable to that of paranacystids occurring in the same levels of the Santa Rosa Formation (see Lefebvre, 2003b).

In specimen MHNC 13358 (Fig. 19b), the preservation of the arm in extended position is unusual in mitrates. In this group, the aulacophore is generally recurved over the theca, in a typical flexed posture, which is usually interpreted as a distressed position or as the result of a post-mortem contraction (e.g. Dehm, 1932; Jefferies, 1984; Parsley, 1988; Ruta and Bartels, 1998; Lefebvre, 2003b). The unusual preservation of Bolivian anomalocystitids with their extended arm (i.e. in its original feeding position) suggests that they were very likely buried alive and in situ by a sudden influx of sediments (see Parsley and Gutiérrez-Marco, 2005; Lefebvre and Botting, 2007; Martin et al., 2015). Their occurrence in very shallow, low intertidal deposits suggest that this interpretation is plausible.

1092 Occurrence. *Perikefalea racheboeufi* is only known from the type-locality (Presto-El
1093 Peral), where it occurs within the uppermost part of the Santa Rosa Formation (Lochkovian).

1094
1095 Material. Besides the holotype (MHNC 13354; Fig. 17), available material comprises four
1096 other specimens. MHNC 13355 (Fig. 18) is an almost complete, fully articulated theca, with
1097 the two aulacophore apophyses anteriorly; spines and aulacophore not preserved. MHNC
1098 13356 (Fig. 19a) preserves the posterior half of a theca, with the pair of spines articulated to
1099 it. The last two individuals, MHNC 13357 and MHNC 13358, are less well-preserved.
1100 However, MHNC 13358 (Fig. 19b) corresponds to an almost complete specimen in lateral
1101 position, showing the theca, proximal aulacophore rings, stylocone, and more than 20
1102 brachials and their articulated cover plates; posterior thecal spines not visible.

1103
1104 ***Perikefalea? cybeleae* Lefebvre et Ausich, sp. nov.**

1105
1106 Figs 22–23

1107
1108 Etymology. The species is named after the lithostratigraphic unit (Cybèle Member), where
1109 the holotype was collected by the junior author, on Anticosti Island, Canada.

1110
1111 Holotype. GSC 126914 (Figs 22-23), specimen preserved in a fine carbonate mudstone.
1112 Exposed is an almost complete lower thecal surface, part of proximal aulacophore, and a
1113 small portion of distally recurved arm. Cybèle Member of the Jupiter Formation (Telychian,
1114 late Llandovery, Silurian), western bank of the Box River (N 49° 08' 53.5" W 62° 21' 13.6"),
1115 eastern part of Anticosti Island, Canada.

1117 Diagnosis. A species of *Perikefalea* with a narrow, sharp posterior M₇ spike, and extensive
1118 thecal sculpture consisting of scale-like riblets.

1119

1120 Description. Almost complete, though slightly disarticulated, lower thecal surface, with drop-
1121 shaped outlines (Fig. 22). Weakly curved, almost straight, abaxial sides. Long, median
1122 posterior process, tapering distally into a sharp spike subdividing posterior margin into two
1123 equal, concave, lateral edges. Anterior thecal margin and aulacophore insertion not preserved.
1124 Lower thecal surface almost flat, with the exception of downwards recurved abaxial edges of
1125 lateral marginals, forming two low longitudinal skate-like flanges.

1126

1127 Lower thecal surface almost bilaterally symmetrical, with 11 marginals and at least one
1128 plate in a central position (Fig. 23a). Anterior marginals M'₁ and M₁ broad, relatively
1129 elongate, subequal in size, and adaxially in contact with each other along straight longitudinal
1130 suture (Fig. 22). Precise morphology of aulacophore insertion and anterior margins of A'₁ and
1131 A₁ unknown. Antero-lateral marginals, M'₂ (on the left) and M₂ (on the right), particularly
1132 wide, fan-shaped, with elongate, strongly convex abaxial margins (Fig. 22). Anterior portions
1133 of M'₂ and M₂ not preserved. Adaxial margins of M'₂ and M₂ particularly long, sinuous to
1134 slightly concave, along sutures with anterior marginals. M'₂ clearly contacting large central
1135 zygial plate (Z) along short, straight suture. Contact between M₂ and Z possible, though not
1136 clearly visible. M'₂ and M₂ in contact posteriorly with next pair of lateral marginals, M'₃ (on
1137 the left) and Mc (on the right) along sinuous, transverse sutures. M'₃ and Mc, broad, elongate,
1138 both wider anteriorly than posteriorly (Fig. 22). M'₃ pentagonal, with long, almost straight
1139 abaxial margin, and shorter, sinuous posterior edge sutured to next marginal (M'₄). Adaxial
1140 margin of M'₃ comprising anteriorly, a long, straight, longitudinal edge probably in contact
1141 with Z, and posteriorly, a shorter, slightly concave, oblique notch along suture with

anomalocystid plate (A). Mc trapezoidal, delimited by two sinuous, almost parallel, transverse sutures, anteriorly (with M₂) and posteriorly (with M₃), and two longer, almost straight, markedly diverging edges, adaxially (along contact with Z) and abaxially. Postero-lateral marginals, M'₄ (on the left) and M₃ (on the right), subequal in size, broad, pentagonal, significantly shorter than all more anterior marginals (Fig. 22). Posterior edges of both M'₄ and M₃ particularly short, concave, forming typical sockets for spine insertion. M'₄ and M₃ both delimited by gently curved abaxial margins, and sinuous sutures with three surrounding thecal plates. M₃ in contact with Mc, Z and M₆. Anterior portion of M'₄ not visible, though certainly sutured to M'₃. M'₄ also in contact with M'₆ and anomalocystid plate. Lateral posterior plates, M'₆ (on the left) and M₆ (on the right), subequal in size, narrow, elongate, slightly shorter anteriorly than posteriorly, with long, subparallel abaxial and adaxial margins (Fig. 22). M'₆ anteriorly in contact with anomalocystid plate, and M₆, with Z. M'₆ and M₆ both adaxially sutured to median posterior plate (M₇). M₇ relatively broad, wide, pentagonal, with anteriorly, a very short, straight transverse margin, and, two long, gently curved, abaxially diverging edges along sutures with M'₆ and M₆ (Fig. 22). Posterior margin of M₇ expanded into long spike-shaped median process, with a wide base, strongly concave edges, distally tapering into a sharp tip. Zygial plate particularly broad, slightly longer than wide, occupying most of lower thecal surface (Fig. 22). Preserved portion of Z indicates contacts with most surrounding marginals (M'₁, M₁, M'₂, Mc, M₃, M₆), and possibly with M₂ (Fig. 23a). Left and posterior part of Z not preserved. Several fragments of skeletal elements (anomalocystid plate? supracentrals?) occurring between left posterior marginals (M'₃, M'₄, M'₆ and M₇) and incomplete, visible portion of Z (Fig. 22). Posterior spines not preserved (Fig. 22).

Extensive external thecal sculpture occurring in two symmetrical, sub-triangular to fan-shaped areas, almost equally distributed on two marginals, on left (M'₂ and M'₃) and right (M₂

and Mc) thecal sides (Fig. 22). Sculpture consisting of irregular, discontinuous, transverse, more or less oblique scale-like riblets. Riblets not parallel to each other but forming two sets of radiating lines abaxially diverging from two points, located close to the M'_2 - M'_3 -Z (on the left) and M_2 -Mc-Z (on the right) triple contacts. Thecal sculpture not extending, abaxially, into downwards recurved, longitudinal skate-like marginal flanges.

No internal thecal characters visible (specimen showing only external, lower aspect of theca).

Proximal aulacophore consisting of at least four, bilaterally symmetrical proximal rings (Fig. 22). Stylocone and arm not preserved, except small portion of recurved distal aulacophore, consisting of six brachials and five associated cover plates (right series). Three distal-most observed ossicles more or less completely sectioned transversely, with relatively high lateral walls on both sides of deep central part with longitudinal median groove (Fig. 23c). Next two more proximal elements well-preserved, with external aspect of ossicles, with low posterior spike and shallow transverse furrow (Fig. 23c). Sixth, proximal-most brachial poorly preserved. Cover plates incompletely preserved, gently arched, smooth, significantly smaller than associated ossicles (Fig. 23c).

Measurements. GSC 126914 (holotype): TL: 14 mm, TW: 8.1 mm.

Remarks. Although posterior spines are not preserved in the Anticosti mitrate (Fig. 22), the presence of typical sockets for spine articulation on the posterior margins of both M'_4 and M_3 clearly indicates that two spines were originally articulated to the theca (Fig. 23a), thus unambiguously supporting the assignment of this fossil to Anomalocystitidae. The two key

characters for subfamilial identification (morphology of stylocone blades and plate pattern of upper thecal) are not available for this specimen (see above, about unsuccessful CT-scan investigations). However, the occurrence of extensive scale-like riblets on lateral marginals (M'_2 , M'_3 , M_2 and M_c ; Fig. 22) strongly suggests allanicytidiine, rather than anomalocystitine, affinities. In anomalocystitines, thecal sculpture almost essentially consists of more or less continuous, straight to sinuous cuesta-shaped ribs and/or pustules, as for example in *Ateleocystites* (Kolata and Jollie, 1982; Parsley, 1991), *Barrandeocarpus* (Ubaghs, 1979; Craske and Jefferies, 1989; Ruta, 1997c; Lefebvre and Gutiérrez-Marco, 2003), *Placocystites* (Jefferies and Lewis, 1978), *Rhenocystis* (Dehm, 1932; Ruta and Bartels, 1998) or *Victoriacystis* (Gill and Caster, 1960; Ruta, 1997b; Ruta and Jell, 1999c, 1999d). In contrast, the external thecal sculpture of allanicytidiines, when present, typically consists either of discontinuous, crescent-shaped to scale-like riblets and/or of pustules, as in *Placocystella africana* (Ruta and Theron, 1997), *P. flemingi* (Ubaghs, 1967a; Ruta and Jell, 1999e) or *P. garratti* (Philip, 1981; Ruta and Jell, 1999e). For this reason, Lindstöm's anomalocystitid (1888; see discussion above) and the Anticosti mitrate, which both display scale-like riblets are here identified as probable allanicytidiines.

A further argument supporting this taxonomic assignment of the Anticosti specimen is its strong similarity with the allanicytidiine genus *Perikefalea* with, in particular, comparable morphologies of posterior marginals M_7 (strong posterior spike), M'_6 and M_6 (particularly narrow and elongate). For this reason, the Anticosti mitrate is interpreted here as a probable allanicytidiine anomalocystitid, which is tentatively assigned to the genus *Perikefalea*. To be confirmed (or not) this identification requires the discovery of additional specimens preserving the upper thecal surface. Although morphologically very close to *P. racheboeufi*,

the Anticosti mitrate is assigned to a distinct species, *P.?* *cybeleae*, because of several differences.

The most obvious difference with *P. racheboeufi* concerns the external thecal sculpture, which is totally absent in *P. racheboeufi* but extensive in the Canadian form. Moreover, as ornamentation in anomalocystitids is always stronger on the upper thecal surface (see Jefferies, 1984; Ruta and Bartels, 1998; Lefebvre, 2003b), the occurrence of widespread riblets on marginals of *P.?* *cybeleae* suggests that a much more extensive sculpture is present on its opposite (upper) thecal surface. This strong ornamentation suggests that *P.?* *cybeleae* was very likely infaunal (see Jefferies and Lewis, 1978; Jefferies, 1984; Lefebvre, 2003b).

Other differences concern the morphology of the M₇ spike (wider and blunt in *P. racheboeufi*, narrower and sharp in *P.?* *cybeleae*), and the relative size of postero-lateral marginals M'₄ and M₃ (much smaller in *P.?* *cybeleae* than in *P. racheboeufi*). Although this is not clearly visible on the holotype (Fig. 22), a single left infracentral element (anomalocystid plate) was probably present in *P.?* *cybeleae*. This interpretation relies on the occurrence of a relatively large skeletal fragment on the left of Z, and mostly, on the morphology of surrounding plates (M'₃, M'₄, M'₆ and possibly M₇), which indicates that they were sutured to a single, relatively large posterior infracentral element. Moreover, the probable occurrence of the anomalocystid plate in *P.?* *cybeleae* would be in good agreement with the situation in other Siluro-Devonian anomalocystitids, all characterized by the loss of the barrandeocarpid plate (see above). In *P.?* *cybeleae*, A is anteriorly largely in contact with M'₃ (Fig. 23a), which is not the case in *P. racheboeufi* (Fig. 21b).

All these morphological differences are considered here as sufficiently significant to justify the erection of a distinct species for the Canadian specimen. Finally, all specimens of *P. racheboeufi* are about twice as smaller and significantly younger (Lochkovian) than the single known individual of *P.? cybeleae* (Telychian).

Contrary to the situation in *P. racheboeufi* (see above), the arm of the only known specimen of *P.? cybeleae* is preserved in the typical flexed position (i.e. taphonomic group 2 of Martin et al., 2015). This posture, along with the partial disarticulation of its lower thecal surface (plates are not in close contact with each other, especially in the posterior part of the specimen), suggest that the holotype of *P.? cybeleae* was not buried alive by a sudden influx of sediments (e.g. tempestites), but more likely, a short time (several days or weeks) after its death.

Occurrence. *Perikefalea? cybeleae* is only known from the type-locality (Box River, Anticosti Island), where it occurs within the Cybèle Member of the Jupiter Formation (Telychian).

Material. *P.? cybeleae* is only known from its holotype.

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FIGURE CAPTIONS

Fig. 1. Location and geology of Anticosti Island: (a) location of Québec in North America; (b) location of Anticosti Island in Québec; (c) geological map of Anticosti Island; the star indicates the position of the locality yielding stylophoran remains (modified from Ausich and Cournoyer, 2019). With the exception of the Vauréal (Katian) and Ellis Bay (Hirnantian) formations, all other lithostratigraphic units are Silurian (Llandovery; see Fig. 2).

Fig. 2. Silurian stratigraphic chart for Anticosti Island (modified from Copper et al., 2013); the star indicates the lithostratigraphic unit yielding mitrate remains.

Fig. 3. Location of Presto El Peral section (Bolivia): (a) location of Bolivia in South America; (b) location of study area in Bolivia; (c) location of the Presto El Peral section (indicated

by a star), where mitrates were found (redrawn from Gaillard and Rachebœuf, 1993; Lefebvre and Rachebœuf, 2007).

Fig. 4. Devonian stratigraphic chart for the Central Subandean Zone of Bolivia (correlations based on Rachebœuf et al., 1993; Troth, 2006; Di Pasquo and Noetinger, 2008); the star indicates the lithostratigraphic unit, where mitrates were collected, at the top of the Santa Rosa Formation.

Fig. 5. Stylophoran morphology; reconstruction of the mitrocystitidan mitrate *Vizcainocarpus dentiger* (late Tremadocian, France), redrawn from holotype (UCBL-FSL 712665) and previous reconstructions (Ruta, 1997d; Lefebvre, 2000b); (a) upper surface; (b) lower surface; the original extension of the arm was probably longer (anterior part missing).

Fig. 6. Plate patterns of the lower thecal surface and homologies in early stylophorans; (a) *Ceratocystis perneri* (Wuliuan, Czech Republic), redrawn from Ubaghs (1967a, 1967b); (b) *Ponticulocarpos robisoni* (Wuliuan, USA), redrawn and modified from Sumrall and Sprinkle (1999); (c) *Flabellicarpus rushtoni* (late Tremadocian, UK) redrawn from Marti Mus (2002). Designations: (A₀) median adoral, (A₁) right adoral, (A'₁) left adoral, (D) digital, (G) glossal, (M₁–M₅) right marginals, (M'₁–M'₅) left marginals, (Mc) cothurnocystid marginal, (Z) zygale plate.

Fig. 7. Plate patterns of the lower thecal surface and homologies in early mitrates and related forms; (a) *Lobocarpus vizcainoi* (Furongian, France), redrawn from Lefebvre (2000b); (b) *Chinianocarpos thoralis* (late Tremadocian, France), redrawn from Ubaghs (1970); (c) *Peltocystis cornuta* (late Tremadocian, France and Morocco), redrawn from Ubaghs

(1970). Designations: (D) digital, (G) glossal, (M₁–M₃, M₆) right marginals, (M'₁–M'₄) left marginals, (Mc) cothurnocystid marginal, (Z) zygale plate.

Fig. 8. Lower thecal surface of a '*Phyllocystis*' *jingxiensis*-like stylophoran (Furongian, France); camera-lucida drawing of specimen UCBL-FSL 712773; (a) interpretation (plate homologies) of plate pattern; (b) main morphological features; the central position of Z results from the joining of both M₃ and G, posteriorly to it. This character (Z in central position), which is shared by amygdalothecids and mitrates, is very likely inherited from a 'cornute-grade' ancestor morphologically similar to '*P.*' *jingxiensis*. Designations: (D) digital, (G) glossal, (M₁–M₃) right marginals, (M'₁–M'₄) left marginals, (Mc) cothurnocystid marginal, (Z) zygale plate.

Fig. 9. Plate patterns of the lower thecal surface and homologies in early mitrocystitids; (a) *Ovocarpus moncereti* (late Floian, France), redrawn from Lefebvre and Gutiérrez-Marco (2003); (b) *Aspidocarpus bohemicus* (Sandbian, Czech Republic), with typical posterior spike on M₇; redrawn from Ubaghs (1979); (c) *Mitrocystites mitra* (Darriwilian, Czech Republic), redrawn from Ubaghs (1967a); the two posterior left infracentrals in *M. mitra* (I'₂ and I'₃) are not considered as homologous to those found in similar position in anomalocystitids (anomalocystid and barrandeocarpid plates), but as the result of convergent evolution towards left infracentral areas made of a reduced and fixed number of large elements. Designations: (D) digital, (G) glossal, (M₁–M₃, M₆) right marginals, (M₇) posterior median marginal, (M'₁–M'₄, M'₆) left marginals, (Mc) cothurnocystid marginal, (Z) zygale plate.

Fig. 10. Lower thecal surface of the earliest known anomalocystitid (middle Floian, Morocco); camera-lucida drawing of specimen UCBL-FSL 711719; (a) interpretation (plate homologies) of plate pattern; (b) main morphological features; two posterior skeletal elements (D and G) are no longer part of the marginal frame, but articulated to it and modified as posterior spines. Designations: (D) digital, (G) glossal, (M₁–M₃, M₆) right marginals, (M₇) posterior median marginal, (M'₁–M'₄, M'₆) left marginals, (Mc) cothurnocystid marginal, (Z) zygial plate.

Fig. 11. Plate patterns of the lower thecal surface and homologies in allanicytidiine anomalocystitids; (a) *Enoploura popei* (Katian, USA), redrawn from Parsley (1991); (b) *Protocytidium elliotiae* (Hirnantian, Australia), redrawn from Ruta and Jell (1999a); (c) *Placocystella garratti* (Ludlow, Australia), redrawn from Ruta (1999a); Ordovician allanicytidiines retain two left infracentral elements, whereas all Siluro-Devonian taxa have only one. Designations: (A) anomalocystid plate, (B) barrandeocarpid plate, (D) digital, (G) glossal, (M₁–M₃, M₆) right marginals, (M₇) posterior median marginal, (M'₁–M'₄, M'₆) left marginals, (Mc) cothurnocystid marginal, (Z) zygial plate.

Fig. 12. Plate patterns of the upper thecal surface and homologies in early stylophorans and mitrates; (a) *Ceratocystis perneri* (Wuliuan, Czech Republic), redrawn from Ubaghs (1967a, 1967b); (b) *Lagynocystis pyramidalis* (Furongian, China; late Tremadocian, Morocco; late Floian, France; Dapingian, UK; Darriwilian, Czech Republic, France and Spain; Sandbian, France and Russia), redrawn from Ubaghs (1967a); (c) *Peltocystis cornuta* (late Tremadocian, France and Morocco), redrawn and modified from Ubaghs (1970) and Lefebvre and Botting (2007). Designations: (D) digital, (G) glossal, (M₁–M₄) right marginals, (M'₁–M'₄) left marginals, (Mc) cothurnocystid marginal, (Z) zygial plate.

1752

1753 **Fig. 13.** Morphology of upper thecal surface of two early anomalocystitids, both with their
1754 supracentral area entirely consisting of numerous, unorganized, imbricate elements; (a)
1755 earliest known anomalocystitid (middle Floian, Morocco), camera-lucida drawing of
1756 specimen UCBL-FSL 711717; (b) *Diamphidiocystis* sp. (Darriwilian, France), camera-
1757 lucida drawing of specimen IGR 15217. Designations: ($A_0?$) possible median adoral, (A_1)
1758 right adoral, (A'_1) left adoral.

1759

1760 **Fig. 14.** Plate patterns of the upper thecal surface and homologies in allanicytidiine
1761 anomalocystitids; (a) *Enoploura popei* (Katian, USA), redrawn from Parsley (1991); (b)
1762 *Protocytidium elliotiae* (Hirnantian, Australia), redrawn from Ruta and Jell (1999a); (c)
1763 *Occultocystis koeneni* (Lower Devonian, Argentina), redrawn from Haude (1995).
1764 Designations: ($A_0?$) possible median adoral, (A_1) right adoral, (A'_1) left adoral, (B_2 , B'_2)
1765 row B supracentrals, (C_1 , C'_1 , C_2 , C'_2) row C supracentrals, (E_0 , E_1 , E'_1 , E_2 , E'_2) row E
1766 supracentrals.

1767

1768 **Fig. 15.** Plate patterns of the upper thecal surface and homologies in Late Ordovician
1769 anomalocystitids; (a) *Willmanocystis denticulatus* (Katian, USA), redrawn and modified
1770 from Kolata and Jollie (1982); (b) *Barrandeocarpus jaekeli* (Sandbian, Czech Republic),
1771 redrawn from Ubaghs (1979); (c) *Ateleocystites guttenbergensis* (Katian, USA), redrawn
1772 from Kolata and Jollie (1982). Designations: ($A_0?$) possible median adoral, (A_1) right
1773 adoral, (A'_1) left adoral, (B_1 , B'_1 , B_2 , B'_2) row B supracentrals, (C_1 , C'_1 , C_2 , C'_2) row C
1774 supracentrals, (E_0 , E_1 , E'_1 , E_2 , E'_2) row E supracentrals, (P) placocystid plate.

1775

Fig. 16. Plate patterns of the upper thecal surface and homologies in Siluro-Devonian anomalcystitine mitrates; (a) *Placocystites forbesianus* (Wenlock, UK), redrawn from Jefferies and Lewis (1978); (b) *Bokkeveldia oosthuizeni* (Emsian, South Africa), redrawn from Ruta and Theron (1997), original size of single known individual not mentioned in Ruta and Theron (1997): dimensions based on specimen of *Bokkeveldia* sp. (Lower Devonian, Morocco) figured by Régnault and Chauvel (1987, fig. 1); (c) *Anomalocystites cornutus* (Lower Devonian, USA), redrawn and modified from Parsley (1991) and Ruta (1999a). Designations: (A₀?) possible median adoral, (A₁) right adoral, (A'₁) left adoral, (B₁, B'₁, B₂, B'₂) row B supracentrals, (III₀, III₁, III'₁, III₂, III'₂) row III supracentrals, (IV₁, IV'₁, IV₂, IV'₂, IV₃, IV'₃) row IV supracentrals, (V₁, V'₁, V₂, V'₂) row V supracentrals, (VI₀, VI₁, VI'₁, VI₂, VI'₂) row VI supracentrals, (P) placocystid plate.

Fig. 17. *Perikefalea racheboeufi* sp. nov., holotype MHNC 13354; (a-b) theca in lower aspect, with articulated spines, proximal aulacophore and ploughshare-shaped stylocone, with expanded distal transverse blade ; (a) photographic view; (b) interpretative camera-lucida drawing; (c-d) theca in upper aspect, with proximal aulacophore and two first pairs of ambulacral cover plates; (c) interpretative camera-lucida drawing; (d) photographic view. Designations: (A) anomalocystid plate, (A₀?) possible median adoral, (A₁) right adoral, (A'₁) left adoral, (C₁, C'₁) supracentrals, (cov. pl.) cover plates, (dig.) digital, (gloss.) glossal, (M₁–M₄, M₆) right marginals, (M₇) posterior median marginal, (M'₁–M'₄, M'₆) left marginals, (Mc) cothurnocystid marginal, (prox.) proximal aulacophore; styl.: stylocone, (Z) zygale plate.

Fig. 18. *Perikefalea racheboeufi* sp. nov., specimen MHNC 13355; (a-b) theca in lower aspect, with aulacophore insertion cavity exposed; (a) photographic view; (b) interpretative

camera-lucida drawing; (c-d) theca in upper aspect; (c) interpretative camera-lucida drawing; (d) photographic view. Designations: (A) anomalocystid plate, (A₀?) possible median adoral, (A₁) right adoral, (A'₁) left adoral, (aul. insert. cav.) aulacophore insertion cavity, (C₁, C'₁) supracentrals, (M₁–M₄, M₆) right marginals, (M₇) posterior median marginal, (M'₁–M'₄, M'₆) left marginals, (Mc) cothurnocystid marginal, (Z) zygale plate.

Fig. 19. *Perikefalea racheboeufi* sp. nov.; (a) MHNC 13356, posterior half of the theca, in lower aspect, showing strong posterior spike on median posterior marginal (M₇) with distal supracentrals (C'₁ and C₁) protruding on both sides of it, and two spines (partially preserved glossal, on the left, and complete digital, on the right) articulated to postero-lateral marginals (M₃ and M'₄); (b) MHNC 13358, almost complete individual in left lateral view, showing the theca and almost complete aulacophore (over twenty brachials and associated cover plates, ploughshare-like stylocone with two strong transverse blades on its lower surface, proximal aulacophore rings); the preservation of the appendage in extended (feeding) position suggests sudden burial by obrution (storm) deposits.

Fig. 20. *Perikefalea racheboeufi* sp. nov., reconstruction of the theca; (a) anterior aspect, with aulacophore insertion; (b) lower surface; (c) upper surface.

Fig. 21. *Perikefalea racheboeufi* sp. nov. thecal plate patterns and homologies; (a) upper thecal surface; (b) lower thecal surface. Designations: (A) anomalocystid plate, (A₀?) possible median adoral, (A₁) right adoral, (A'₁) left adoral, (C₁, C'₁) supracentrals, (D) digital, (G) glossal, (M₁–M₃, M₆) right marginals, (M₇) posterior median marginal, (M'₁–M'₄, M'₆) left marginals, (Mc) cothurnocystid marginal, (Z) zygale plate.

1826 **Fig. 22.** *Perikefalea? cybeleae* sp. nov., holotype GSC 126914, almost complete lower thecal
1827 surface (spines missing), with partially preserved proximal aulacophore and small, distal
1828 portion of recurved feeding arm; (a) interpretative camera-lucida drawing; (b)
1829 photographic view. Designations: (A?) probable large fragment of anomalocystid plate,
1830 (M₇) posterior median marginal; (prox. aulacophore) proximal aulacophore.

1831

1832 **Fig. 23.** *Perikefalea? cybeleae* sp. nov., holotype GSC 126914; (a) tentative reconstruction of
1833 lower thecal surface, with dashed areas corresponding to missing or unobserved parts; (b)
1834 photographic view of the slab containing the holotype of *P.? cybeleae* closely associated to
1835 a portion of crinoid stem; (c) interpretative camera-lucida drawing of small portion of
1836 distal arm, in lateral view. Designations: (A) anomalocystid plate, (cov. pl.) cover plate,
1837 (M₁–M₃, M₆) right marginals, (M₇) posterior median marginal, (M'₁–M'₄, M'₆) left
1838 marginals, (Mc) cothurnocystid marginal, (Z) zygale plate.

System	Series	Stage	Formation	Member
Silurian	Llandovery	Telychian	Chicotte	
			Jupiter	Pavillon
				Ferrum
				Cybèle
				Richardson
		Aeronian	Menier	East Point
				Goéland
				Macgilvray
			Gun River	Sandtop
				Innommée
				Lachute
		Rhuddanian	Merrimack	
			Becscie	Chabot
				Fox Point

System	Series	Stage	Formation
Devonian	Upper	Famennian	Saipuru
		Frasnian	
	Middle	Givetian	Iquiri
		Eifelian	Los Monos
	Lower	Emsian	Huamampampa
		Pragian	Icla
		Lochkovian	Santa Rosa

aulacophore

ambulacral cover plate

brachial

stylocone

proximal rings

hydropore

adoral

marginal
frame

zygal bar

right
infracentral area

supracentral area

left infracentral area

glossal

anus

0 1 mm

arm

theca

(a)

(b)

0 2 mm

0 2 mm

0 2 mm

(a)

0 5 mm

(b)

0 5 mm

(c)

0 5 mm

(a)

0 5 mm

(b)

0 5 mm

A'_1

$A_0?$

A_1

row B

posterior rows (C and E)

posterior rows

imbricate supracentrals

(a) 0 5 mm

(b) 0 5 mm

(c) 0 5 mm

A'₁
A₀?
 A₁

row B
placocystid plate

row III
row IV

row V
row VI

(a)

0

5 mm

(b)

(c)