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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**

4
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13
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

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

34

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

37

38

INTRODUCTION

39

40 Stylophorans are an extinct clade of single-armed, vagile, benthic echinoderms, which
41 flourished on soft substrates from the Wuliuan (Miaolingian, middle Cambrian) to the
42 Bashkirian (Lower Pennsylvanian, Carboniferous) (Ubaghs, 1967a; Kolata et al., 1991;
43 Zamora et al., 2013a; Lefebvre et al., 2019). In the late Guzhangian–late Tremadocian interval
44 immediately preceding the major diversification of crinoids, stylophorans were a major
45 component of worldwide echinoderm communities (Sumrall et al., 1997; Guensburg and
46 Sprinkle, 2000; Lefebvre and Fatka, 2003; Lefebvre et al., 2013). All main stylophoran
47 clades, including anomalocystitid mitrates, appeared and diversified during this late
48 Cambrian–Early Ordovician interval (Lefebvre, 2007a; Lefebvre et al., 2013; Zamora et al.,
49 2013b). In Middle Ordovician times, the paleobiogeographic distribution of stylophorans was
50 limited to high-latitude (peri-) Gondwanan areas and relatively deep settings of Avalonia

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

60

61 Stylophorans were severely affected by the Hirnantian mass extinction, with only four
62 clades reported from younger deposits (Lefebvre, 2007a). Although they are sometimes
63 locally abundant (e.g. *Placocystites forbesianus*, in the Dudley Limestone of Britain;
64 *Rhenocystis latipedunculata*, in the Hunsrück Slate of Germany; Jefferies and Lewis, 1978;
65 Ruta and Bartels, 1998), post-Ordovician stylophorans are generally extremely rare, and their
66 fossil record particularly sparse. For example, peltocystidans, which are one of the most
67 abundant and widespread clades of Ordovician stylophorans, are only known from three
68 younger occurrences: '*Mitrocystites*' *styloideus* (Emsian, Germany; Dehm, 1934; Lefebvre,
69 2007a), yet undescribed Middle Devonian forms (Eifelian–Givetian, Germany; Haude, 1983)
70 and *Jaekelocarpus oklahomaensis* (Bashkirian, USA; Kolata et al., 1991). Similarly, the
71 paleobiogeographic distribution of Siluro-Devonian mitrocystitidans (Anomalocystitidae and
72 Paranacystidae) is poorly known and suffers from a strong sampling bias. For example,
73 paranacystids were long considered as typical members of the Early–Middle Devonian high-
74 latitude Malvinokaffric faunas (e.g. Derstler, 1979; Haude, 1995; Ruta, 1997a; Penn-Clarke,
75 2019; but see Boucot and Rachebœuf, 1993). This interpretation is based on a very small

76 number of occurrences from Argentina (*Yachalicystis triangularis*; Haude, 1995), Brazil
77 (*Paranacystis petrii*; Caster, 1954a; Caster and Eaton, 1956), and South Africa (*P. simoneae*;
78 Ruta, 1997a; Reid et al., 2015). However, the reinterpretation of the Middle Devonian genus
79 *Dalejocystis* (Czech Republic, Germany; Prokop, 1963; Haude, 1983) as a paranacystid, as
80 well as the discovery of several new occurrences in the Wenlock of Sweden (Reich et al.,
81 2008), the Ludlow of Australia (Ruta and Jell, 1999b), the Lochkovian of Australia and
82 Bolivia (Ruta and Jell, 1999b; Lefebvre and Rachebœuf, 2007) and the Givetian of France
83 (Lefebvre, 1999, 2000a) suggest a more complex and widespread distribution of
84 paranacystids.

85
86 In the two main clades of anomalocystitids (Allanicystidiinae and Anomalocystitinae), the
87 evolutionary transition from Late Ordovician to younger taxa, as well as their Siluro-
88 Devonian paleobiogeographic distribution are similarly poorly understood. Post-Ordovician
89 anomalocystitines were traditionally considered as a 'boreal' group, restricted to low-latitude
90 regions of the 'Old World' and 'North Eastern Americas' faunal realms *sensu* Boucot (1988)
91 (see e.g. Gill and Caster, 1960; Derstler, 1979; Parsley, 1991; Ruta, 1997b; Ruta and Bartels,
92 1998). This interpretation relied on the very low number of Siluro-Devonian anomalocystitine
93 taxa described between the late 1850s and the late 1990s: *Anomalocystites cornutus* Hall,
94 1859 (Lower Devonian, North America; Parsley, 1991), *Placocystites forbesianus* de
95 Koninck, 1869 (Wenlock, Britain; Jefferies and Lewis, 1978), *Rhenocystis latipedunculata*
96 Dehm, 1932 (Emsian, Germany; Ruta and Bartels, 1998), and *Victoriacystis wilkinsi* Gill and
97 Caster, 1960 (Ludlow, Australia; Ruta, 1997b; Ruta and Jell, 1999d). However, the
98 reinterpretation of *Mongolocarpos minzhini* (Ludlow, Mongolia; Rozhnov, 1990) as a
99 probable anomalocystitine (Ruta, 1999a), as well as new discoveries in regions (Bolivia,
100 South Africa) belonging to the Devonian Malvinokaffric faunal realm (see Ruta and Theron,

101 1997; Lefebvre and Rachebœuf, 2007) suggest a more cosmopolitan distribution for Siluro-
102 Devonian Anomalocystitinae.

103

104 The second clade of post-Ordovician anomalocystitids, Allanicystidiinae, has been long
105 considered as an 'austral' group of stylophorans, restricted to (peri-) Gondwanan regions
106 belonging either to the eastern part of the Old World faunal realm (Australia, New Zealand)
107 or to the higher latitude Malvinokaffric Realm (Argentina, Brazil, South Africa) (see Caster,
108 1954b, 1983; Ubaghs, 1967a; Philip, 1981; Parsley, 1991; Haude, 1995; Ruta, 1997b; Ruta
109 and Theron, 1997; Ruta and Jell, 1999e; Lefebvre and Rachebœuf, 2007; Jell, 2013; Penn-
110 Clarke, 2019; Scheffler et al., 2019; but see Boucot and Rachebœuf, 1993). In this context,
111 the two mitrates described here from the late Llandovery of Anticosti Island (Canada) and the
112 Lochkovian of Bolivia are particularly important. The Canadian occurrence represents both
113 the first stylophoran described in Silurian deposits from North America and also the first
114 report of post-Ordovician Allanicystidiinae outside of (peri) Gondwanan regions. The
115 Anticosti mitrate is here tentatively assigned to a new genus of allanicystidiines, described
116 from better-preserved and more complete material from Bolivia. The morphology of the
117 Bolivian stylophoran suggests stronger affinities with *Occultocystis* (Lower Devonian;
118 Argentina) than with the widespread coeval genus *Placocystella* (late Llandovery–early
119 Givetian; Australia, Brazil, New-Zealand, South Africa).

120

121 Consequently, the main objective of this paper is to describe the morphology of the two
122 new allanicystidiines from Bolivia and Canada. However, so as to compare them properly with
123 other mitrates, a reevaluation of the two main models of plate homologies elaborated by Ruta
124 (1999a) for supracentrals, and Lefebvre (2001) for adorals and marginals, is a necessary pre-

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

127

128 GEOLOGICAL SETTING

129

130 *Anticosti Island, Canada*

131

132 Anticosti Island is in the Gulf of St. Lawrence and part of Québec, Canada (Fig. 1). The
133 section on Anticosti Island is a nearly complete Katian (Ordovician) through Llandovery
134 (Silurian) stratigraphic section (Fig. 1c), and the most complete section known in shelly
135 facies. A long history of stratigraphic and paleontological studies has clarified the geology of
136 Anticosti Island (see e.g. Richardson, 1857; Schuchert and Twenhofel, 1910; Twenhofel,
137 1928; Bolton, 1961; Cocks and Copper, 1981; Petryk, 1981; Long and Copper, 1987; Barnes,
138 1988; Copper, 1989, 2001; Jin and Copper, 2008; Desrochers et al., 2008, 2010; Copper et al.,
139 2013). Recent investigations have identified the position of the Ordovician-Silurian boundary
140 and, significant to this study, revised the east-west correlation of Aeronian-Telychian
141 stratigraphy based on a combination of biostratigraphy and sequence stratigraphy (Fig. 2;
142 Copper et al., 2013).

143

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

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

151

152 *Bolivia*

153

154 During Devonian times, most of Bolivia was part of an intracratonic basin on the western
155 margin of Gondwana (Isaacson and Díaz-Martinez, 1995; Di Pasquo and Noetinger, 2008).
156 About 50 km northeast of Sucre (Fig. 3), the classical section of Presto-El Peral exposes the
157 three lowermost units of the Devonian succession in the Eastern Cordillera area (Fig. 4): the
158 Santa Rosa, Icla and Huamampampa formations (Rachebœuf et al., 1993; Gaillard and
159 Rachebœuf, 2006). The Santa Rosa Formation (Lochokovian) is a thick siliciclastic unit
160 consisting mostly of fluvio-deltaic and coastal deposits, yielding abundant land plant remains,
161 associated to rare marine palynomorphs and low diversity trace fossils (Rachebœuf et al.,
162 1993; Gaillard and Rachebœuf, 2006; Di Pasquo and Noetinger, 2008). However, abundant
163 trace fossils (*Palaeophycus* association) and a relatively diverse, fully marine assemblage
164 occur in the finer-grained sandstones and siltstones of the uppermost part of the Santa Rosa
165 Formation (Rachebœuf et al., 1993; Gaillard and Rachebœuf, 2006). These levels have
166 yielded abundant brachiopods (e.g. *Australostrophia* sp., *Derbyina* sp., *Proboscidina arcei*,
167 *Scaphiocoelia boliviensis*), associated with asterozoans, bivalves (*Nuculites* sp., *Modiolopsis*
168 sp.), crinoid ossicles, gastropods, trilobites and disarticulated vertebrate remains (Rachebœuf
169 et al., 1993; Gaillard and Rachebœuf, 2006; Janvier and Maisey, 2010). Both trace fossils and
170 brachiopods are suggestive of low intertidal environmental conditions (Gaillard and
171 Rachebœuf, 2006). In the early 2000s, fully-articulated remains of two different stylophoran
172 taxa were found by Patrick Rachebœuf in these levels (Gaillard and Rachebœuf, 2006;
173 Lefebvre and Rachebœuf, 2007): a *Paranacystis*-like mitrocystitid, and the new, herein

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

179

180

MATERIAL AND METHODS

181

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

188

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

198

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

213

214 THECAL PLATE TERMINOLOGY AND HOMOLOGIES

215

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

222

223 The lower side (Fig. 5b) is characterized by a frame of thick skeletal elements (marginals),
224 which also forms the lateral walls of the test. In various stylophoran clades, some of these
225 marginals can bear long flattened posterior spikes or be modified into posterior spines (Kirk,
226 1911; Ubaghs, 1967a; Lefebvre, 2001). The number of marginal plates is constant throughout
227 ontogeny, but their respective proportions can be variable (Ubaghs, 1967a). In all
228 stylophorans, an asymmetrical internal structure (the zygial crest or septum) is consistently
229 borne by two plates (forming together the zygial bar or strut), and extends from left of the
230 aulacophore insertion (anteriorly) to right of the anal opening (posteriorly). The marginal
231 frame and the zygial strut delimit two polyplated surfaces: the left and right infracentral areas
232 (Ubaghs, 1967a, 1981; Lefebvre 2001). Both areas are present in most stylophorans, but the
233 right one is frequently lost, independently in various derived taxa (e.g. Anomalocystitidae,
234 *Chinianocarpus*, Kirkocystidae, *Lyricocarpus*). The number and shape of infracentral
235 elements are generally highly variable in stylophorans (e.g. *Aspidocarpus*, *Cothurnocystis*),
236 but they tend to become constant, independently, in various mitrate taxa (e.g.
237 Anomalocystitidae, *Mitrocystella*, Paranacystidae, *Peltocystis*).

238

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

248 generally numerous and unorganized, forming a flexible pavement of tessellate (e.g.
249 *Chinianocarpos*, *Phyllocystis*) and/or imbricate elements (e.g. *Eumitrocystella*, *Lagyncystis*).
250 In derived mitrocystitidan mitrates (anomalocystitids and paranacystids), supracentral areas
251 consist of a reduced and constant number of elements (Caster, 1952; Ubaghs, 1967a; Parsley,
252 1991; Ruta, 1999a).

253

254 Along with some aulacophore-related features, the morphology and number of major
255 skeletal elements (adorals and marginals) are used as primary key characters for the
256 systematics of stylophorans (Ubaghs, 1967a; Lefebvre, 2001). In derived mitrocystitidans, the
257 identification also relies largely on the number, morphology and position of both infracentrals
258 and supracentrals (Caster, 1952; Ubaghs, 1967a; Parsley, 1991; Ruta, 1999a). Unsurprisingly,
259 various plate nomenclatures have been proposed for stylophorans (e.g. Bather, 1913; Jaekel,
260 1918; Gislen, 1930; Dehm, 1932; Caster, 1952; Ubaghs, 1963; Jefferies, 1968; Jefferies and
261 Prokop, 1972; Philip, 1981; Ruta and Theron, 1997; Ruta and Bartels, 1998; Lefebvre and
262 Vizcaïno, 1999; Ruta, 1999a; Lefebvre, 2000b, 2001). Most of them, however, are either
263 simply descriptive and do not imply any homology (e.g. Jaekel, 1918; Ubaghs, 1963;
264 Jefferies, 1968) and/or can be applied only to a limited group of taxa but not to the whole
265 class Stylophora (e.g. Bather, 1913; Dehm, 1932; Caster, 1952; Philip, 1981; Ruta, 1999a).

266

267 In this paper, we largely follow the plate terminology proposed by Lefebvre and Vizcaïno
268 (1999) for cornutes, and extended to mitrates by Lefebvre (2000b, 2001, 2003a). This model
269 implies class-level homologies between major skeletal elements (adorals, marginals), based
270 on their morphology, position, and associated internal structures (Lefebvre et al., 1998;
271 Lefebvre, 2000c, 2001). A similar and complementary plate terminology was elaborated by
272 Ruta (1997b, 1999a) to identify homologies in skeletal elements (adorals, supracentrals)

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

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

286

287 *Marginals and infracentrals*

288

289 All anomalocystitid mitrates are characterized by a marginal frame made of 11 massive
290 skeletal elements, which can be considered as homologous at the family level (e.g. Dehm,
291 1932; Caster, 1952, 1954b, 1983; Gill and Caster, 1960; Ubaghs, 1967a, 1979; Jefferies and
292 Lewis, 1978; Philip, 1981; Craske and Jefferies, 1989; Parsley, 1991; Haude, 1995; Ruta,
293 1997b, 1999a; Ruta and Theron, 1997; Ruta and Bartels, 1998; Ruta and Jell, 1999a, 1999c,
294 1999d, 1999e; Lefebvre, 2000b, 2001; Jell, 2013; McDermott and Paul, 2017; Scheffler et al.,
295 2019). In all described anomalocystitids, these marginals enclose a large, septum-bearing
296 central plate and a left infracentral area consisting of one ('anomalocystid plate' of Siluro-
297 Devonian taxa) or two elements (Mid-Late Ordovician forms). The right infracentral area is

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

302

303 Most of these anomalocystitid skeletal elements (marginals, centrals, spines) can be readily
304 identified in other mitrocystitidans (Jefferies and Lewis, 1978; Craske and Jefferies, 1989;
305 Parsley, 1991; Ruta and Theron, 1997), and more tentatively, at class-level (Lefebvre, 2000b,
306 2001). The model of stylophoran plate homologies proposed by Lefebvre and Vizcaïno
307 (1999) and Lefebvre (2000b, 2001) interprets *Lobocarpus vizcainoi* as a basal mitrate, and
308 considers that mitrates derive from a *Ceratocystis*-like ancestor (Fig. 6a), with large marginals
309 and small infracentral areas. The application of this model to anomalocystitids suggests that:
310 (1) their left series of marginals corresponds to M'₁, M'₂, M'₃, and M'₄; (2) their right
311 marginals can be identified as M₁, M₂, M₃, and M₄; (3) their two posterior spines are
312 homologous to the digital (D) and the glossal (G); (4) their large central septum-bearing
313 element is the zygial plate (Z); and (5) their three posterior plates correspond to M'₅ (on the
314 left) and to two additional platelets of infracentral origin, inserted successively between M₄
315 and M'₅ (right element PP₁), and between PP₁ and M'₅ (median element PP₂).

316

317 All putative mitrate-like features of the Furongian stylophoran *Lobocarpus* (e.g. wide
318 marginals, reduced infracentral areas; Fig. 7a) are plesiomorphic, as they occur in
319 *Ceratocystis* (Fig. 6a), which is almost universally considered as the most basal representative
320 of the class (Ubaghs, 1967b; Jefferies, 1969; Derstler, 1979; Cripps, 1991; Parsley, 1997;
321 Lefebvre and Vizcaïno, 1999; Marti Mus 2002; Ruta, 2003; Lefebvre, 2005; Rahman et al.,
322 2010). Moreover, *Lobocarpus* lacks all apomorphies defining the mitrates: in particular, it

323 retains small, narrow adorals, and its distal aulacophore is made of unornamented (smooth)
324 ossicles with undifferentiated, flat interbrachial articulations (Ubaghs, 1998). In marked
325 contrast, abundant remains of definitive mitrates have been discovered recently in late
326 Guzhangian to Furongian deposits of Korea (Lefebvre, 2007a) and South China (Chen et al.,
327 2013; Zamora et al., 2013b; Zhu et al., 2016; Peng et al., in press).

328

329 *'Nanocarpus' guoleensis*; from the Furongian Guole Biota of South China, was initially
330 described as an amygdalothecid cornute (Chen and Han, 2013). This identification mostly
331 relied on its thecal outlines, a posteriorly open marginal frame (no M₅-M'₅ bar), the presence
332 of large infracentral areas, a zygal plate in central (not marginal) position, and spikes on the
333 lower surface of brachials. However, its upper surface has two extremely wide adorals (see
334 e.g. Zamora et al., 2013b, fig. 2E). Moreover, well-differentiated interbrachial articulations
335 are present on aulacophore ossicles, allowing the arm to be preserved in recurved position
336 (see e.g. Chen and Han, 2013, figs 2.1-2), which is a typical post-mortem posture of mitrates
337 (Dehm, 1932; Parsley, 1988; Lefebvre, 2003b). All these characters (large adorals, strongly
338 ornamented ossicles with interbrachial articulations) unambiguously support the identification
339 of '*N.*' *guoleensis* as a mitrate, with strong morphological similarities to late Tremadocian taxa
340 such as *Chinianocarpus* (Fig. 7b) and/or *Vizcainocarpus* (Fig. 5). The occurrence of other,
341 similar-looking undescribed stylophorans in the late Guzhangian of South China (Peng et al.,
342 in press) and the Furongian of Korea (Lefebvre, 2007a) suggests that early mitrates were
343 morphologically closer to *Vizcainocarpus* (Fig. 5), with large infracentral areas, and a
344 relatively narrow, posteriorly open marginal frame, than to a heavily-plated, *Lobocarpus*-like
345 form (Fig. 7a).

346

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

371

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

382

383 The 'cornute-grade' origin of mitrates implies that their plate homologies have to be
384 reconsidered. This scenario confirms the identification of the left series of marginals as M'₁,
385 M'₂, M'₃ and M'₄, as well as the homology of the posterior zygial plate in all mitrates, whatever
386 its position: central (e.g. anomalocystitids, *Ovocarpus*, *Vizcainocarpus*; Figs 5, 9) or marginal
387 (e.g. *Chinianocarpos*, *Peltocystis*; Fig. 7b-c) (Lefebvre et al., 1998; Lefebvre, 2000b, 2000c,
388 2001; Lefebvre and Gutiérrez-Marco, 2003). However, comparison with '*Phyllocystis*'
389 *jingxiensis*-like stylophorans (Fig. 8) suggests that the right series of marginal elements in
390 *Vizcainocarpus*-like mitrates (including anomalocystitids) should be identified as M₁, M₂, M_c
391 and M₃, rather than as M₁, M₂, M₃ and M₄ (Figs 5, 7c, 9a). Similarly, the posterior skeletal
392 element inserted between D and G (e.g. *Chinianocarpos*, *Ovocarpus*; Figs 7b, 9a) cannot
393 represent M'₅, as suggested by Lefebvre (2000b, 2001), because this plate is absent in '*P.*'
394 *jingxiensis*-like stylophorans (Fig. 8) and all known Cambrian mitrates (e.g. '*Nanocarpus*'
395 *guoleensis*). This skeletal element more likely corresponds to an infracentral plate, inserted in
396 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

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

429

430 In *Mitrocystites* (Fig. 9c) and other mitrocystitidans with three posterior marginals (e.g.
431 Anomalocystitidae), the right element very likely corresponds to M₆, because it shows the
432 same morphology (with a rounded posterior edge) and contacts (with both G and Z) as in
433 *Ovocarpus* and *Aspidocarpus*. The identification of the two other posterior plates is more
434 problematic. They are both anteriorly in contact with the left infracentral area, so that any of
435 them can correspond to a plate of infracentral origin inserted into the marginal frame. A first
436 possibility is to consider the skeletal element in median position as an additional plate (PP₂),
437 inserted between M₆ (on the right) and M₇ (on the left) (Lefebvre, 2000b, 2001, 2003a).
438 Alternatively, the right posterior plate could be an additional element inserted between M₇ (on
439 the right) and D (on the left). There are no definitive clues to decipher between these two
440 scenarios. However, two lines of indirect evidence suggest that the second interpretation is
441 more likely (Fig. 9c). First, the teratological specimen of *Mitrocystites* figured by Lefebvre
442 (2003a, fig. 3D) shows that its right and median posterior plates are both anteriorly in contact
443 with Z, which is similar to the situation in *Aspidocarpus*, and could support their
444 identification as M₆ and M₇, respectively. Moreover, in several anomalocystitids, including
445 yet undescribed specimens from the Letná Formation (Sandbian) of Czech Republic (B.
446 Lefebvre, pers. obs.), *Protocytidium elliottae* (see Ruta and Jell, 1999a), and the two herein

447 described new allanicytidiines (see below), their median posterior marginal has a strong spike,
448 which is very similar in morphology to the one borne by M₇ in *Aspidocarpus bohemicus* (Fig.
449 9b). For these reasons, the median posterior marginal of *Mitrocystites* and anomalocystitids is
450 here tentatively identified as M₇ (Fig. 9c). Consequently, the left posterior plate of these
451 mitrates is interpreted as an infracentral element inserted between M₇ (on the right) and the
452 digital (on the left). So as to avoid any confusion with plate homologies suggested by
453 Lefebvre (2000b, 2001, 2003a), the left posterior plate is here designated M'₆ (Fig. 9c). If this
454 interpretation is correct, it would imply that infracentrals (M₆, then M₇, and finally M'₆) have
455 been repeatedly inserted into the marginal frame, along the right margin of the digital. This
456 region could represent an area of weakness and/or of reduced mechanical constraints, which
457 might result from the loss of the M₅-M'₅ bar, which forms the posterior frame of the left
458 infracentral area in other stylophorans (plesiomorphic condition; e.g. *Arauricystis*,
459 *Cothurnocystis*, *Ponticulocarpus*, *Protocystites*; Fig. 6b).

460

461 The nature, origin, and homology of the two posterior spines of anomalocystitid mitrates
462 have been long debated (see e.g. Haeckel, 1896; Kirk, 1911; Caster, 1952; Ubaghs, 1967a;
463 Jefferies and Lewis, 1978; Jefferies, 1984; Parsley, 1991; Ruta, 1999a; Lefebvre 2000b,
464 2001). Lefebvre (2000b, 2001) suggested that these two spines are homologous to the digital
465 and glossal of cornutes: D and G would have the possibility to be either incorporated in the
466 thecal frame as regular marginals (e.g. *Milonicystis*, *Mitrocystites*) or articulated to it and
467 modified as movable spines (e.g. anomalocystitids, *Cothurnocystis*). In this context, the
468 recent discovery of abundant remains of the earliest, yet undescribed anomalocystitid mitrate
469 in the middle Floian of Morocco (Fig. 10) is particularly informative (Lefebvre, 2007a;
470 Noailles and Lefebvre, 2012; Lefebvre et al., 2013, 2016). Its morphology is a mixture of
471 characters typical of anomalocystitids (e.g. possession of two posterior spines) and

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

481

482 As in *Aspidocarpus* (Fig. 9b), the left infracentral area of the new Moroccan mitrate is
483 made of numerous, unorganized platelets (Fig. 10). This observation implies that similar-
484 looking plate patterns consisting of a reduced number of infracentral elements (1 to 3) were
485 acquired independently from irregular, polyplated surfaces in younger anomalocystitids (e.g.
486 *Ateleocystites*, *Barrandeocarpus*, *Diamphidiocystis*, *Enoploura*; Fig. 11) and in *Mitrocystites*
487 (Fig. 9c) and related forms (e.g. *Eumitrocystella*, *Mitrocystella*, Parancystidae).
488 Consequently, although they are frequently considered as homologous (e.g. Jefferies and
489 Lewis, 1978; Craske and Jefferies, 1989; Parsley, 1991, 1997; Ruta and Theron, 1997; Ruta,
490 1999a; Lefebvre, 2000b), the two posterior infracentrals occurring in anomalocystitids (Fig.
491 11a-b) and other mitrocystitidans (Fig. 9c) are more likely the result of convergent evolution
492 (reduction of the number of infracentrals) in the two lineages. The terminology introduced by
493 Ruta (1999a) for the two infracentrals in anomalocystitids is retained here, with A for the
494 anterior element, and B for the posterior one (Fig. 11). These letters are convenient, because
495 A is almost universally identified as the 'anomalocystid' plate (e.g. Caster, 1952, 1983;
496 Ubaghs, 1967a, 1979; Philip, 1981; Parsley, 1991; Haude, 1995; Ruta and Bartels, 1998;

497 Ruta, 1999a; Jell, 2013; Scheffler et al., 2019), and the name 'barrandeocarpid plate' is
498 suggested here for the B element. In *Mitrocystites* (Fig. 9c) and related mitrocystitidans, the
499 distinct terminology (with I₁, I₂ and I₃) introduced by Lefebvre (2003a) should be
500 maintained, so as to avoid any confusion with anomalocystitid infracentrals.

501

502 *Adorals*

503

504 In anomalocystitids, the anterior margin of the upper thecal surface is invariably consisting
505 of two large skeletal elements, universally considered as homologous at family level (e.g.
506 Dehm, 1932; Caster, 1952, 1954b, 1983; Gill and Caster, 1960; Ubaghs, 1967a, 1979;
507 Jefferies and Lewis, 1978; Kolata and Guensburg, 1979; Philip, 1981; Kolata and Jollie,
508 1982; Jefferies, 1984; Craske and Jefferies, 1989; Rozhnov, 1990; Parsley, 1991, 1997;
509 Haude, 1995; Ruta, 1997b, 1999a; Ruta and Theron, 1997; Ruta and Bartels, 1998; Ruta and
510 Jell, 1999a, 1999c, 1999d, 1999e; Lefebvre, 2000b, 2001; Jell, 2013; McDermott and Paul,
511 2017; Scheffler et al., 2019). These two (left and right) elements can be confidently identified
512 as homologous to the left and right adorals (A'₁ and A₁) of other mitrates (Fig. 12b-c), based
513 on the presence of the same internal structures (co-opercula) on their lower (inner) side (see
514 e.g. Chauvel, 1941, 1981; Ubaghs, 1967a, 1979; Jefferies and Lewis, 1978; Kolata and Jollie,
515 1982; Parsley, 1991, 1997; Lefebvre, 2000b, 2001, 2005). Class-level homology of A₁ and A'₁
516 (Fig. 12) relies on similarities in position (framing the aulacophore insertion on the anterior
517 edge of the upper thecal side), comparable contacts with the same two underlying marginals
518 (M'₁ and M₁), and also the occurrence of the hydropore on A₁ in most cornutes (e.g.
519 *Cothurnocystis*, *Phyllocystis*) and basal mitrocystitidans (e.g. *Chinianocarpos*, *Mitrocystites*,
520 *Ovocarpus*, *Vizcainocarpus*; Fig. 5a) (Ubaghs, 1967a, 1981, 1994; Parsley, 1991, 1997;
521 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

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

580

581

Supracentrals

582

583 All anomalocystitids have similar plate patterns for their lower thecal surface, with
584 consistently the same 14 homologous skeletal elements: four marginals on the left (M'₁, M'₂,
585 M'₃, M'₄), four ones on the right (M₁, M₂, M_c, M₃), a central zygale (Z), three posterior plates
586 (M'₆, M₇, M₆), and two posterior spines (D and G) (see above; Fig. 11). In all taxa, but the
587 new Floian anomalocystitid from Morocco, the right infracentral area is absent, and the left
588 one consists of A (Siluro-Devonian forms; Fig. 11c), or A and B (Mid-Late Ordovician taxa;
589 Fig. 11a-b) (see above). Consequently, the systematics of anomalocystitids mostly relies on
590 the plate pattern of their upper thecal surface, and in particular on the number, extent and
591 arrangement of their supracentrals (e.g. Dehm, 1932; Gill and Caster, 1960; Parsley, 1991;
592 Ruta and Theron, 1997; Ruta and Bartels, 1998; Ruta, 1999a; Lefebvre, 2001; McDermott
593 and Paul, 2017). Contrary to the situation in most other stylophorans, anomalocystitid
594 supracentrals are frequently arranged into regular transverse rows, each made of a limited and
595 fixed number of relatively large plates. Various terminologies have been introduced to
596 identify supracentrals in Allanicystidiinae (e.g. Caster, 1952, 1954b; Philip, 1981),

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

602

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

614

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

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

624

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

636

637 Allanicytidiinae (Fig. 14) are defined by the possession of a distinctive ploughshare-like
638 stylocone with transverse blades (Ubaghs, 1967a; Caster, 1983; Haude, 1995; Lefebvre, 1999,
639 2001; Ruta, 1999a; Ruta and Jell, 1999a; Jell, 2013; Scheffler et al., 2017). Contrary to the
640 situation in most other mitrocystitidans, $A_0?$ is also generally inserted between A'_1 and A_1 ,
641 and framing the aulacophore insertion (e.g. *Enoploura*, *Protocytidium*, *Placocystella*; Fig.
642 14a-b). In the earliest known representatives of the subfamily Allanicytidiinae (*Enoploura*
643 spp., late Sandbian–Katian of North America), the supracentral area has an almost bilaterally
644 symmetrical plate pattern (Fig. 14a), characterized by a fixed number of tessellate elements
645 (11), organized into three incomplete rows (Caster, 1952; Parsley, 1982, 1991). The plate
646 pattern of *Enoploura* can be readily compared with those of all younger allanicytidiines, and a

647 well-defined set of homologies can be established at sub-family level (see discussions in
648 Haude, 1995; Ruta and Theron, 1997; Ruta, 1999a; Ruta and Jell, 1999a; Lefebvre, 2001; Jell,
649 2013; Scheffler et al., 2017). For example, the reduced number of supracentrals (nine) in
650 *Protocytidium elliotiae* (Hirnantian, Australia; Fig. 14b) most likely results from the loss of
651 two posterior supracentrals (Ruta and Jell, 1999a). Similarly, the plate patterns of
652 *Occultocystis* (Lower Devonian, Argentina; Fig. 14c) and *Placocystella* spp. (late
653 Llandovery–early Givetian; Australia, Brazil, New Zealand, South Africa) can be both
654 interpreted as resulting from further drastic reductions of the number of supracentrals from
655 nine elements (*Protocytidium*) to five and six, respectively (Haude, 1995; Ruta and Theron,
656 1997; Ruta, 1999a; Ruta and Jell, 1999a; Lefebvre, 2001; Jell, 2013; Scheffler et al., 2017).

657

658 Anomalocystitinae (Figs 15b-c, 16) are characterized by the possession of a highly
659 distinctive supracentral element with rounded to elliptical outlines: the placocystid plate (P).
660 The spineless genus *Barrandeocarpus* (with an obvious plate P on its upper thecal surface;
661 Fig. 15b) is thus interpreted here as an anomalocystitine mitrate, in which both D and G have
662 been secondarily lost (Lefebvre, 1999; Lefebvre and Gutiérrez-Marco, 2003; McDermott and
663 Paul, 2017; but see Ubaghs, 1979; Craske and Jefferies, 1989; Ruta, 1997c, 1999a).
664 Anomalocystitines also retain many plesiomorphic mitrocystitidan features, such as
665 longitudinally compressed styloid blades and, in most taxa, a median anterior plate A_0 ?
666 located posteriorly to A'_1 and A_1 and, thus, not in contact with the aulacophore insertion (Figs.
667 15b-c, 16a; Lefebvre, 1999). The earliest known representatives of this subfamily,
668 *Barrandeocarpus jaekeli* (Sandbian, Czech Republic; Fig. 15b), *B.* sp. (Sandbian, UK),
669 *Ateleocystites* spp. (early Katian, Canada and USA; Fig. 15c) and *A? lansae* (late Katian, UK)
670 are all characterized by two anterior, relatively regular rows of supracentrals, each made of a
671 fixed number of elements (Ubaghs, 1979; Kolata and Jollie, 1982; Parsley, 1991; Ruta,

672 1997c; McDermott and Paul, 2017). In both *Ateleocystites* and *Barrandeocarpus*, the most
673 anterior transverse row of supracentrals always comprises five plates, including P in central
674 position, whereas the next, more posterior row is made of four elements (Fig. 15b-c).
675 However, in some specimens of *A. huxleyi* (and possibly also in some individuals of *B.*
676 *jaekeli*), a fifth plate can be sometimes more or less deeply inserted posteriorly and in
677 between the two large median supracentrals of the second row (Kolata and Jollie, 1982;
678 Parsley, 1991). In the two genera *Ateleocystites* (Fig. 15c) and *Barrandeocarpus* (Fig. 15b),
679 the posterior part of the supracentral area mostly consists of imbricate, irregularly arranged
680 elements in variable number (Ubaghs, 1979; Kolata and Jollie, 1982; McDermott and Paul,
681 2017). In this respect, the very nice reconstructions of both *A. guttenbergensis* and *B. jaekeli*
682 provided by Kolata and Jollie (1982, fig. 3) and Ubaghs (1979, fig. 5), respectively, are partly
683 misleading, because they suggest the existence of a more or less regular arrangement for
684 posterior supracentrals, which is not the case. As stated by Kolata and Jollie (1982, p. 640),
685 the total number of supracentrals varies between 20 and 25 in *Ateleocystites* (i.e. between 11
686 and 16 in the posterior, imbricate region; see also McDermott and Paul, 2017, p. 7).

687

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

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

698

699 Similarly to Dehm's terminology (1932), the new system relies primarily on the
700 organization of the upper thecal surface into regular transverse rows of tessellate plates (Figs.
701 14-15). Within a given row, each plate is assigned a number indicating its position away from
702 the midline, in the same way this is already done for identifying marginals and adorals (see
703 e.g. Lefebvre and Vizcaïno, 1999; Lefebvre, 2001). In all anomalocystitids, the most anterior
704 row (row A) consists of three homologous plates: A'_1 (on the left), $A_0?$ (in median position),
705 and A_1 (on the right). In Ordovician anomalocystitines, the next row (here designated as row
706 B) contains five plates, which are from left to right: B'_2 , B'_1 , P (placocystid plate, in median
707 position), B_1 and B_2 (Fig. 15b-c). Similarly, the second row of supracentrals (row C) typically
708 contains four elements in both *Ateleocystites* and *Barrandeocarpus*, with from left to right:
709 C'_2 , C'_1 , C_1 and C_2 (Fig. 15b-c).

710

711 Comparison of plate patterns in Ordovician allanicytidiines (Fig. 14a-b) and
712 anomalocystitines (Fig. 15b-c), suggests that supracentrals C'_1 and C_1 in *Ateleocystites* and
713 *Barrandeocarpus* are very likely homologous to the pair of similarly shaped, wide median
714 supracentrals anteriorly in contact with $A_0?$ in both *Enoploura* and *Protocytidium*.
715 Comparison with the situation in Ordovician anomalocystitines indicates that the lateral
716 element in contact with both A'_1 and C'_1 in *Enoploura* and *Protocytidium* can be identified as
717 B'_2 (same position and same contacts with surrounding plates). Similarly, on the right side of
718 allanicytidiine thecae, B_2 corresponds to the supracentral in contact with both A_1 and C_1 (Fig.
719 14a-b). These identifications imply that, in *Enoploura* (Fig. 14a) and *Protocytidium* (Fig.
720 14b), the first row of supracentrals consists of only two plates (B'_2 and B_2), instead of five in

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

727

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

746 both allanicytidiines and anomalocystitines. Alternatively, this five-plated row might be an
747 autapomorphy of *W. denticulatus* (row absent or lost in e.g. *Enoploura* and *Ateleocystites*),
748 and the next, four-plated row could then be equivalent to row C of Late Ordovician
749 allanicytidiines and anomalocystitines. In *Willmanocystis* (Fig. 15a), the posterior, regularly
750 arranged row of five tessellate supracentrals has no obvious equivalent in the morphology of
751 coeval anomalocystitines, but it is very likely homologous to the similarly positioned row of
752 *Enoploura* (Fig. 14a), which is also made of five small plates along the anal opening. The
753 upper surface of *Willmanocystis* (Fig. 15a) suggests that the arrangement on the upper thecal
754 surface of *Enoploura* (Fig. 14a) results from a drastic reduction in the number of plates (from
755 18 to 11) and the probable loss of one row of supracentrals (either the second or the third one,
756 by comparison with *W. denticulatus*; see discussion above). For this reason, the third,
757 posterior supracentral row of *Enoploura* is here designated E (Fig. 14a), and its five plates,
758 E₂, E₁, E₀, E₁, and E₂ (from left to right). Finally, the plate pattern of the upper thecal surface
759 of *Willmanocystis* (Fig. 15a) has some troubling similarities with those of much younger,
760 Early Devonian anomalocystitines (e.g. *Anomalocystites* and, mostly, *Bokkeveldia*; Fig. 16b).
761 At this stage, it remains difficult to decipher if these similarities in plating are the result of
762 fortuitous convergence or of iterative evolution, possibly due to heterochronic processes.

763

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

771 1999a; Ruta and Theron, 1997; Ruta and Bartels, 1998; Ruta and Jell, 1999c, 1999d; Lefebvre
772 and Rachebœuf, 2007; Parsley and Sumrall, 2007). Plate patterns of Siluro-Devonian
773 anomalocystitines (Fig. 16) can be easily compared to each other, and a set of robust
774 homologies was proposed by Ruta (1999a; see also Ruta, 1997b; Ruta and Theron, 1997; Ruta
775 and Bartels, 1998). However, the numerical terminology for supracentrals elaborated by Ruta
776 (1999a), which is based on *Bokkeveldia*, with four rows of plates, posteriorly to adorals (Fig.
777 16b), cannot be applied to taxa such as *Anomalocystites*, with one more row of supracentrals
778 (Fig. 16c; see Parsley, 1991; Ruta 1999a, fig. 9A).

779

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

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

801

802 The highest total number of transverse rows (six) is present on the upper thecal surface of
803 *Anomalocystites* (Fig. 16c; see Ubaghs, 1967a; Parsley, 1991; Ruta, 1999a). Its two anterior-
804 most rows are homologous to rows A and B in other anomalocystitids (see above). Although
805 it was not shown on Parsley's reconstruction (1991, fig. 5) of *A. cornutus*, the placocystid
806 plate is clearly present in median position, within row B (see e.g. Parsley, 1991, pl. 1 figs 4,
807 14; Ruta, 1999a). The next four rows are designated III, IV, V and VI (Fig. 16c). Row and
808 plate homologies in all other Siluro-Devonian anomalocystitines (Fig. 16a-b) can be deduced
809 from a comparison with the upper surface of *Anomalocystites* (Fig. 16c). Although their fossil
810 record remains relatively sparse, post-Ordovician anomalocystitines seem to show a more or
811 less regular increase of their number of supracentrals through time, and correlatively of their
812 number of transverse rows (Gill and Caster, 1960; but see Ruta and Bartels, 1998): four-
813 rowed taxa (Fig. 16a) occur in the late Llandovery (A, B, III, and VI; e.g. *Placocystites*
814 *forbesianus*), whereas five-rowed ones (Fig. 16b) are not documented before the Ludlow (A,
815 B, III, V, and VI; e.g. *Mongolocarpos minzhini*, *Victoriacystis wilkinsi*) and six-rowed forms
816 (Fig. 16c) are only known from the Early Devonian (A, B, III, IV, V, and VI; *Anomalocystites*
817 *cornutus*). More data are probably necessary to decipher whether this apparent increase in the
818 number of plates and rows in post-Ordovician anomalocystitines represents an actual trend, or
819 if it simply results from a strong sampling bias.

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SYSTEMATIC PALEONTOLOGY

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

CLASS STYLOPHORA GILL & CASTER, 1960

Order Mitrata Jaekel, 1918

Suborder Mitrocystitida Caster, 1952

Family Anomalocystitidae Bassler, 1938

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

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

846 and Lefebvre, 2012; Lefebvre et al., 2013, 2016). Three main subdivisions are here identified
847 within anomalocystitids, based on the literature, previous phylogenetic analyses and, mostly,
848 plate homologies: Allanicystidiinae, Anomalocystitinae and Diamphidiocystinae (see above;
849 e.g. Ubaghs, 1967a; Kolata and Guensburg, 1979; Kolata and Jollie, 1982; Parsley, 1991,
850 1997; Ruta, 1999a, 2003; Lefebvre, 2000b, 2001, 2005). The subfamily Allanicystidiinae (Figs
851 11, 14) includes all taxa possessing a ploughshare-shaped stylocone with transverse blades
852 (see below). Anomalocystitines (Figs 15b-c, 16) are defined by the presence of the
853 placocystid plate on their upper thecal surface (see above; *Anomalocystites*, *Ateleocystites*,
854 *Barrandeocarpus*, *Bokkeveldia*, *Mongolocarpos*, *Placocystites*, *Rhenocystis*, *Victoriacystis*).
855 Finally, the subfamily Diamphidiocystinae (Fig. 13b) corresponds to a small clade of
856 anomalocystitids with a markedly asymmetrical, sinistrally flexed theca (*Diamphidiocystis*).

857

858 Three Late Ordovician anomalocystitids from North America are not assigned to any
859 subfamily. *Willmanocystis denticulatus* (Fig. 15a) is a possible sister-taxon of Allanicystidiinae
860 (see discussion above; Kolata and Jollie, 1982). The upper thecal surface of *Kopficystis*
861 *kirkfieldi* suggests probable affinities with Anomalocystitinae; the single known specimen of
862 *Kopficystis* could even represent a poorly preserved individual of *Ateleocystites*. Similarly, the
863 morphology of the type and only specimen of *Kierocystis inserta* is extremely poorly known.
864 This genus was defined on the erroneous identification of two tectals (elements of the
865 proximal aulacophore) as a pair of small, additional anterior thecal plates (PSI in Parsley,
866 1991; but see Ruta, 1999a). The plate pattern of its upper thecal surface is anteriorly poorly
867 preserved, so that it is difficult to identify whether one single large median element $A_0?$ is
868 present (thus suggesting affinities with *Enoploura* and allanicystidiines), or if this area rather
869 corresponds to four plates (see Ruta, 1999a), with a small $A_0?$, B'_1 , B_1 and possibly, P (in this
870 case, *Kierocystis* would be a badly preserved specimen of *Ateleocystites*).

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

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

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

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

903

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

905

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

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

908

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

912

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

914

915 Diagnosis. A genus of allanicytidiine mitrate with a long posterior spike on M_7 ; left
916 infracentral area made of one plate (A); upper thecal surface consisting of five extensive
917 skeletal elements; A_0 ? diamond-shaped, posteriorly inserted to A'_1 and A_1 , not in contact
918 with aulacophore insertion; posterior half of upper thecal surface formed by two supracentrals
919 (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 allanicystidiines (ploughshare
927 stylocone with transverse blades). The plating of its upper thecal surface differs from those of
928 most other allanicystidiines 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

945 mitrocystitidans characterized by a leftward directed anal opening, and a strong expansion of
946 M₆, which is modified into a large posterior marginal process (Lefebvre, 1999, 2000b;
947 Lefebvre and Rachebœuf, 2007). Consequently, the similar-looking upper thecal surfaces of
948 paranacystids and *Perikefalea* were acquired independently, through convergent, drastic
949 reductions of their numbers of supracentrals.

950

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

952

953 Figs 17–21

954

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

958

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

964

965 Diagnosis. A species of *Perikefalea* with a wide, blunt posterior M₇ spike, and reticulate
966 thecal plates with no obvious thecal sculpture.

967

968 Description. Relatively broad, almost bilaterally symmetrical theca, with gently curved
969 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 M₇ (Figs 17a-b, 18a-b, 19a). Lower thecal surface almost flat, except crescent-
973 shaped raised anterior lip borne by M'₁ and M₁ 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 M₂, Mc and M₃) (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 M₁ 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 M₁
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 M₂ (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 Mc (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 M₃ (on the right) unequal in size, with slightly different outlines (Figs 17a-b, 18a-b, 19a).
992 M'₄ and M₃ with similar long, almost straight abaxial edges, and very short posterior margin,
993 corresponding to sockets for spine articulation. M₃ pentagonal, wider than M'₄, largely in
994 contact with Mc, Z and M₆ along straight sutures. M'₄ with very short suture along Z, concave

995 adaxial margin along anomalocystitid plate A, and relatively short, straight contact with M'₆.
996 Lateral posterior plates M'₆ (on the left) and M₆ (on the right) subequal in size, similarly
997 shaped, elongate, narrow, quadrangular elements, slightly wider posteriorly than anteriorly
998 (Figs 17a-b, 18a-b, 19a). M'₆ in contact with M₇ (adaxially), Z (anteriorly), and both A and
999 M'₄ (abaxially). M₆ sutured to M₃ (abaxially), Z (anteriorly) and M₇ (adaxially). Median
1000 posterior marginal M₇, particularly elongate, subpentagonal, with short anterior margin in
1001 contact with Z, long, posteriorly diverging, gently concave sutures along M'₆ (on the left) and
1002 M₆ (on the right), and two long marginal edges converging posteriorly towards a blunt,
1003 rounded tip (Figs 17a-b, 18a-b, 19a). Posterior part of M₇ thus forming wide, protruding
1004 spike-shaped expansion of marginal frame. Zygale plate particularly large, subhexagonal,
1005 occupying most of central part of lower thecal surface, in contact with anomalocystid plate
1006 and all marginals (Figs 17a-b, 20b). Anomalocystitid plate small central subtrapezoidal
1007 skeletal element in close contact with M'₄ (abaxially), and also sutured to both Z (adaxially)
1008 and M'₆ (posteriorly) (Figs 17a-b, 18a-b, 19a). Posterior spines, D (digital, on the left) and G
1009 (glossal, on the right), elongate, rod-shaped, moderately decreasing in width antero-
1010 posteriorly, with rounded proximal ball for articulation with marginal frame, and distal blunt
1011 extremity (Figs 17a-b, 19a). Digital almost straight, but glossal possibly weakly curved (Figs
1012 17a-b, 20b).

1013

1014 Bilaterally symmetrical upper thecal surface (Fig. 20c) entirely made of five large, gently
1015 domed plates: two adorals (A'₁ and A₁), one median element (A₀?), and two supracentrals
1016 (C'₁, C₁). Lateral adorals, A'₁ (on the left) and A₁ (on the right), wide, particularly elongate,
1017 forming together most of anterior half of upper thecal surface (Figs 17c-d, 18c-d). A'₁ and A₁
1018 with relatively short, straight anterior margins forming wide, shallow, V-shaped, concave
1019 notch above aulacophore insertion. Abaxial margins of lateral adorals particularly elongate,

1020 convex, regularly curved, closely sutured to lateral walls of underlying marginals (M'_1 - M_1 ,
1021 M'_2 - M_2 and anterior half of M'_3 - M_3). Adaxial margins of A'_1 and A_1 anteriorly sutured to each
1022 other along thecal longitudinal midline, and posteriorly diverging abaxially along A_0 ?. Each
1023 lateral adoral posteriorly in contact with one supracentral along short, straight, transverse
1024 suture. A_0 ? large, elongate, diamond- to fan-shaped skeletal element in central position,
1025 sutured to all other plates of upper thecal surface (Figs 17c-d, 18c-d). Maximum width of A_0 ?
1026 at contact between adorals and supracentrals. Maximum length of A_0 ? along longitudinal
1027 midline. Anterior margins of A_0 ?, long, sinuous and converging anteriorly to triple junction
1028 with A'_1 and A_1 along thecal longitudinal midline. Posterior margins of A_0 ?, much shorter,
1029 gently convex, similarly converging posteriorly to triple junction with C'_1 (on the left) and C_1
1030 (on the right) along longitudinal midline. Supracentrals C'_1 and C_1 almost as extensive as
1031 adorals, particularly elongate, sub-triangular to fan-shaped, forming together most of posterior
1032 half of upper thecal surface (Figs 17c-d, 18c-d). Long, straight, adaxial suture between C'_1
1033 and C_1 along thecal longitudinal midline. Each supracentral anteriorly in contact with A_0 ? and
1034 one lateral adoral. Abaxial margins of C'_1 and C_1 particularly long, convex, regularly flexed,
1035 laterally in contact with underlying marginals (posterior half of M'_3 - M_3 , M'_4 - M_4), but forming
1036 posteriorly a large vault expanding beyond M'_6 and M_6 , up to distal extremity of M_7 spike
1037 (Fig. 19a).

1038

1039 Internal thecal features (e.g. infundibulum, septum, scutulae and associated co-opercula)
1040 not observed (all specimens fully articulated, no internal moulds, no isolated plates). Anal
1041 opening slit-like, narrow, in transversely elongate space roofed by C'_1 - C_1 vault, and floored
1042 by distal margin of posterior marginals (M'_6 , M_7 , M_6). Internal thecal cavity anteriorly in
1043 contact with lumen of proximal aulacophore through narrow, transversely elongate

1044 passageway between high aulacophore apophyses borne by M'_1 and M_1 (below) and low vault
1045 provided by A'_1 and A_1 (above) (Fig. 20a).

1046

1047 Proximal aulacophore relatively short, cylindrical, consisting of four telescopic, bilaterally
1048 symmetrical, transverse rings, each made of four plates (Fig. 17): two tectals (above), and two
1049 inferolaterals (below). Left and right series of tectals in contact along longitudinal midline
1050 (Fig. 17c-d). Left and right series of inferolaterals similarly sutured along longitudinal midline
1051 (Fig. 17a-b). Inferolaterals and tectals contributing equally to height of lateral walls of
1052 proximal rings (Fig. 19b). Each ring comprising a slightly narrower, depressed proximal neck,
1053 and a slightly wider, raised distal lip. No intercalated integumentary platelets observed in
1054 between successive rings. Stylocone ploughshare-shaped, with two transverse, oblique blades.
1055 Anterior (distal) stylocone blade much more extensive and wider than posterior (proximal)
1056 one (Figs 17a-b, 19b). Upper surface of stylocone and more distal brachials not observed. In
1057 best preserved aulacophore (Fig. 19b), anterior portion of arm, consisting of more than 20
1058 high, clearly spinose brachials and associated cover plates. Fine details of arm plates obscured
1059 by preservation in coarse siliciclastic deposits.

1060

1061 Measurements. Thecal length (TL) is measured between the anterior-most extremity of
1062 anterior marginals (M'_1 , M_1) and the posterior tip of the M_7 spike. Thecal width (TW) is
1063 estimated perpendicularly to TL, where width is maximum (i.e. along the M'_2 - M_3 and M_2 - M_3
1064 sutures). Spine length (SpL) and width (SpW) are measured along and across, respectively,
1065 posterior spines. Maximum width of the stylocone (StylW) is estimated along its anterior
1066 (distal) transverse blade. MHNC 13354 (holotype): TL: 8.5 mm, TW: 5.4 mm, SpL: 3.3 mm,
1067 SpW: 0.6 mm, StylW: 2.6 mm; MHNC 13355: TL: 8.5 mm, TW: 6.2 mm; MHNC 13356:

1068 TW: 6.2 mm, SpW: 0.6 mm. In the holotype, TW is probably underestimated, because left
1069 marginals are slightly shifted adaxially.

1070

1071 Remarks. The occurrence of a new allanicytidiine mitrate in the Lochkovian of Bolivia
1072 was originally reported by Lefebvre and Rachebœuf (2007), and later mentioned by Scheffler
1073 et al. (2019). Although specimens occur in relatively coarse siliciclastic deposits, the absence
1074 of any obvious external skeletal sculpture is probably original in *P. racheboeufi*. Minute
1075 details can be preserved, as evidenced by the relatively loose, porous stereom microstructure,
1076 which is visible on most thecal plates and that is similar to the 'punctate' morphology
1077 described in some Ordovician allanicytidiines (e.g. *Enoploura punctata*; Bassler, 1932;
1078 Parsley, 1991). The absence of ornamentation in *P. racheboeufi* is possibly related to an
1079 epibenthic, vagile, mode of life, comparable to that of paranacystids occurring in the same
1080 levels of the Santa Rosa Formation (see Lefebvre, 2003b).

1081

1082 In specimen MHNC 13358 (Fig. 19b), the preservation of the arm in extended position is
1083 unusual in mitrates. In this group, the aulacophore is generally recurved over the theca, in a
1084 typical flexed posture, which is usually interpreted as a distressed position or as the result of a
1085 post-mortem contraction (e.g. Dehm, 1932; Jefferies, 1984; Parsley, 1988; Ruta and Bartels,
1086 1998; Lefebvre, 2003b). The unusual preservation of Bolivian anomalocystitids with their
1087 extended arm (i.e. in its original feeding position) suggests that they were very likely buried
1088 alive and in situ by a sudden influx of sediments (see Parsley and Gutiérrez-Marco, 2005;
1089 Lefebvre and Botting, 2007; Martin et al., 2015). Their occurrence in very shallow, low
1090 intertidal deposits suggest that this interpretation is plausible.

1091

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.

1116

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

1142 anomalocystid plate (A). Mc trapezoidal, delimited by two sinuous, almost parallel, transverse
1143 sutures, anteriorly (with M₂) and posteriorly (with M₃), and two longer, almost straight,
1144 markedly diverging edges, adaxially (along contact with Z) and abaxially. Postero-lateral
1145 marginals, M'₄ (on the left) and M₃ (on the right), subequal in size, broad, pentagonal,
1146 significantly shorter than all more anterior marginals (Fig. 22). Posterior edges of both M'₄
1147 and M₃ particularly short, concave, forming typical sockets for spine insertion. M'₄ and M₃
1148 both delimited by gently curved abaxial margins, and sinuous sutures with three surrounding
1149 thecal plates. M₃ in contact with Mc, Z and M₆. Anterior portion of M'₄ not visible, though
1150 certainly sutured to M'₃. M'₄ also in contact with M'₆ and anomalocystid plate. Lateral
1151 posterior plates, M'₆ (on the left) and M₆ (on the right), subequal in size, narrow, elongate,
1152 slightly shorter anteriorly than posteriorly, with long, subparallel abaxial and adaxial margins
1153 (Fig. 22). M'₆ anteriorly in contact with anomalocystid plate, and M₆, with Z. M'₆ and M₆ both
1154 adaxially sutured to median posterior plate (M₇). M₇ relatively broad, wide, pentagonal, with
1155 anteriorly, a very short, straight transverse margin, and, two long, gently curved, abaxially
1156 diverging edges along sutures with M'₆ and M₆ (Fig. 22). Posterior margin of M₇ expanded
1157 into long spike-shaped median process, with a wide base, strongly concave edges, distally
1158 tapering into a sharp tip. Zygial plate particularly broad, slightly longer than wide, occupying
1159 most of lower thecal surface (Fig. 22). Preserved portion of Z indicates contacts with most
1160 surrounding marginals (M'₁, M₁, M'₂, Mc, M₃, M₆), and possibly with M₂ (Fig. 23a). Left and
1161 posterior part of Z not preserved. Several fragments of skeletal elements (anomalocystid
1162 plate? supracentrals?) occurring between left posterior marginals (M'₃, M'₄, M'₆ and M₇) and
1163 incomplete, visible portion of Z (Fig. 22). Posterior spines not preserved (Fig. 22).

1164

1165 Extensive external thecal sculpture occurring in two symmetrical, sub-triangular to fan-
1166 shaped areas, almost equally distributed on two marginals, on left (M'₂ and M'₃) and right (M₂

1167 and Mc) thecal sides (Fig. 22). Sculpture consisting of irregular, discontinuous, transverse,
1168 more or less oblique scale-like riblets. Riblets not parallel to each other but forming two sets
1169 of radiating lines abaxially diverging from two points, located close to the M'₂-M'₃-Z (on the
1170 left) and M₂-Mc-Z (on the right) triple contacts. Thecal sculpture not extending, abaxially,
1171 into downwards recurved, longitudinal skate-like marginal flanges.

1172

1173 No internal thecal characters visible (specimen showing only external, lower aspect of
1174 theca).

1175

1176 Proximal aulacophore consisting of at least four, bilaterally symmetrical proximal rings
1177 (Fig. 22). Stylocone and arm not preserved, except small portion of recurved distal
1178 aulacophore, consisting of six brachials and five associated cover plates (right series). Three
1179 distal-most observed ossicles more or less completely sectioned transversely, with relatively
1180 high lateral walls on both sides of deep central part with longitudinal median groove (Fig.
1181 23c). Next two more proximal elements well-preserved, with external aspect of ossicles, with
1182 low posterior spike and shallow transverse furrow (Fig. 23c). Sixth, proximal-most brachial
1183 poorly preserved. Cover plates incompletely preserved, gently arched, smooth, significantly
1184 smaller than associated ossicles (Fig. 23c).

1185

1186 Measurements. GSC 126914 (holotype): TL: 14 mm, TW: 8.1 mm.

1187

1188 Remarks. Although posterior spines are not preserved in the Anticosti mitrate (Fig. 22), the
1189 presence of typical sockets for spine articulation on the posterior margins of both M'₄ and M₃
1190 clearly indicates that two spines were originally articulated to the theca (Fig. 23a), thus
1191 unambiguously supporting the assignment of this fossil to Anomalocystitidae. The two key

1192 characters for subfamilial identification (morphology of stylocone blades and plate pattern of
1193 upper thecal) are not available for this specimen (see above, about unsuccessful CT-scan
1194 investigations). However, the occurrence of extensive scale-like riblets on lateral marginals
1195 (M'_2 , M'_3 , M_2 and M_c ; Fig. 22) strongly suggests allanicytidiine, rather than anomalocystitine,
1196 affinities. In anomalocystitines, thecal sculpture almost essentially consists of more or less
1197 continuous, straight to sinuous cuesta-shaped ribs and/or pustules, as for exemple in
1198 *Ateleocystites* (Kolata and Jollie, 1982; Parsley, 1991), *Barrandeocarpus* (Ubaghs, 1979;
1199 Craske and Jefferies, 1989; Ruta, 1997c; Lefebvre and Gutiérrez-Marco, 2003), *Placocystites*
1200 (Jefferies and Lewis, 1978), *Rhenocystis* (Dehm, 1932; Ruta and Bartels, 1998) or
1201 *Victoriacystis* (Gill and Caster, 1960; Ruta, 1997b; Ruta and Jell, 1999c, 1999d). In contrast,
1202 the external thecal sculpture of allanicytidiines, when present, typically consists either of
1203 discontinuous, crescent-shaped to scale-like riblets and/or of pustules, as in *Placocystella*
1204 *africana* (Ruta and Theron, 1997), *P. flemingi* (Ubaghs, 1967a; Ruta and Jell, 1999e) or *P.*
1205 *garratti* (Philip, 1981; Ruta and Jell, 1999e). For this reason, Lindstöm's anomalocystitid
1206 (1888; see discussion above) and the Anticosti mitrate, which both display scale-like riblets
1207 are here identified as probable allanicytidiines.

1208

1209 A further argument supporting this taxonomic assignment of the Anticosti specimen is its
1210 strong similarity with the allanicytidiine genus *Perikefalea* with, in particular, comparable
1211 morphologies of posterior marginals M_7 (strong posterior spike), M'_6 and M_6 (particularly
1212 narrow and elongate). For this reason, the Anticosti mitrate is interpreted here as a probable
1213 allanicytidiine anomalocystitid, which is tentatively assigned to the genus *Perikefalea*. To be
1214 confirmed (or not) this identification requires the discovery of additional specimens
1215 preserving the upper thecal surface. Although morphologically very close to *P. racheboeufi*,

1216 the Anticosti mitrate is assigned to a distinct species, *P.?* *cybeleae*, because of several
1217 differences.

1218

1219 The most obvious difference with *P. racheboeufi* concerns the external thecal sculpture,
1220 which is totally absent in *P. racheboeufi* but extensive in the Canadian form. Moreover, as
1221 ornamentation in anomalocystitids is always stronger on the upper thecal surface (see
1222 Jefferies, 1984; Ruta and Bartels, 1998; Lefebvre, 2003b), the occurrence of widespread
1223 riblets on marginals of *P.?* *cybeleae* suggests that a much more extensive sculpture is present
1224 on its opposite (upper) thecal surface. This strong ornamentation suggests that *P.?* *cybeleae*
1225 was very likely infaunal (see Jefferies and Lewis, 1978; Jefferies, 1984; Lefebvre, 2003b).

1226

1227 Other differences concern the morphology of the M₇ spike (wider and blunt in *P.*
1228 *racheboeufi*, narrower and sharp in *P.?* *cybeleae*), and the relative size of postero-lateral
1229 marginals M'₄ and M₃ (much smaller in *P.?* *cybeleae* than in *P. racheboeufi*). Although this is
1230 not clearly visible on the holotype (Fig. 22), a single left infracentral element (anomalocystid
1231 plate) was probably present in *P.?* *cybeleae*. This interpretation relies on the occurrence of a
1232 relatively large skeletal fragment on the left of Z, and mostly, on the morphology of
1233 surrounding plates (M'₃, M'₄, M'₆ and possibly M₇), which indicates that they were sutured to
1234 a single, relatively large posterior infracentral element. Moreover, the probable occurrence of
1235 the anomalocystid plate in *P.?* *cybeleae* would be in good agreement with the situation in
1236 other Siluro-Devonian anomalocystitids, all characterized by the loss of the barrandeocarpid
1237 plate (see above). In *P.?* *cybeleae*, A is anteriorly largely in contact with M'₃ (Fig. 23a), which
1238 is not the case in *P. racheboeufi* (Fig. 21b).

1239

1240 All these morphological differences are considered here as sufficiently significant to justify
1241 the erection of a distinct species for the Canadian specimen. Finally, all specimens of *P.*
1242 *racheboeufi* are about twice as smaller and significantly younger (Lochkovian) than the single
1243 known individual of *P.?* *cybeleae* (Telychian).

1244

1245 Contrary to the situation in *P. racheboeufi* (see above), the arm of the only known
1246 specimen of *P.?* *cybeleae* is preserved in the typical flexed position (i.e. taphonomic group 2
1247 of Martin et al., 2015). This posture, along with the partial disarticulation of its lower thecal
1248 surface (plates are not in close contact with each other, especially in the posterior part of the
1249 specimen), suggest that the holotype of *P.?* *cybeleae* was not buried alive by a sudden influx
1250 of sediments (e.g. tempestites), but more likely, a short time (several days or weeks) after its
1251 death.

1252

1253 Occurrence. *Perikefalea?* *cybeleae* is only known from the type-locality (Box River,
1254 Anticosti Island), where it occurs within the Cybèle Member of the Jupiter Formation
1255 (Telychian).

1256

1257 Material. *P.?* *cybeleae* is only known from its holotype.

1258

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1280

1281

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1663

1664 FIGURE CAPTIONS

1665

1666 **Fig. 1.** Location and geology of Anticosti Island: (a) location of Québec in North America;
1667 (b) location of Anticosti Island in Québec; (c) geological map of Anticosti Island; the star
1668 indicates the position of the locality yielding stylophoran remains (modified from Ausich
1669 and Cournoyer, 2019). With the exception of the Vauréal (Katian) and Ellis Bay
1670 (Hirnantian) formations, all other lithostratigraphic units are Silurian (Llandovery; see Fig.
1671 2).

1672

1673 **Fig. 2.** Silurian stratigraphic chart for Anticosti Island (modified from Copper et al., 2013);
1674 the star indicates the lithostratigraphic unit yielding mitrate remains.

1675

1676 **Fig. 3.** Location of Presto El Peral section (Bolivia): (a) location of Bolivia in South America;
1677 (b) location of study area in Bolivia; (c) location of the Presto El Peral section (indicated

1678 by a star), where mitrates were found (redrawn from Gaillard and Rachebœuf, 1993;
1679 Lefebvre and Rachebœuf, 2007).

1680

1681 **Fig. 4.** Devonian stratigraphic chart for the Central Subandean Zone of Bolivia (correlations
1682 based on Rachebœuf et al., 1993; Troth, 2006; Di Pasquo and Noetinger, 2008); the star
1683 indicates the lithostratigraphic unit, where mitrates were collected, at the top of the Santa
1684 Rosa Formation.

1685

1686 **Fig. 5.** Stylophoran morphology; reconstruction of the mitrocystitidan mitrate *Vizcainocarpus*
1687 *dentiger* (late Tremadocian, France), redrawn from holotype (UCBL-FSL 712665) and
1688 previous reconstructions (Ruta, 1997d; Lefebvre, 2000b); (a) upper surface; (b) lower
1689 surface; the original extension of the arm was probably longer (anterior part missing).

1690

1691 **Fig. 6.** Plate patterns of the lower thecal surface and homologies in early stylophorans; (a)
1692 *Ceratocystis perneri* (Wuliuan, Czech Republic), redrawn from Ubaghs (1967a, 1967b);
1693 (b) *Ponticulocarpus robisoni* (Wuliuan, USA), redrawn and modified from Sumrall and
1694 Sprinkle (1999); (c) *Flabelllicarpus rushtoni* (late Tremadocian, UK) redrawn from Marti
1695 Mus (2002). Designations: (A₀) median adoral, (A₁) right adoral, (A'₁) left adoral, (D)
1696 digital, (G) glossal, (M₁–M₅) right marginals, (M'₁–M'₅) left marginals, (Mc)
1697 cothurnocystid marginal, (Z) zygial plate.

1698

1699 **Fig. 7.** Plate patterns of the lower thecal surface and homologies in early mitrates and related
1700 forms; (a) *Lobocarpus vizcainoi* (Furongian, France), redrawn from Lefebvre (2000b); (b)
1701 *Chinianocarpus thoralis* (late Tremadocian, France), redrawn from Ubaghs (1970); (c)
1702 *Peltocystis cornuta* (late Tremadocian, France and Morocco), redrawn from Ubaghs

1703 (1970). Designations: (D) digital, (G) glossal, (M₁–M₃, M₆) right marginals, (M'₁–M'₄) left
1704 marginals, (Mc) cothurnocystid marginal, (Z) zygial plate.

1705

1706 **Fig. 8.** Lower thecal surface of a '*Phyllocystis*' *jingxiensis*-like stylophoran (Furongian,
1707 France); camera-lucida drawing of specimen UCBL-FSL 712773; (a) interpretation (plate
1708 homologies) of plate pattern; (b) main morphological features; the central position of Z
1709 results from the joining of both M₃ and G, posteriorly to it. This character (Z in central
1710 position), which is shared by amygdalothecids and mitrates, is very likely inherited from a
1711 'cornute-grade' ancestor morphologically similar to '*P.*' *jingxiensis*. Designations: (D)
1712 digital, (G) glossal, (M₁–M₃) right marginals, (M'₁–M'₄) left marginals, (Mc)
1713 cothurnocystid marginal, (Z) zygial plate.

1714

1715 **Fig. 9.** Plate patterns of the lower thecal surface and homologies in early mitrocystitidans; (a)
1716 *Ovocarpus moncereti* (late Floian, France), redrawn from Lefebvre and Gutiérrez-Marco
1717 (2003); (b) *Aspidocarpus bohemicus* (Sandbian, Czech Republic), with typical posterior
1718 spike on M₇; redrawn from Ubaghs (1979); (c) *Mitrocystites mitra* (Darriwilian, Czech
1719 Republic), redrawn from Ubaghs (1967a); the two posterior left infracentrals in *M. mitra*
1720 (I'₂ and I'₃) are not considered as homologous to those found in similar position in
1721 anomalocystitids (anomalocystid and barrandeocarpid plates), but as the result of
1722 convergent evolution towards left infracentral areas made of a reduced and fixed number
1723 of large elements. Designations: (D) digital, (G) glossal, (M₁–M₃, M₆) right marginals,
1724 (M₇) posterior median marginal, (M'₁–M'₄, M'₆) left marginals, (Mc) cothurnocystid
1725 marginal, (Z) zygial plate.

1726

1727 **Fig. 10.** Lower thecal surface of the earliest known anomalocystitid (middle Floian,
1728 Morocco); camera-lucida drawing of specimen UCBL-FSL 711719; (a) interpretation
1729 (plate homologies) of plate pattern; (b) main morphological features; two posterior skeletal
1730 elements (D and G) are no longer part of the marginal frame, but articulated to it and
1731 modified as posterior spines. Designations: (D) digital, (G) glossal, (M₁–M₃, M₆) right
1732 marginals, (M₇) posterior median marginal, (M'₁–M'₄, M'₆) left marginals, (Mc)
1733 cothurnocystid marginal, (Z) zygial plate.

1734

1735 **Fig. 11.** Plate patterns of the lower thecal surface and homologies in allanicytidiine
1736 anomalocystitids; (a) *Enoploura popei* (Katian, USA), redrawn from Parsley (1991); (b)
1737 *Protocytidium elliottae* (Hirnantian, Australia), redrawn from Ruta and Jell (1999a); (c)
1738 *Placocystella garratti* (Ludlow, Australia), redrawn from Ruta (1999a); Ordovician
1739 allanicytidiines retain two left infracentral elements, whereas all Siluro-Devonian taxa
1740 have only one. Designations: (A) anomalocystid plate, (B) barrandeocarpid plate, (D)
1741 digital, (G) glossal, (M₁–M₃, M₆) right marginals, (M₇) posterior median marginal, (M'₁–
1742 M'₄, M'₆) left marginals, (Mc) cothurnocystid marginal, (Z) zygial plate.

1743

1744 **Fig. 12.** Plate patterns of the upper thecal surface and homologies in early stylophorans and
1745 mitrates; (a) *Ceratocystis perneri* (Wuliuan, Czech Republic), redrawn from Ubaghs
1746 (1967a, 1967b); (b) *Lagynocystis pyramidalis* (Furongian, China; late Tremadocian,
1747 Morocco; late Floian, France; Dapingian, UK; Darriwilian, Czech Republic, France and
1748 Spain; Sandbian, France and Russia), redrawn from Ubaghs (1967a); (c) *Peltocystis*
1749 *cornuta* (late Tremadocian, France and Morocco), redrawn and modified from Ubaghs
1750 (1970) and Lefebvre and Botting (2007). Designations: (D) digital, (G) glossal, (M₁–M₄)
1751 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: (A₀?) possible median adoral, (A₁)
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 elliottae* (Hirnantian, Australia), redrawn from Ruta and Jell (1999a); (c)
1763 *Occultocystis koeneni* (Lower Devonian, Argentina), redrawn from Haude (1995).
1764 Designations: (A₀?) possible median adoral, (A₁) right adoral, (A'₁) left adoral, (B₂, B'₂)
1765 row B supracentrals, (C₁, C'₁, C₂, C'₂) row C supracentrals, (E₀, E₁, E'₁, E₂, 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: (A₀?) possible median adoral, (A₁) right
1773 adoral, (A'₁) left adoral, (B₁, B'₁, B₂, B'₂) row B supracentrals, (C₁, C'₁, C₂, C'₂) row C
1774 supracentrals, (E₀, E₁, E'₁, E₂, E'₂) row E supracentrals, (P) placocystid plate.

1775

1776 **Fig. 16.** Plate patterns of the upper thecal surface and homologies in Siluro-Devonian
1777 anomalocystitine mitrates; (a) *Placocystites forbesianus* (Wenlock, UK), redrawn from
1778 Jefferies and Lewis (1978); (b) *Bokkeveldia oosthuizeni* (Emsian, South Africa), redrawn
1779 from Ruta and Theron (1997), original size of single known individual not mentioned in
1780 Ruta and Theron (1997): dimensions based on specimen of *Bokkeveldia* sp. (Lower
1781 Devonian, Morocco) figured by Régnault and Chauvel (1987, fig. 1); (c) *Anomalocystites*
1782 *cornutus* (Lower Devonian, USA), redrawn and modified from Parsley (1991) and Ruta
1783 (1999a). Designations: (A₀?) possible median adoral, (A₁) right adoral, (A'₁) left adoral,
1784 (B₁, B'₁, B₂, B'₂) row B supracentrals, (III₀, III₁, III'₁, III₂, III'₂) row III supracentrals, (IV₁,
1785 IV'₁, IV₂, IV'₂, IV₃, IV'₃) row IV supracentrals, (V₁, V'₁, V₂, V'₂) row V supracentrals, (VI₀,
1786 VI₁, VI'₁, VI₂, VI'₂) row VI supracentrals, (P) placocystid plate.

1787
1788 **Fig. 17.** *Perikefalea racheboeufi* sp. nov., holotype MHNC 13354; (a-b) theca in lower
1789 aspect, with articulated spines, proximal aulacophore and ploughshare-shaped stylocone,
1790 with expanded distal transverse blade ; (a) photographic view; (b) interpretative camera-
1791 lucida drawing; (c-d) theca in upper aspect, with proximal aulacophore and two first pairs
1792 of ambulacral cover plates; (c) interpretative camera-lucida drawing; (d) photographic
1793 view. Designations: (A) anomalocystid plate, (A₀?) possible median adoral, (A₁) right
1794 adoral, (A'₁) left adoral, (C₁, C'₁) supracentrals, (cov. pl.) cover plates, (dig.) digital,
1795 (gloss.) glossal, (M₁–M₄, M₆) right marginals, (M₇) posterior median marginal, (M'₁–M'₄,
1796 M'₆) left marginals, (Mc) cothurnocystid marginal, (prox.) proximal aulacophore; styl.:
1797 stylocone, (Z) zygial plate.

1798
1799 **Fig. 18.** *Perikefalea racheboeufi* sp. nov., specimen MHNC 13355; (a-b) theca in lower
1800 aspect, with aulacophore insertion cavity exposed; (a) photographic view; (b) interpretative

1801 camera-lucida drawing; (c-d) theca in upper aspect; (c) interpretative camera-lucida
1802 drawing; (d) photographic view. Designations: (A) anomalocystid plate, (A₀?) possible
1803 median adoral, (A₁) right adoral, (A'₁) left adoral, (aul. insert. cav.) aulacophore insertion
1804 cavity, (C₁, C'₁) supracentrals, (M₁–M₄, M₆) right marginals, (M₇) posterior median
1805 marginal, (M'₁–M'₄, M'₆) left marginals, (Mc) cothurnocystid marginal, (Z) zygale plate.

1806

1807 **Fig. 19.** *Perikefalea racheboeufi* sp. nov.; (a) MHNC 13356, posterior half of the theca, in
1808 lower aspect, showing strong posterior spike on median posterior marginal (M₇) with distal
1809 supracentrals (C'₁ and C₁) protruding on both sides of it, and two spines (partially
1810 preserved glossal, on the left, and complete digital, on the right) articulated to postero-
1811 lateral marginals (M₃ and M'₄); (b) MHNC 13358, almost complete individual in left
1812 lateral view, showing the theca and almost complete aulacophore (over twenty brachials
1813 and associated cover plates, ploughshare-like stylocone with two strong transverse blades
1814 on its lower surface, proximal aulacophore rings); the preservation of the appendage in
1815 extended (feeding) position suggests sudden burial by obrution (storm) deposits.

1816

1817 **Fig. 20.** *Perikefalea racheboeufi* sp. nov., reconstruction of the theca; (a) anterior aspect, with
1818 aulacophore insertion; (b) lower surface; (c) upper surface.

1819

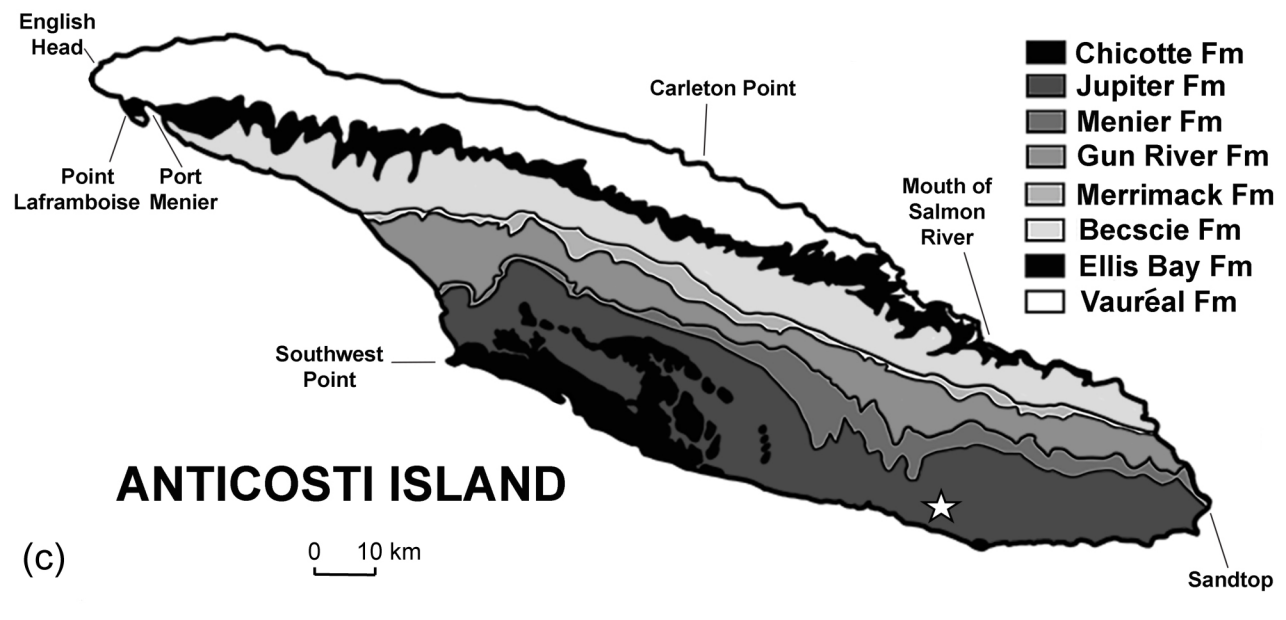
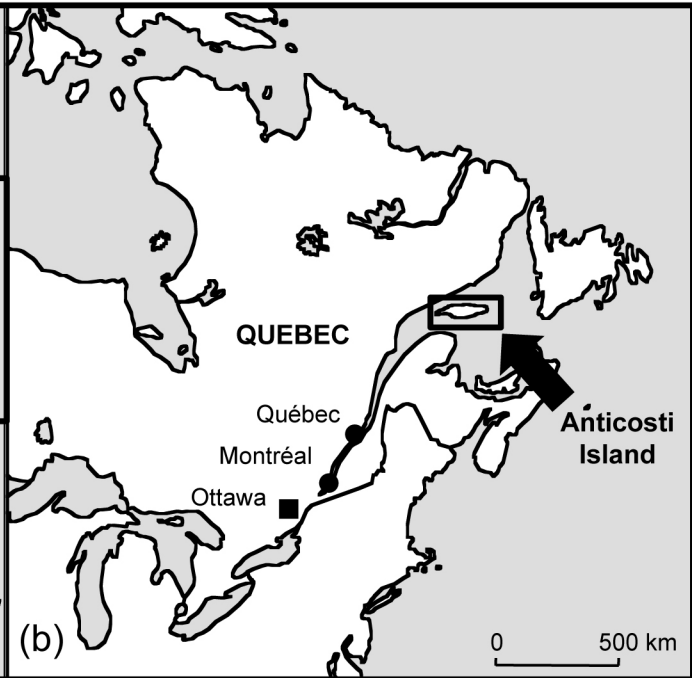
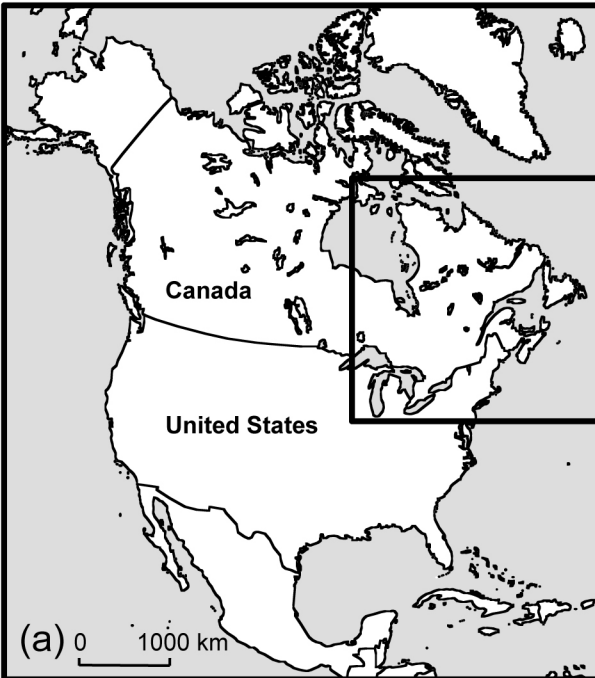
1820 **Fig. 21.** *Perikefalea racheboeufi* sp. nov. thecal plate patterns and homologies; (a) upper
1821 thecal surface; (b) lower thecal surface. Designations: (A) anomalocystid plate, (A₀?)
1822 possible median adoral, (A₁) right adoral, (A'₁) left adoral, (C₁, C'₁) supracentrals, (D)
1823 digital, (G) glossal, (M₁–M₃, M₆) right marginals, (M₇) posterior median marginal, (M'₁–
1824 M'₄, M'₆) left marginals, (Mc) cothurnocystid marginal, (Z) zygale plate.


1825

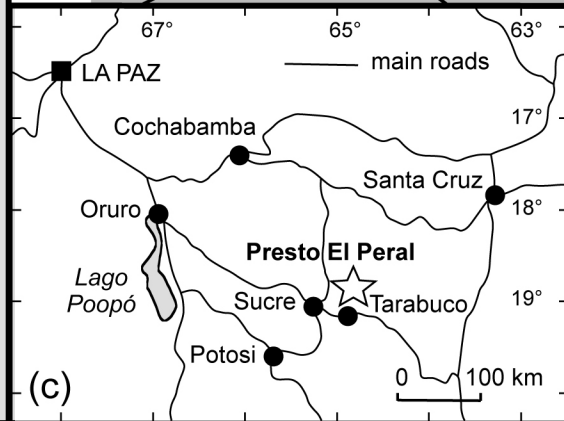
1826 **Fig. 22.** *Perikefalea? cybeleae* sp. nov., holotype GSC 126914, almost complete lower thecal
1827 surface (spines missing), with partially preserved proximal aulacophore and small, distal
1828 portion of recurved feeding arm; (a) interpretative camera-lucida drawing; (b)
1829 photographic view. 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 
		Aeronian	Richardson	
			Menier	East Point
				Goéland
			Gun River	Macgilvray
				Sandtop
				Innommée
			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

arm

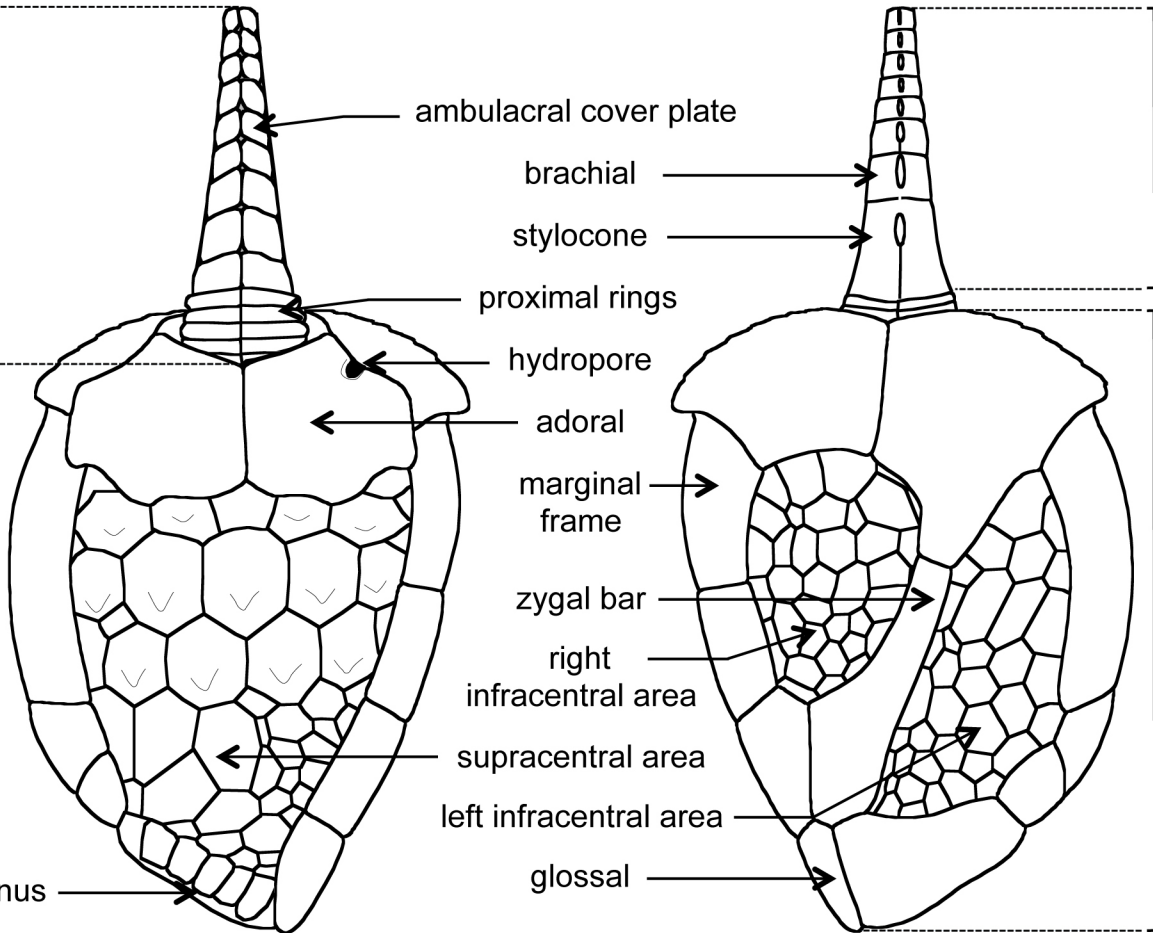
theca

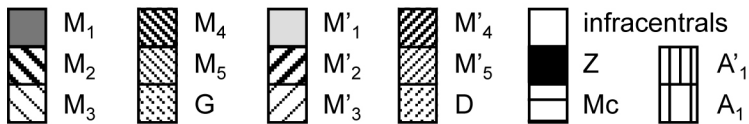
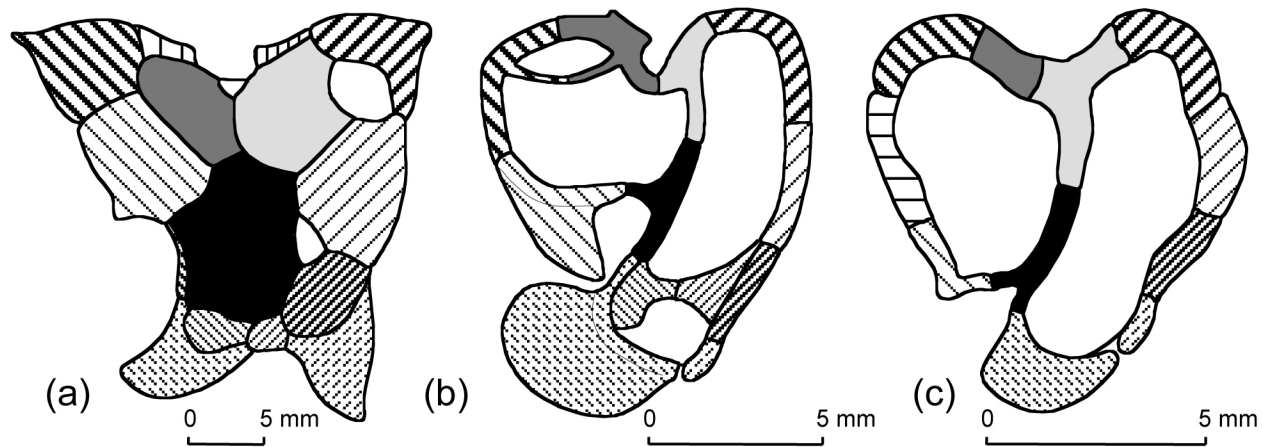
anus

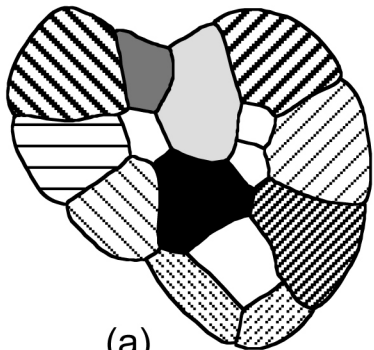
0 1 mm

(a)

(b)

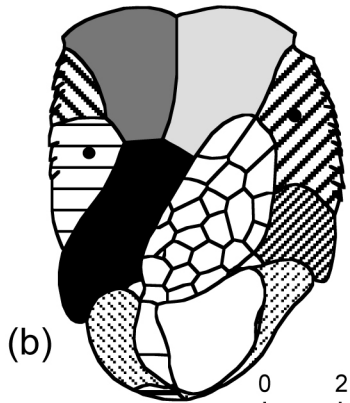






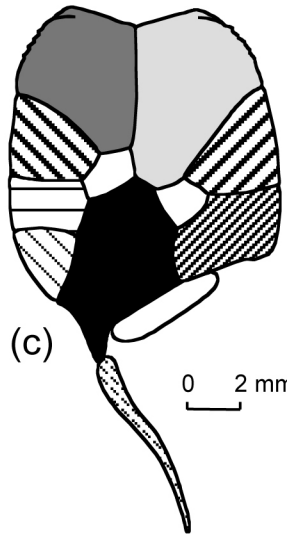
(a)

0 2 mm



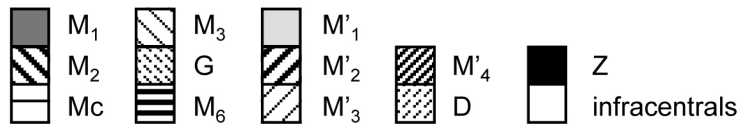
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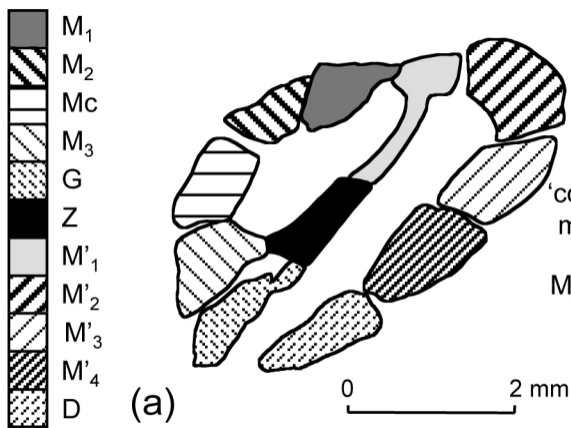
0 2 mm



(c)

0 2 mm





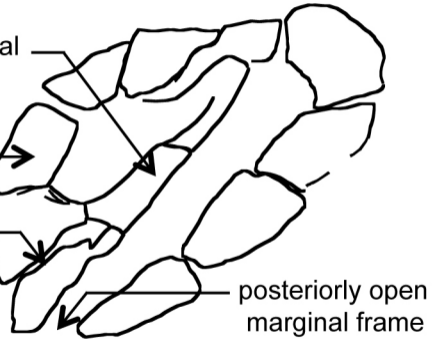
(a)

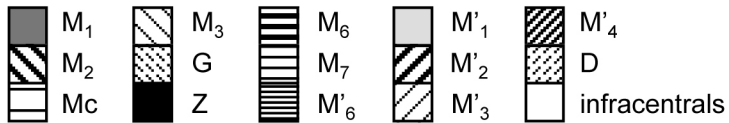
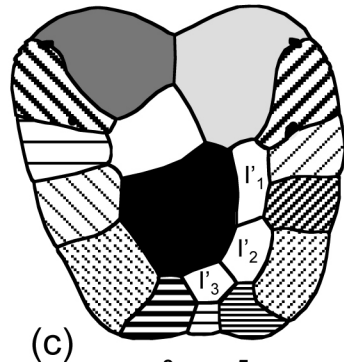
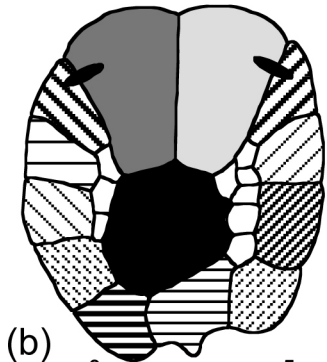
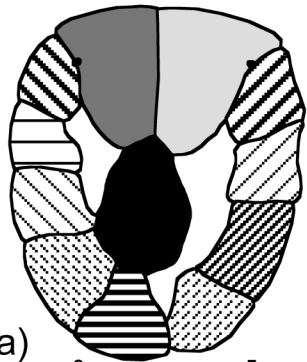
zygal in central
position

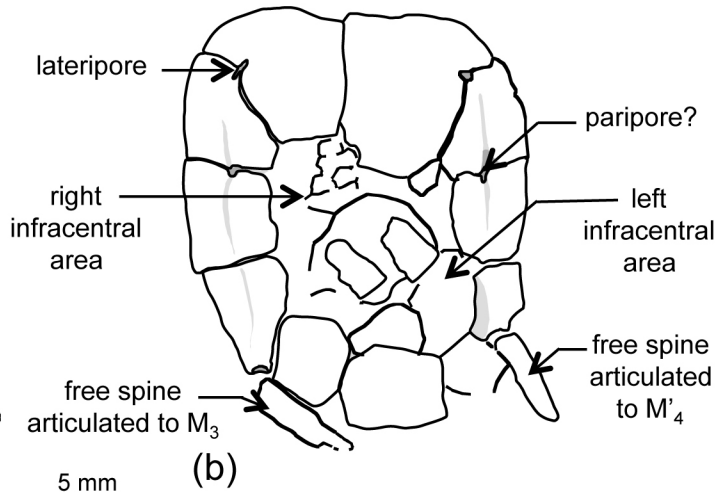
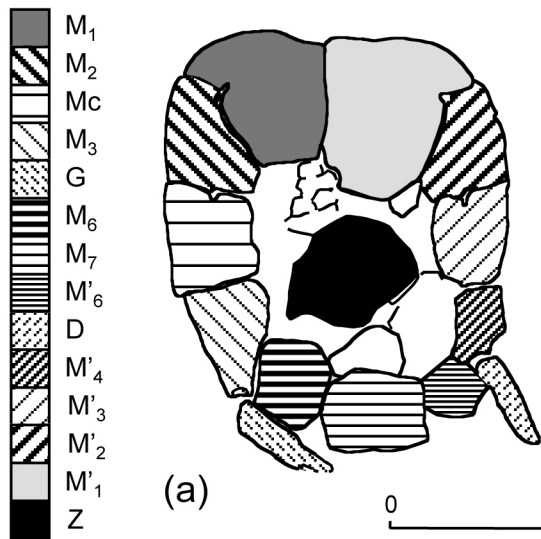
'cothurnocystid'
marginal (Mc)

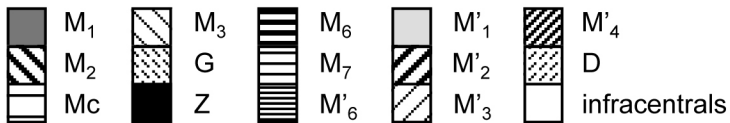
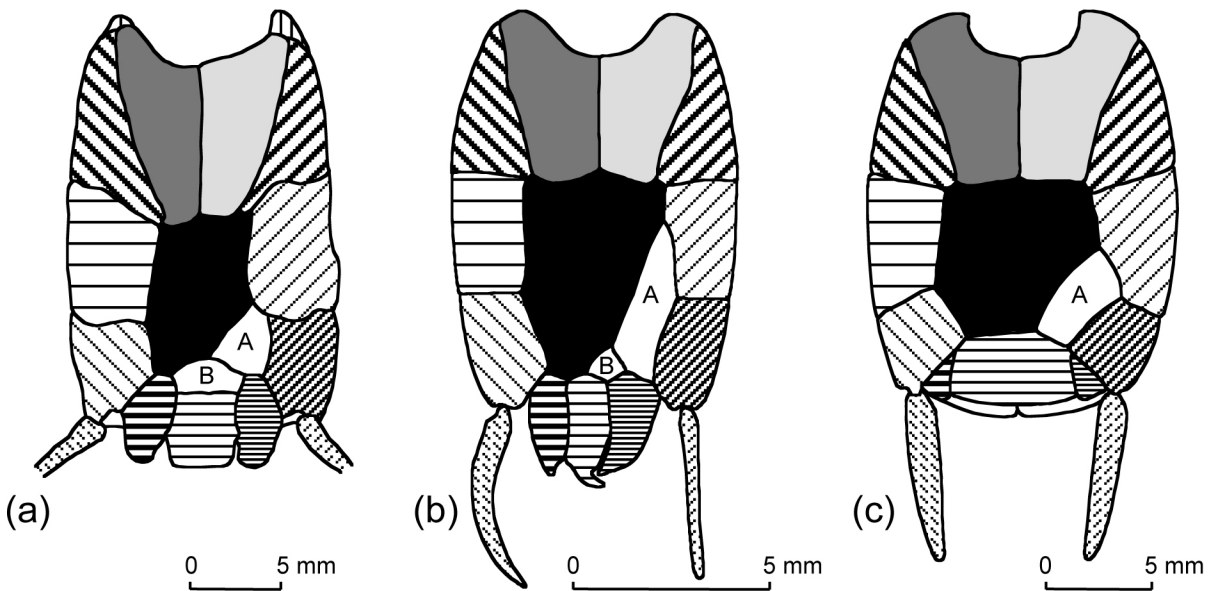
M₃-G contact

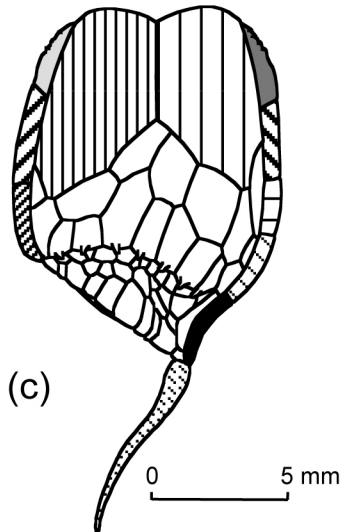
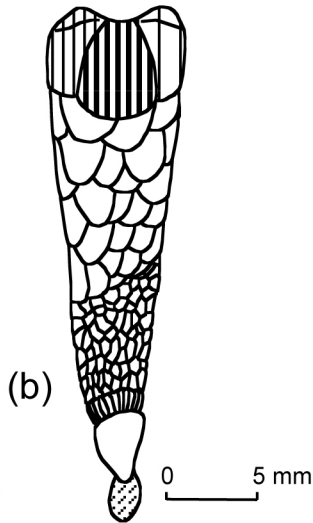
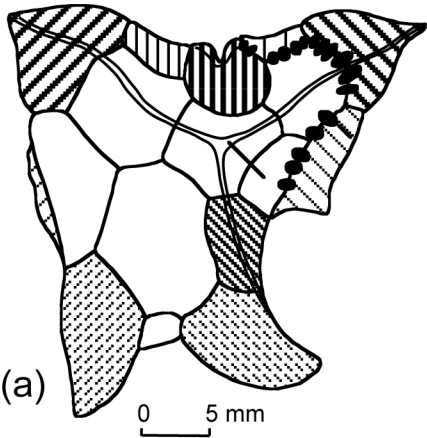
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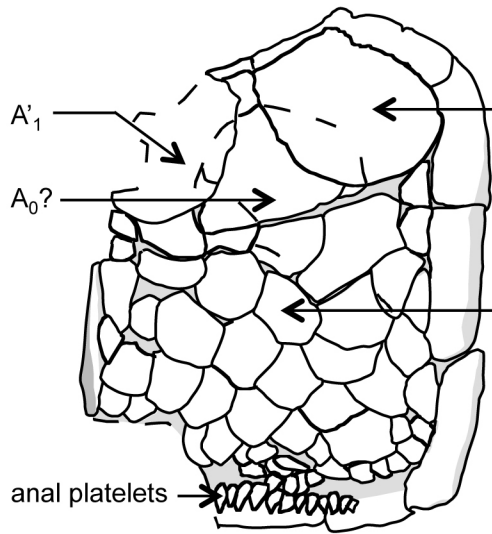






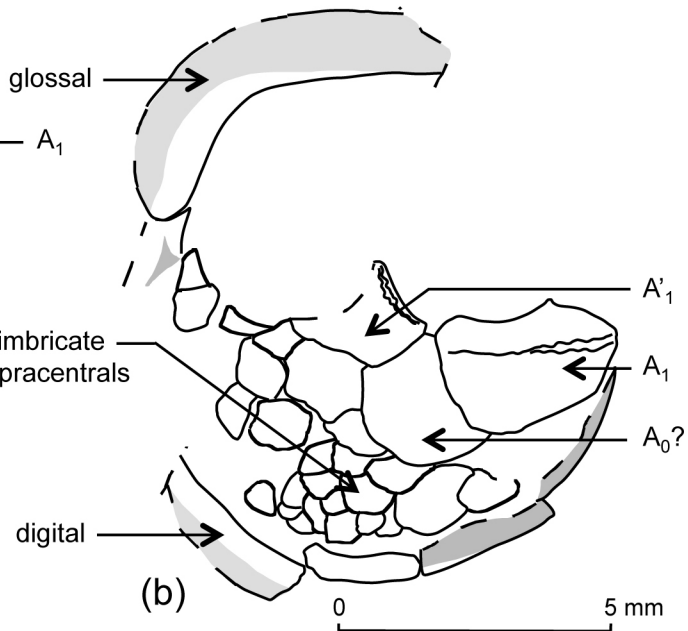






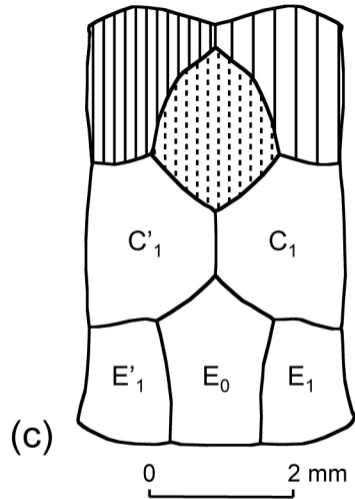
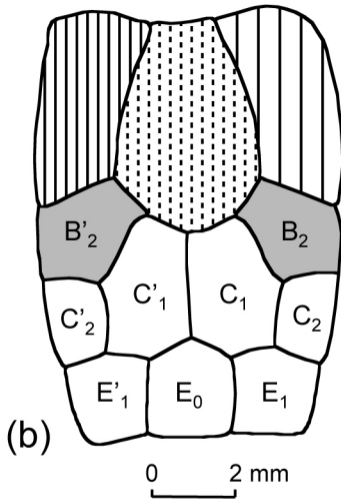
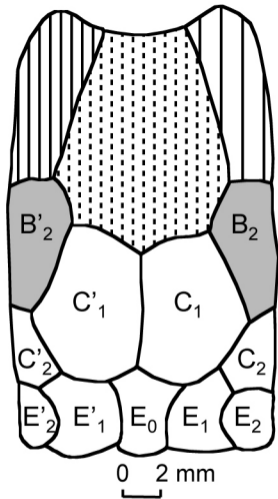
(a)

0 5 mm

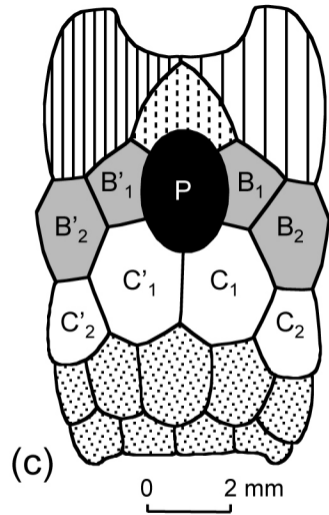
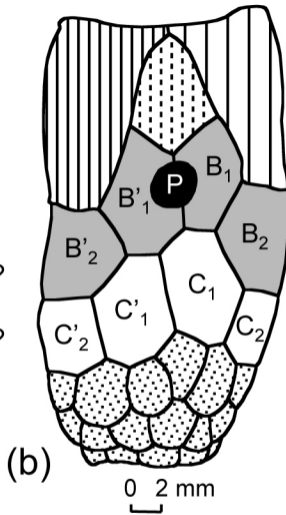
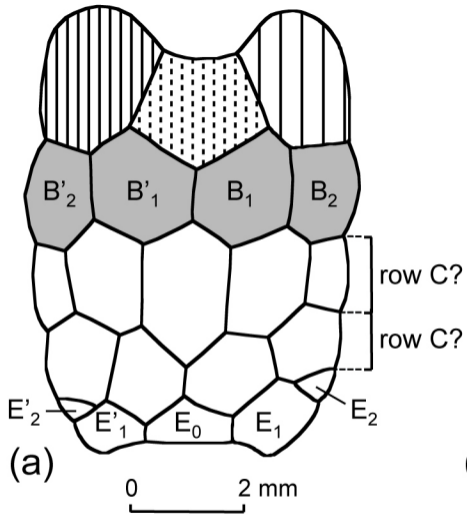


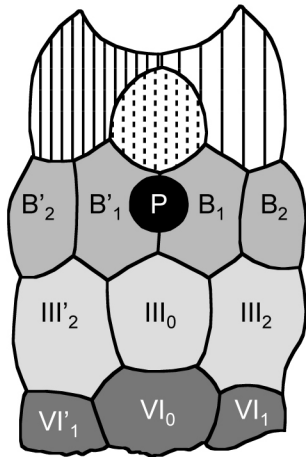
(b)

0 5 mm

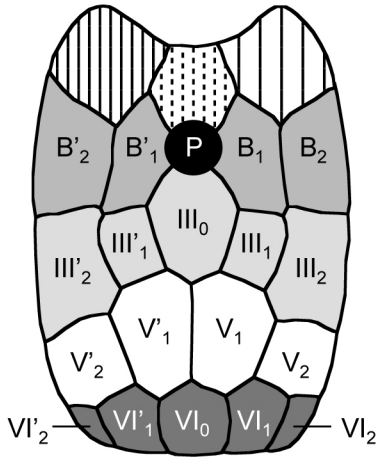


 A₁
 A₀?
  A₁
 row B
  posterior rows (C and E)

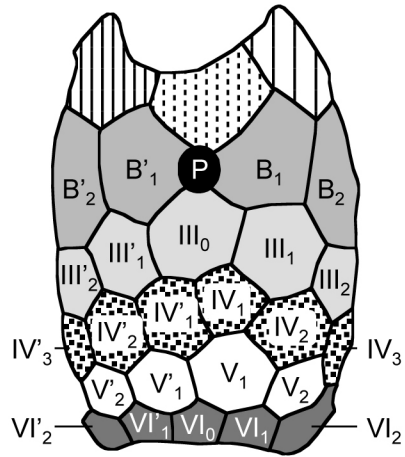




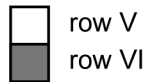
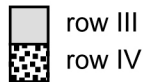
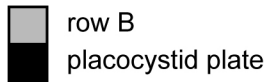
(a) 0 5 mm

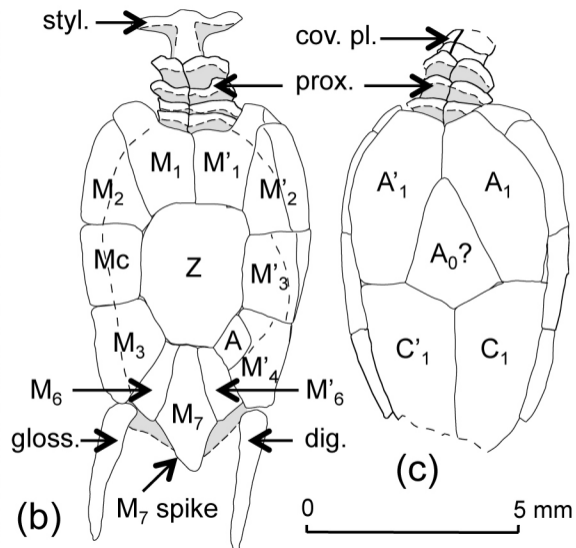


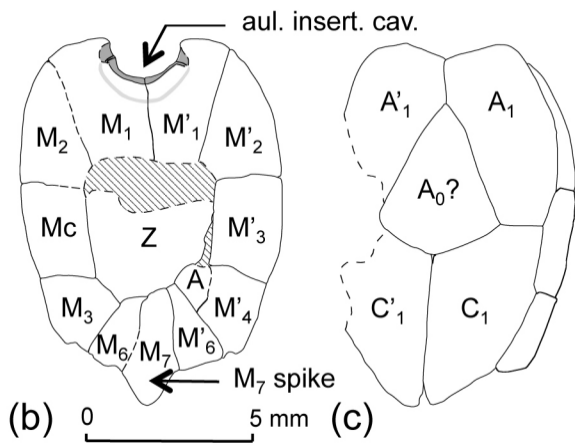
(b) 0 5 mm

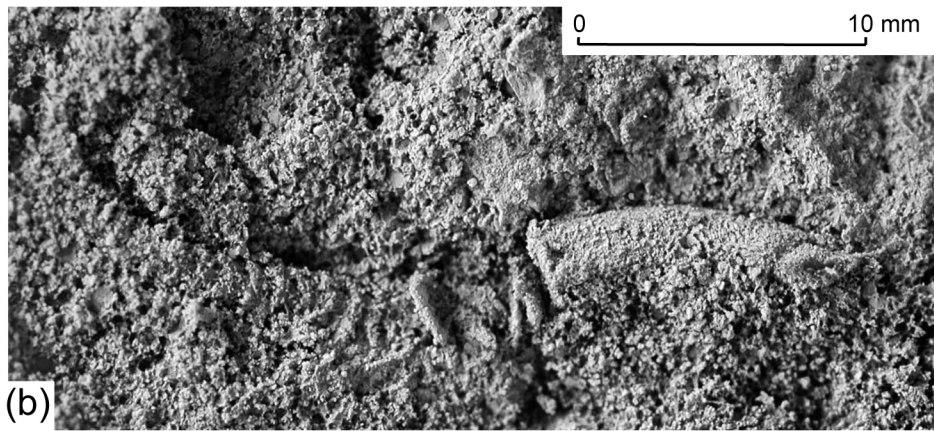
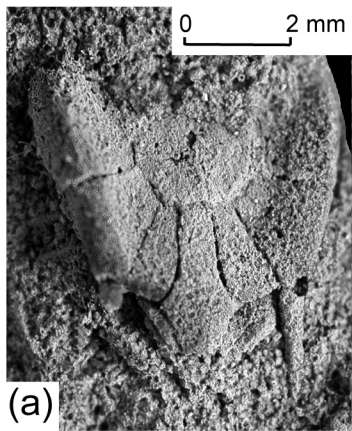


(c) 0 5 mm

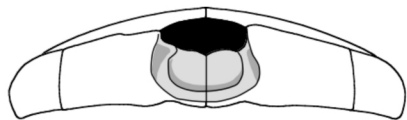








(a)

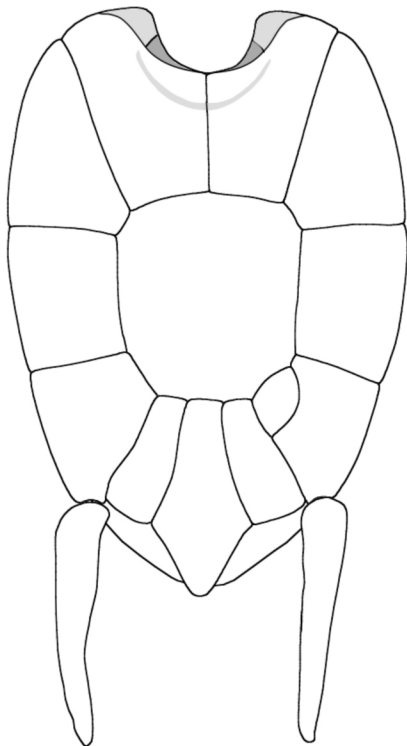


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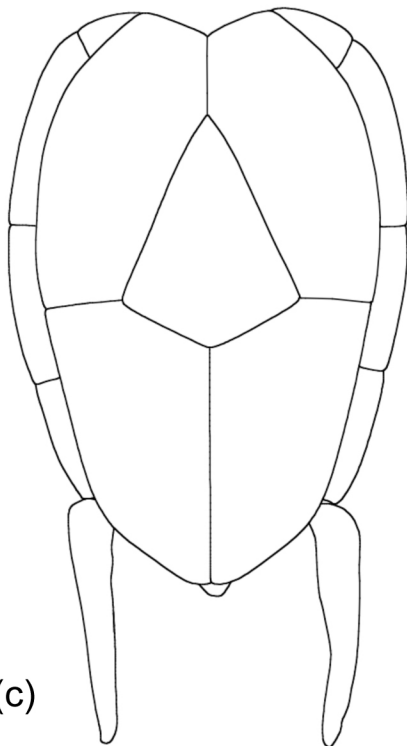
5 mm

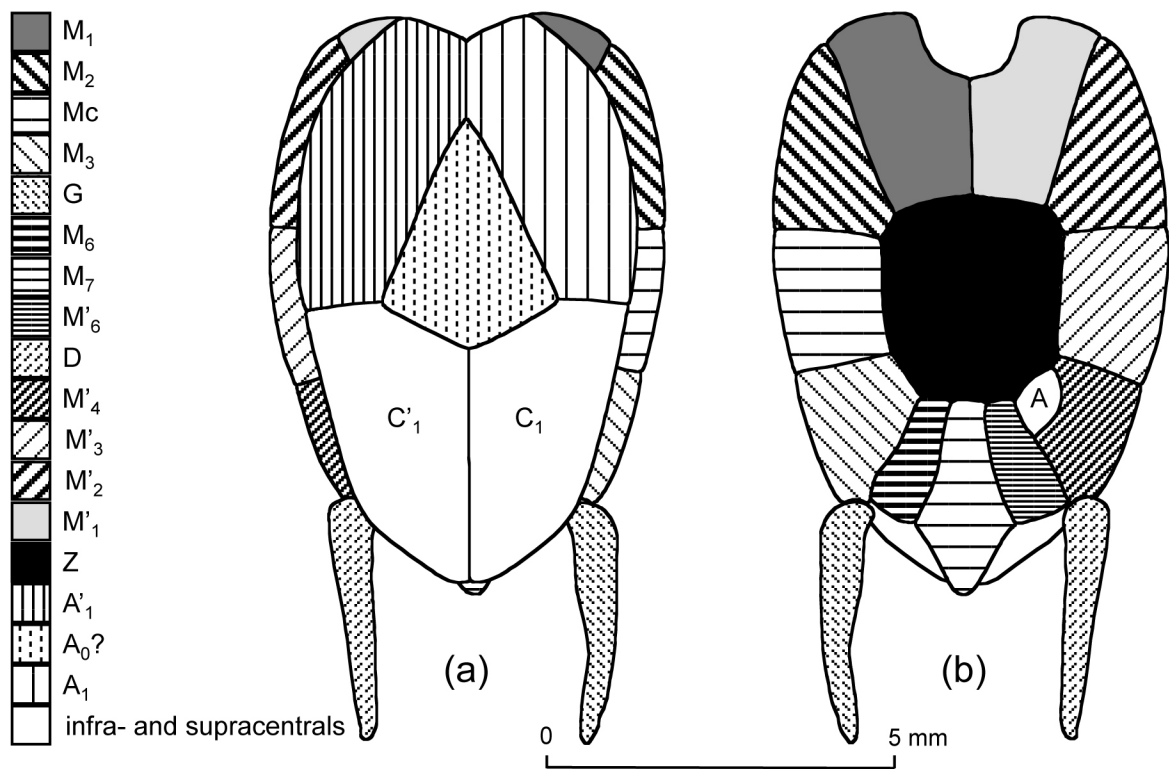


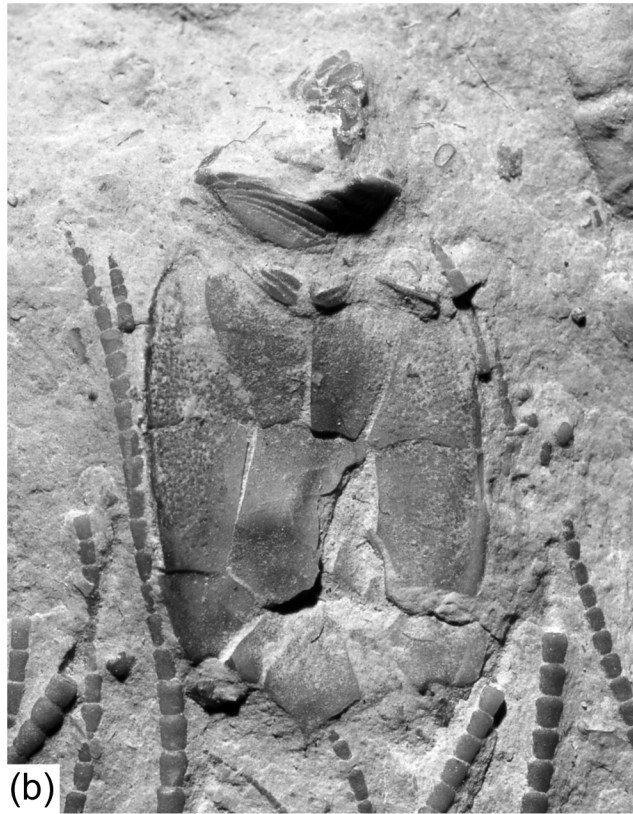
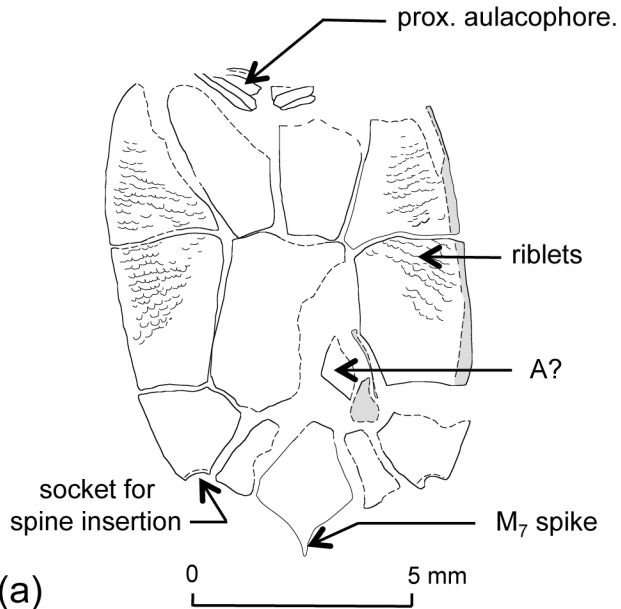
(b)

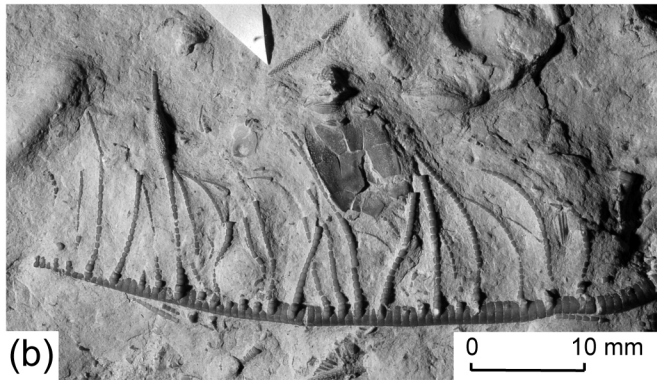
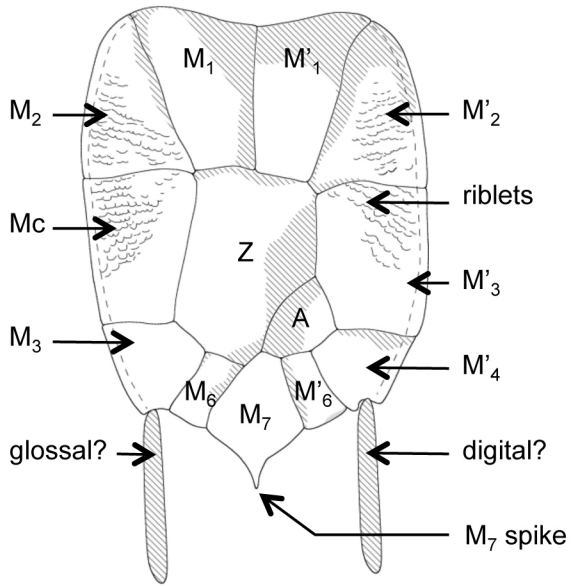


(c)



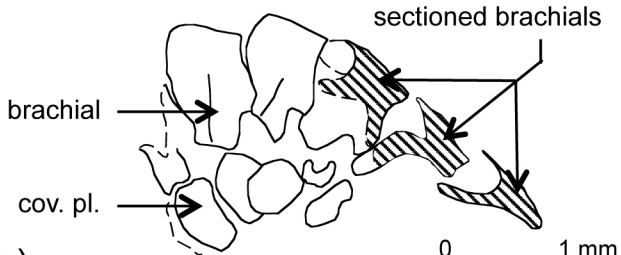






(b)

(a)



(c)