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2 **Late Ordovician solutan echinoderms from the western Tafilalt, Morocco**

3  
4 MARTINA NOHEJLOVÁ<sup>1,2\*</sup> & BERTRAND LEFEBVRE<sup>1</sup>

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6 <sup>1</sup>*Univ Lyon, Univ Lyon 1, ENSL, CNRS, LGL-TPE, F-69622, Villeurbanne, France*

7 <sup>2</sup>*Czech Geological Survey, Klárov 3, 11821, Praha 1, Czech Republic*

8  
9 Orcid identifier: <https://orcid.org/0000-0001-7972-8165>

10  
11 \* *Correspondence: martina.nohejlova@geology.cz*

12  
13 **Abstract:** In the western Tafilalt area, eastern Anti-Atlas (Morocco), solutan echinoderms are  
14 a major faunal element of most echinoderm Lagerstätten occurring within the Lower Ktaoua  
15 Formation (late Sandbian–early Katian). For the first time, members of the class Soluta are  
16 formally described from Morocco and Africa. All solutans from the Lower Ktaoua Formation  
17 are identified as *Dendrocystites aff. sedgwicki*. Three size-related morphotypes, probably  
18 corresponding to successive growth stages ('juvenile', 'adult' and 'gerontic'), could be  
19 distinguished within the abundant and well-preserved material from Morocco. The occurrence  
20 of the genus *Dendrocystites* in the western Tafilalt confirms the strong faunal affinities  
21 between Morocco and other regions of the Mediterranean Province (Czech Republic and  
22 Spain) in Late Ordovician times. In high palaeolatitude (peri-)Gondwanan areas,  
23 *Dendrocystites* was a gregarious solutan living in shallow, siliciclastic settings at or above  
24 storm-wave base.

25  
26 **Keywords:** Echinoderm Lagerstätte, Soluta, Upper Ordovician, Morocco

28 In the last 15 years, several spectacular echinoderm Lagerstätten (also informally designated  
29 'starfish beds', even when starfish are absent) were discovered and exploited for commercial  
30 purposes in Upper Ordovician sandstones of the eastern Anti-Atlas (western Tafilalt),  
31 Morocco (Lefebvre *et al.* 2010; Lebrun 2018; Gutiérrez-Marco *et al.* 2020; Gutiérrez-Marco  
32 & García-Bellido this volume). These localities have yielded abundant, fully articulated  
33 echinoderms with their finest morphological details preserved, such as complete blastozoan  
34 feeding appendages (brachioles) or delicate pinnules on crinoid arms (see e.g. Lefebvre *et al.*  
35 2007, 2008, this volume; Hunter *et al.* 2010; Nardin & Régnault 2015; Botting this volume;  
36 Zamora *et al.* this volume). The discovery of these numerous starfish beds dramatically  
37 altered previous estimates of echinoderm diversity and palaeocology in the Upper Ordovician  
38 of the western Tafilalt area. All previous studies on Late Ordovician echinoderms from the  
39 eastern Anti-Atlas had described moderately diverse assemblages dominated by diploporite  
40 blastozoans (mostly aristocystitids and sphaeronitids) and associated with moderately deep  
41 (shelf) environmental conditions (Chauvel 1966, 1977, 1978; Termier & Termier 1970;  
42 Lefebvre & Fatka 2003; Álvaro *et al.* 2007). The Tafilalt starfish beds yielded markedly  
43 different associations dominated by other echinoderm groups (e.g. asterozoans, eocrinoids,  
44 solutans, stylophorans) and corresponding to the sudden burial of *in-situ* or, more often,  
45 downslope transported dense populations of echinoderms originally living in shallow settings  
46 (Lefebvre *et al.* 2007, 2008, 2010, this volume; Nardin 2007; Régnault 2007; Hunter *et al.*  
47 2010; Nardin & Régnault 2015; Botting this volume; Zamora *et al.* this volume). Although  
48 echinoderms usually occur as mass occurrences with little or no associated fauna, other levels  
49 within the Upper Ordovician of the western Tafilalt have also provided abundant and diverse  
50 remains of many other invertebrates, such as brachiopods (Havlíček 1971; Colmenar *et al.*  
51 this volume; Villas & Colmenar this volume), bryozoans (Destombes *et al.* 1971; Ernst this  
52 volume), conulariids (Van Iten *et al.* this volume), molluscs (Babin & Destombes 1990;

53 Horný 1997; Ebbestad *et al.* this volume), and trilobites (Destombes 1972; Gutiérrez-Marco *et*  
54 *al. a* this volume). Some localities have also yielded exquisitely preserved lightly sclerotized  
55 arthropods (e.g. cheloniellids; Van Roy 2006), paropsonemid eldonioids (Van Roy 2006;  
56 MacGabhann 2012), hydroids (Gutiérrez-Marco *et al. b* this volume), machaeridian annelids  
57 (Vinther *et al.* 2008) and palaeoscolecid worms (Gutiérrez-Marco & García-Bellido 2015).

58 This study focuses on the locally abundant, well-preserved material of solutans occurring  
59 in the Lower Ktaoua Formation (Sandbian–early Katian) of the Tafilalt area. Solutans are a  
60 small clade of non-radiate blastozoan echinoderms ranging from the middle Cambrian  
61 (Drumian) to the Lower Devonian (Emsian) (Dehm 1934; Caster 1968; Ubaghs & Robison  
62 1988; Daley 1996; Parsley 1997; Domínguez *et al.* 2002; Rahman & Lintz 2012; Noailles *et*  
63 *al.* 2014). The class probably originated in Laurentia (Drumian–Guzhangian; Ubaghs &  
64 Robison 1985, 1988; Daley 1995, 1996; Lefebvre & Lerosey-Aubril 2018) before spreading  
65 to peri-Gondwanan areas in the Furongian (South China; Zamora *et al.* 2013*b*; Zhu *et al.*  
66 2016) and the Lower Ordovician (France, Morocco; Thoräl 1935; Ubaghs 1969; Lefebvre *et*  
67 *al.* 2016). In Middle Ordovician times, the fossil record of solutans is restricted to peri-  
68 Gondwanan areas (e.g. Bohemia; Prokop & Petr 2003; Lefebvre *et al.* 2012) and Avalonia  
69 (Lefebvre *et al.* 2012). Solutan diversity and palaeobiogeographic distribution both peaked in  
70 Late Ordovician times with abundant remains described in Baltica (Rozhnov & Jefferies  
71 1996), several peri-Gondwanan areas (Barrande 1887; Gil Cid *et al.* 1996; Lefebvre *et al.*  
72 2007, 2010; Hunter *et al.* 2010; Noailles *et al.* 2014), and mostly in Laurentia, where this  
73 class underwent a major diversification (Bather 1913; Parsley & Caster 1965; Parsley 1972;  
74 Kolata 1973; Kolata *et al.* 1977; Jefferies 1990; Daley 1992). No solutan taxa have been  
75 described so far from Silurian strata, suggesting that this class was very likely severely  
76 impacted by the Hirnantian mass-extinction (Domínguez *et al.* 2002). However, yet  
77 undescribed solutan remains have been found in the Silurian - Wenlock of Wales (B.

78 Lefebvre, pers. obs., 2008), and several occurrences of this class were described in the Lower  
79 Devonian of Australia (Gill & Caster 1960), Germany (Dehm 1934; Rahman & Lintz 2012)  
80 and North America (Parsley & Sumrall 2007). This macroevolutionary pattern with two  
81 distinct peaks in diversity in the Upper Ordovician and the Lower Devonian separated by a  
82 Silurian gap is not unique to solutans, but is also observed in other groups of flattened,  
83 asymmetrical and unattached echinoderms (e.g. pleurocystitid rhombiferans, mitrate  
84 stylophorans; see e.g. Lefebvre 2007a; Parsley & Sumrall 2007).

85 Although solutans have been regularly mentioned as the dominant faunal element of  
86 several Moroccan echinoderm dense beds in the Lower Ordovician of the Central Anti-Atlas  
87 (see e.g. Lefebvre & Fatka 2003; Lefebvre 2007a; Lefebvre *et al.* 2016) and the Upper  
88 Ordovician of the western Tafilalt (see e.g. Lefebvre *et al.* 2007, 2008; Hunter *et al.* 2010),  
89 their taxonomy and palaeoecology have never been investigated so far. Consequently, this  
90 preliminary study aims at partly filling this gap in knowledge, by providing the first  
91 taxonomic description of Late Ordovician solutans from Morocco and from Africa, as well as  
92 the first detailed discussion of their palaeoecology, taphonomy and palaeobiogeographic  
93 affinities. Contrary to the Fezouata Shale (Tremadocian–Floian), which has yielded a  
94 relatively diverse solutan remains belonging to at least three distinct genera (*Castericystis?*,  
95 *Minervaecystis* and *Plasiacystis*; Lefebvre *et al.* 2016), all solutans found so far in the Lower  
96 Ktaoua Formation belong to one single genus (*Dendrocystites*).

97

## 98 **Geological setting and stratigraphy**

99

100 The study material was collected from eight distinct localities, all situated within the western  
101 Tafilalt area, eastern Anti-Atlas (Morocco). Seven of these sites occur within a narrow and  
102 elongate area (about 3 km wide and 25 km long), orientated about N10 road, extending from

103 the western flank of Jbel Tijarfaïouine (to the North) to Isthlou and Jbel Signit (to the South),  
104 on both sides of the N12 road between Msissi (about 25 km to the West) and Rissani (about  
105 30 km to the East) (see Fig. 1). The other locality (Jbel Taklimt) is situated slightly eastwards,  
106 about 4 km south of the N12 road and 16 km W of Rissani (Fig. 1).

107 The stratigraphic position of each locality was difficult to identify precisely, due to the  
108 rarity or even lack of associated faunal elements useful for stratigraphic purposes (e.g.  
109 brachiopods, graptolites, trilobites) within echinoderm dense beds, and also because of the  
110 widespread occurrence of homogeneous, sandstone-dominated lithologies throughout most of  
111 the Upper Ordovician succession in this area (Destombes 2006*a, b*; Álvaro *et al.* this volume).  
112 In spite of these difficulties and pending a detailed sedimentological and stratigraphic re-  
113 evaluation of the Upper Ordovician in this area is performed, the stratigraphic positions of  
114 solutan localities could be evaluated based on field observations made with J. Destombes,  
115 while visiting most of these sites (Oct. 2010), and also through the careful report of their GPS  
116 coordinates on the two corresponding 1:200.000 geological maps of Tafilalt-Taouz (Service  
117 géologique du Maroc 1986) and Todrha-Maïder (Service géologique du Maroc 1988). In the  
118 western Tafilalt area, solutan occurrences can be assigned to four successive stratigraphic  
119 intervals, all situated within the Lower Ktaoua Formation (Fig. 2).

120 The Piste de Jorf locality (ECR-F3; Fig. 1b) corresponds to a long and deep trench quarried  
121 within sandstones identified as 'Or5a' (lower part of the Lower Ktaoua Formation; Fig. 2) on  
122 the 1:200.000 geological map (Todrha-Maïder; Service géologique du Maroc 1988), along the  
123 banks of a dried oued. This site was exploited by local fossil dealers to extract large slabs of  
124 sandstones covered with particularly abundant, fully articulated specimens of ophiuroids and  
125 paranacystid mitrates (Lefebvre *et al.* 2007, 2010; Hunter *et al.* 2010). Other faunal elements  
126 are particularly rare and comprise eocrinoids (*Cardiocystites*; Nardin 2007) and the oldest

127 solutans documented so far in the Upper Ordovician of the eastern Anti-Atlas (Lefebvre *et al.*  
128 2007, 2010; Noailles-Gobry 2008; Hunter *et al.* 2010; Lebrun 2018).

129 Jbel Taklimt (ECR-F9; Fig. 1b) is a classical section for the Upper Ordovician succession  
130 in the western Tafilalt area (see Destombes 2006b). Solutans were sampled on sandstone slabs  
131 in the middle part of the Lower Ktaoua Formation (Fig. 2), around the boundary between  
132 units mapped as 'Or5a' and 'Or5b' on the 1:200.000 geological map (Tafilalt-Taouz; Service  
133 géologique du Maroc 1986). In ECR-F9, fully articulated solutans are locally abundant,  
134 densely packed and current-oriented. Other faunal elements include brachiopods, ophiuroids,  
135 trilobites, as well as large conulariids encrusted by numerous edrioasteroids. About 20 km  
136 SW of Jbel Taklimt, two other localities (ECR-F12 and ECR-F13; Fig. 1b), both located on  
137 the western flank of Jbel Signit, have yielded abundant and well-preserved assemblages from  
138 the same stratigraphic interval as ECR-F9 (middle part of the Lower Ktaoua Formation; Fig.  
139 2). In both ECR-F12 and ECR-F13, solutans are a minor component of a diverse invertebrate  
140 fauna comprising asterozoans (asteroids and ophiuroids), brachiopods, bryozoans, crinoids,  
141 glyptocystitids (*Homocystites*), fully articulated machaeridian annelids (*Plumulites*), mitrate  
142 stylophorans (kirkocystids, mitrocystitids), and trilobites.

143 In Tizi n'Mourghi ('the cricket's pass', ECR-F1; Fig. 1b), two main fossiliferous intervals  
144 have been intensively quarried by local fossil traders to extract large slabs of sandstones with  
145 ophiuroids and/or solutans (Lebrun 2018). This hill is the only locality in the western Tafilalt  
146 area, which yielded low-diversity, solutan-dominated assemblages. These solutan dense beds  
147 occur in the upper part of the section, in sandstones mapped as 'Or5b' (upper part of the Lower  
148 Ktaoua Formation; Fig. 2) on 1:200.000 geological maps (Service géologique du Maroc 1986,  
149 1988). Other faunal elements are particularly rare and consist almost exclusively of other  
150 echinoderms: crinoids, diploporites (*Asterocystis*), glyptocystitids (*Homocystites*), ophiuroids,  
151 and stylophorans (mitrocystitid mitrates) (Lefebvre *et al.* 2007, 2010; Hunter *et al.* 2010;

152 Zamora *et al.* this volume). In the upper part of the Tizi n'Mourghi section, solutans are fully  
153 articulated, more or less densely packed and generally current-oriented (Noailles-Gobry  
154 2008). Lower in the section, solutans are also present, but they are isolated and represent  
155 minor elements of an ophiuroid-dominated assemblage. About 5 km SW of ECR-F1, rare  
156 solutan specimens were collected near the dried river Oued El Caïd Rami (ECR-F7; Fig. 1b),  
157 in sandstones from the same stratigraphic interval (upper part of the Lower Ktaoua  
158 Formation). This locality yielded a moderately diverse assemblage comprising glyptocystitid  
159 rhombiferans (*Homocystites*), ophiuroids and trilobites. Rare, fully articulated solutans were  
160 also found at locality ECR-F19 (Jbel Signit; Fig. 1b), within sandstones mapped as 'Or5b'  
161 (upper part of the Lower Ktaoua Formation; Fig. 2) on the 1:200.000 geological map of  
162 Todrha-Maïder (Service géologique du Maroc 1988). These levels provided a well-preserved,  
163 relatively diverse invertebrate fauna comprising asterozoans, crinoids, edrioasteroids, and  
164 machaeridians (*Plumulites*).

165 Few, well-preserved specimens of the youngest known Moroccan solutans were found at  
166 Isthlou (ECR-F6; Fig. 1b), in the uppermost levels of the Lower Ktaoua Formation (Fig. 2),  
167 i.e. immediately below the contact with the overlying Upper Tiouririne Formation (Or5b–  
168 Or5c boundary on the 1:200.000 Todrha-Maïder geological map; Service géologique du  
169 Maroc 1988). No solutan remains were found in the particularly fossiliferous overlying levels  
170 of the Upper Tiouririne Formation, in which abundant and diverse echinoderms (asteroids,  
171 crinoids, diploporites, edrioasteroids, ophiuroids, rhombiferans, mitrate stylophorans) occur  
172 along with brachiopods, bryozoans, conulariids (*Pseudoconularia*), and various trilobites (e.g.  
173 illaenids, trinucleids) (see e.g. Lebrun 2018; Botting this volume; Sumrall & Zamora this  
174 volume).

175

## 176 **Material and methods**



177

178 Over 100 individuals of *Dendrocystites* were collected from eight distinct localities (see  
179 above; Fig. 1). All of them are preserved as natural moulds in sandstones. Most specimens are  
180 complete and fully articulated, with their homoiostele and/or brachiole still attached to the  
181 theca (Figs 3–6). Specimens were casted with latex, so as to reveal their original, three-  
182 dimensional morphology. Latex casts were then whitened with ammonium chloride (NH<sub>4</sub>Cl)  
183 and photographed with a Canon EOS 70 D digital camera. Graphic work was done using the  
184 software Corel Draw X8 and GIMP 2.10.8. Classical morphological measurements (thecal  
185 height TH, brachiole length BL, and homoiostele length HL) were made with the software  
186 ImageJ on a selection of the thirty best preserved and most complete individuals.

187

188 *Institutional abbreviations.* Specimens used in this study are housed in the following public  
189 scientific collections: Université Cadi-Ayyad, Marrakesh, Morocco (AA); Muséum d'Histoire  
190 Naturelle, Marseille, France (MHNM); Muséum d'Histoire Naturelle de Nantes, France  
191 (MHNN); Muséum d'Histoire Naturelle, Toulouse, France (MHNT); Musée des Confluences,  
192 Lyon, France (ML); and Collections de Paléontologie, Université Lyon 1, Villeurbanne,  
193 France (UCBL.FSL).

194

## 195 **Systematic palaeontology**

196

197 Solutans are considered herein as a distinct class of blastozoan echinoderms characterized by  
198 the possession of a single free ambulacral structure (brachiole) and a longitudinally  
199 differentiated stem-like appendage (homoiostele) (David *et al.* 2000; Sprinkle & Guensburg  
200 2004; Nardin *et al.* 2009; Lefebvre *et al.* 2013; Noailles *et al.* 2014; for alternative

201 interpretations see e.g. Jefferies 1990; Smith 2005). Solutan systematics and morphological  
202 terminology are following Noailles *et al.* (2014).

203

204                   Phylum **Echinodermata** Bruguière, 1791 (ex Klein, 1734)

205                               Subphylum **Blastozoa** Sprinkle, 1973

206                                       Class **Soluta** Jaekel, 1901

207   Order **Dendrocystitida** Noailles, Lefebvre & Kašička, 2014

208   Family **Dendrocystitidae** Bassler, 1938

209   Genus *Dendrocystites* Barrande, 1887

210 *Type species.* *Cystidea sedgwicki* Barrande, 1867 from the Upper Ordovician of the  
211 Barrandian area, Czech Republic.

212

213 *Remarks.* All Late Ordovician Moroccan solutans can be unambiguously assigned to the order  
214 Dendrocystitida, based on the narrow, elongate and cylindrical morphology of their dististele,  
215 which clearly departs from the morphology found in *Coleicarpus* (longitudinally  
216 undifferentiated holdfast) and syringocrinids (with a flattened and enlarged dististele). Within  
217 dendrocystitids, the Tafilalt material can be affiliated to the family Dendrocystitidae, and  
218 specifically to the genus *Dendrocystites*, based on its cordiform to pear-shaped thecal  
219 outlines, the presence of a large anal lobe containing a single 'sugar-loaf' skeletal element, and  
220 the absence of any antibrachial lobe.

221

222   *Dendrocystites* aff. *sedgwicki* Barrande, 1867

223   Figures 3–6

224

225 2007b *Dendrocystites* sp. – Lefebvre, p. 243, fig. 1.3

- 226 2007 *Dendrocystites* sp. – Lefebvre *et al.*, p. 130, table 2
- 227 2008 *Dendrocystites sedgwicki* (Barrande) – Noailles-Gobry, p. 15, fig. 8, pl. 1,3,4
- 228 2008 solute indet., gen. et sp. nov. – Noailles-Gobry, p. 17, pl. 2
- 229 2010 *Dendrocystites* sp. – Hunter *et al.*, p. 25, figs 4,5
- 230 2010 *Dendrocystites*-like solute – Hunter *et al.*, p. 25
- 231 2010 *Dendrocystites sedgwicki* (Barrande) – Lefebvre *et al.*, p. 9, fig. 7A
- 232 2010 solute indet. – Lefebvre *et al.*, p. 8, fig. 6A
- 233 2014 *Dendrocystites sedgwicki* (Barrande) – Noailles *et al.*, p. 466
- 234 2018 *Dendrocystites* sp. – Lebrun, p. 129, fig. C
- 235 2018 *Dendrocystites sedgwicki* (Barrande) – Lebrun, p. 129, fig. E

236

237 *Material.* The study material of *Dendrocystites* aff. *sedgwicki* comprises 87 registered  
 238 specimens (some of them preserving several individuals) collected in eight distinct localities,  
 239 all from the Lower Ktaoua Formation (late Sandbian–early Katian) of the western Tafilalt  
 240 area, eastern Anti-Atlas, Morocco (see above; Figs 1–2). Most specimens (67) are from ECR-  
 241 F1, Tizi n'Mourghi (Ka2, early Katian): AA.TNMa.OS.1 (coll. Lefebvre); AA.TNMb.OS.1–5,  
 242 10–12, 16–17, 19–21, 23, 30–31 (coll. Lefebvre); AA.TNMc.OS.1 (coll. Lefebvre);  
 243 UCBL.FSL.712888–712889 (coll. Reboul); MHNm.15406.1, 10, 15, 19, 33 (coll. Reboul);  
 244 MHNm.15690.111 (coll. Reboul); MHNT.PAL.2005.0.138, 150–151 (coll. Reboul);  
 245 ML20.269416, 269419–269432, 269434–259456 (coll. Reboul). Five specimens were  
 246 collected in ECR-F3, Piste de Jorf (Sa2, late Katian): AA.PDJ.OS.4 (coll. Lefebvre);  
 247 MHNm.15406.2, 13 (coll. Reboul); MHNN.P.045601, 045611 (coll. Reboul). Three  
 248 specimens are from ECR-F6, Isthlou (Ka2, early Katian): AA.IST.OS.13 (coll. Lefebvre);  
 249 UCBL.FSL.711732, 711739 (coll. Reboul). Two specimens were found in ECR-F7, Oued El  
 250 Caïd Rami (Ka2, early Katian): AA.OCR.OS.15–16 (coll. Lefebvre). One specimen on a slab

251 was collected in ECR-F9, Jbel Taklimt (Ka1, early Katian): AA.JTK.OS.1 (coll. Lefebvre).  
252 Six specimens are from ECR-F12, Tarafin Signit (Ka1, early Katian): UCBL.FSL.712080,  
253 712858 (coll. Reboul); UCBL.FSL.712911, 713028–29, 713053 (coll. Auvray). Two  
254 specimens were collected in ECR-F13, Tarafin (Ka1, early Katian): UCBL.FSL.712068 (coll.  
255 Reboul); UCBL.FSL.713037 (coll. Auvray). The last specimen was found in ECR-19,  
256 Kraouia (Ka2, early Katian): UCBL.FSL.712832 (coll. Reboul).

257

258 *Occurrence.* Lower Ktaoua Formation (late Sandbian–early Katian), Tafilalt area, eastern  
259 Anti-Atlas (Morocco) (see above; Fig. 2).

260

261 *Description.* Theca flattened, asymmetrical, generally cordiform (Fig. 5) or pear-shaped, with  
262 well-defined pre-anal lobe (see Fig. 6), rarely with more rounded outlines and no distinct pre-  
263 anal lobe (e.g. MHNN.P.045601; see Fig. 4a). Theca made of numerous polygonal plates  
264 (around 50 in smallest individuals, over 100 in large ones), forming tessellate, unorganized  
265 pavement displaying typical rosetting pattern, with large skeletal elements separated by  
266 smaller, intercalated ones (Fig. 5–6). Thecal plates smooth, without any ornamentation  
267 (knobs, ridges), even in largest observed specimens (Fig. 6). Thecal height (TH) ranging from  
268 10 mm in smallest individuals (Fig. 3) to almost 40 mm in largest one (MHNM.15406.1) with  
269 mean estimated value around 21 mm. Anal opening covered by single, large sugar-loaf plate  
270 (Fig. 5c). Hydropore at summit of small tubercle (e.g. ML20.269419), next to brachiole  
271 insertion. Gonopore not observed. Brachiole and homoiostele inserted sharply, at opposite  
272 ends of theca.

273 Single, distally tapering, uni- or biserial brachiole inserted in apical position. Brachiole  
274 length variable, ranging from 7.4 to 23.9 mm (estimated mean value: 11.8 mm), often longer

275 than thecal height in small individuals (Fig. 3a), shorter than TH, in larger specimens (Fig. 5c,  
276 6a, c, e).

277 Homoiostele, elongate, distally tapering, hollow, multimeric stem-like structure  
278 longitudinally differentiated into proxistele and dististele. Proxistele shorter and wider than  
279 dististele. Proxistele consisting of distinct, telescopic tetrameric rings in variable number,  
280 generally six to eight in medium-sized specimens (Fig. 5). In large individuals, proximal rings  
281 more numerous, with abundant, small scale-like integumentary platelets intercalated in  
282 between them (Fig. 6). Dististele made of two longitudinal rows (upper and lower series) of  
283 quadrangular plates (Fig. 4–6). No complete homoiostele preserved (distal tips always  
284 missing), but HL consistently longer than TH, and varying from 10 to almost 100 mm (mean  
285 estimated value for HL: 36.4 mm). No attachment structure or distal hook observed in  
286 available material.

287

288 *Ontogeny*. Three main size-related morphotypes can be identified within the specimens of  
289 Moroccan *Dendrocystites*, based on differences in proxistele organization and in thecal  
290 height, plating and outlines. As all three morphotypes occur together at the same localities  
291 (when sample size is large enough) and can be observed throughout the succession from the  
292 stratigraphically lowest (e.g. ECR-F3) to the stratigraphically highest occurrences (e.g. ECR-  
293 F6) in the Lower Ktaoua Formation, it is very likely that they correspond to successive  
294 ontogenetic stages of one single species. Ontogenetic development is a continual process  
295 without strict boundaries between the different, successive growth stages. However, terms  
296 such as 'juvenile', 'adult', and 'gerontic' have been widely used in the literature to informally  
297 describe size-related morphotypes (small, medium-sized, and large, respectively) observed in  
298 various blastozoans (e.g. eocrinoids, rhombiferans) (see e.g. Parsley 2009, 2012; Zamora *et*  
299 *al.* 2013a, this volume; Nohejlová & Fatka 2016).

300 The 'juvenile morphotype' (Fig. 4) can be observed in two individuals from ECR-F1 and  
301 two others from ECR-F3, all characterized by the particularly small size of their theca (TH  $\approx$   
302 10 mm) compared to other specimens of Moroccan *Dendrocystites*. These four 'juvenile'  
303 individuals are lacking a well-developed pre-anal lobe. Consequently, their thecal outlines are  
304 regularly convex, almost rounded (MHNN.P.045601; Fig. 4a) to cordiform (Fig. 4b, c). Their  
305 thecal plates are few in number (around 50), smooth and all more or less of the same size.  
306 Their proxistele consists of few, well-organized tetramerous rings with no intercalated  
307 platelets. These four Moroccan individuals are morphologically very similar to small-sized,  
308 juvenile specimens of *Dendrocystites barrandei* Bather, 1913 from the Barrandian area of the  
309 Czech Republic (see Noailles *et al.* 2014, fig. 9B).

310 The medium-sized 'adult morphotype' (Fig. 5) is more widely distributed (about 40 percent  
311 of study material) within most Moroccan assemblages (e.g. ECR-F1, ECR-F6, ECR-F7, ECR-  
312 F9, ECR-F12). Specimens are characterized by a relatively large cordiform theca (10 mm <  
313 TH < 20 mm) made of numerous, smooth skeletal elements (around 100) of unequal sizes.  
314 Their proxistele is made of several rings with few intercalated platelets. These Moroccan  
315 individuals of *Dendrocystites* look very similar to the largest observed specimens of *D.*  
316 *barrandei* and also to medium-sized individuals of *D. sedgwicki* from the Barrandian area,  
317 Czech Republic (see Noailles *et al.* 2014, fig. 5).

318 The large 'gerontic morphotype' (Fig. 6) is the most frequently observed within the  
319 Moroccan material and it occurs from the base to the top of the Lower Ktaoua Formation (e.g.  
320 in ECR-F1, ECR-F3, ECR-F6, ECR-F7, ECR-F13). It corresponds to large-sized individuals  
321 (TH > 20 mm), with a pear-shaped theca and a prominent, well-distinct pre-anal lobe. Thecal  
322 plates are numerous, strongly unequal in size, and consistently smooth. The proxistele is made  
323 of unorganized rings, largely separated from each other by extremely abundant small, scale-  
324 like platelets (Fig. 6b). The Moroccan 'gerontic morphotype' shares several similarities with

325 the morphology of the largest specimens of *Dendrocystites sedgwicki* from the Barrandian  
326 area, Czech Republic (see Noailles *et al.* 2014, fig.6): comparable thecal pear-shaped outlines,  
327 largely developed pre-anal lobe, several generations of thecal plates, largely unorganized  
328 proxistele with abundant platelets. However, all 'gerontic' specimens from Morocco lack the  
329 typical thecal ornamentation occurring in large individuals of *D. sedgwicki*, consisting of fine  
330 ridges radiating from a central knob (see Barrande 1887; Bather 1913; Caster 1968; Noailles  
331 *et al.* 2014).

332

333 *Discussion.* The Moroccan material of *Dendrocystites* is morphologically close to the two  
334 Bohemian solutans *Dendrocystites barrandei* from the Letná Formation (late Sandbian) and *D.*  
335 *sedgwicki* from the Záhořany Formation (early Katian). The two Czech taxa differ in  
336 proxistele organization, as well as in thecal size, outlines, ornamentation and plating (see  
337 Bather 1913; Caster 1968; Noailles-Gobry 2008; Noailles *et al.* 2014). In the largest known  
338 specimens of *D. barrandei*, TH is about one third smaller than in the largest individuals of *D.*  
339 *sedgwicki* (Noailles *et al.* 2014). Thecal outlines are cordiform in *D. barrandei*, but more  
340 asymmetrical and pear-shaped in *D. sedgwicki*, because of the more prominent pre-anal lobe  
341 (Bather 1913; Caster 1968; Noailles *et al.* 2014). The theca of *D. barrandei* is made of few,  
342 relatively large skeletal elements, whereas *D. sedgwicki* has usually more thecal plates,  
343 including small 'secondary' platelets intercalated between larger 'primary' ones ('rosetting  
344 pattern'; Noailles *et al.* 2014). Moreover, all thecal plates are smooth in *D. barrandei*, whereas  
345 they typically display a central knob with radiating ridges in the largest individuals of *D.*  
346 *sedgwicki* (Bather 1913; Caster 1968; Noailles *et al.* 2014). Finally, the proxistele of *D.*  
347 *barrandei* consists of distinct, tetramerous rings with few integumentary platelets, whereas in  
348 large specimens of *D. sedgwicki*, rings are more discontinuous and separated by abundant  
349 small scale-like elements (Bather 1913; Caster 1968; Noailles *et al.* 2014). The two taxa have

350 also a distinct stratigraphic distribution, with *D. barrandei* occurring in older levels than *D.*  
351 *sedgwicki* (Bather 1913; Caster 1968). However, the *D. barrandei*-like morphology of small  
352 and medium-sized specimens of *D. sedgwicki* lead Noailles *et al.* (2014) to suggest that the  
353 characteristic features observed in the largest specimens of *D. sedgwicki* were possibly  
354 hyperadult characters and the result of heterochronic processes (hypermorphosis).

355 The situation is different in Morocco, where no obvious morphological transition can be  
356 observed between the successive assemblages of *Dendrocystites*, although their relatively  
357 long stratigraphic range (late Sandbian–early Katian; Fig. 2) is equivalent to that of both *D.*  
358 *barrandei* and *D. sedgwicki* in the Barrandian area. Contrary to the situation in Bohemia,  
359 where only two morphotypes ('juvenile' and 'adult') are originally occurring in the late  
360 Sandbian (Letná Formation; *D. barrandei*), and the third one ('gerontic') appears later in the  
361 early Katian (Záhořany Formation; *D. sedgwicki*), all three morphotypes are continuously  
362 present during the same stratigraphic interval in Morocco. Although small and medium-sized  
363 solutans from the Tafilalt area are morphologically very similar to *D. barrandei*, Moroccan  
364 *Dendrocystites* cannot be assigned to that species, because of the existence of a large-sized  
365 'gerontic' morphotype, with a lobate, pear-shaped theca and an unorganized proxistele.  
366 Similarly, in spite of numerous morphological similarities with *D. sedgwicki*, the Tafilalt  
367 dendrocystitids cannot be affiliated to this species, because they lack the highly distinctive  
368 ornamentation on thecal plates of 'gerontic' individuals. The Moroccan material is thus  
369 identified here as *Dendrocystites* aff. *sedgwicki* to stress that, although morphologically close  
370 to *D. sedgwicki* (e.g. 'gerontic' morphotype), it also retains features characteristic of *D.*  
371 *barrandei* (e.g. smooth, unornamented thecal plates). Consequently, hyperadult, 'gerontic'  
372 morphologies were acquired earlier in Morocco (late Sandbian) than in Bohemia (early  
373 Katian). It is possible that Moroccan solutans represent an ecophenotypic variation of *D.*  
374 *sedgwicki*: observed differences in the strength of thecal ornamentation would then simply



375 result from distinct environmental conditions. It is also possible that *D. aff. sedgwicki*  
376 corresponds to a transitional evolutionary stage between *D. barrandei* and *D. sedgwicki*. This  
377 hypothesis could be tested, if 'intermediate', *D. aff. sedgwicki*-like morphologies were  
378 recovered in the Vinice Formation of Bohemia, i.e. in between the Letná and the Záhofány  
379 formations.

380

### 381 **Palaeobiogeography, taphonomy and palaeoecology**

382

383 All known occurrences of the genus *Dendrocystites* are restricted to a relatively narrow time  
384 interval (late Sandbian–early Katian) and a small set of (peri-)Gondwanan areas, all situated  
385 within the Mediterranean Province, i.e. at high palaeolatitudes in the southern hemisphere  
386 (Lefebvre *et al.* 2013). *Dendrocystites barrandei* is known from the Letná Formation (late  
387 Sandbian), Barrandian area, Czech Republic (Bather 1913; Caster 1968; Noailles *et al.* 2014)  
388 and the Cantera Shale (latest Sandbian–earliest Katian), Central Iberian Zone, Spain (Gil Cid  
389 *et al.* 1996; Gutiérrez-Marco *et al.* 2018). Yet undescribed solutan remains from the Vinice  
390 Formation (latest Sandbian–earliest Katian) possibly represent the youngest occurrence of *D.*  
391 *barrandei* in Bohemia (Noailles *et al.* 2014). *Dendrocystites aff. sedgwicki* occurs in several  
392 stratigraphic intervals (late Sandbian–early Katian) within the lower Ktaoua Formation, in the  
393 western Tafilalt, Morocco (Lefebvre *et al.*, 2007, 2010; Noailles-Gobry 2008; Hunter *et al.*  
394 2010; Lebrun 2018). Finally, *D. sedgwicki* was described from the Záhofány Formation (early  
395 Katian), Prague Basin, Czech Republic (Barrande 1887; Bather 1913; Caster 1968; Noailles *et*  
396 *al.* 2014). Yet undescribed dendrocystitids from the overlying Bohdalec Formation (early  
397 Katian) could represent the youngest occurrence of *D. sedgwicki* in the Barrandian area  
398 (Noailles *et al.* 2014).

399 The occurrence of *Dendrocystites* in Czech Republic, Morocco and Spain supports the  
400 existence of strong faunal affinities between Late Ordovician echinoderm assemblages from  
401 these three regions (see e.g. Lefebvre 2007b; Lefebvre *et al.* 2007, 2013, this volume; Nardin  
402 2007; Zamora & Sumrall this volume; Zamora *et al.* this volume). The absence of  
403 *Dendrocystites* in other regions of the Mediterranean Province yielding otherwise very similar  
404 Late Ordovician faunas (e.g. France, Portugal) could be a result of sampling bias and/or  
405 variations in environmental conditions. *Dendrocystites* represents the single known  
406 dendrocystitid genus documented so far in the Upper Ordovician of (peri-)Gondwanan  
407 regions. Elsewhere, Late Ordovician dendrocystitids are taxonomically diverse and  
408 palaeogeographically widespread with occurrences in Avalonia (e.g. *Girvanicystis casteri*;  
409 Daley 1992), Baltica (e.g. *Heckericystis kuckersiana*, *Maennilia estonica*; Gill & Caster 1960;  
410 Caster 1968; Rozhnov & Jefferies 1996; Parsley *et al.* 2012) and Laurentia (e.g.  
411 *Dendrocystoides scoticus*, *Girvanicystis batheri*; Bather 1913; Caster 1968; Jefferies 1990;  
412 Daley 1992; Jefferies & Daley 1996). It is thought that this Late Ordovician peak in  
413 dendrocystitid diversity and palaeobiogeographic distribution is partly a result of their  
414 expansion onto Laurentian shores, although this could also be a result of an extremely poor  
415 fossil record in older strata (Lefebvre *et al.* 2013). For example, '*Dendrocystites*' *rossicus* is  
416 only species of dendrocystitid described so far in the Darriwilian (Bather 1913; Rozhnov &  
417 Jefferies, 1996). However, an as yet undescribed solutan remains from the Hope Shale of  
418 Shropshire, England, UK (B. Lefebvre, pers. obs.) and the Šárka Formation of the Prague  
419 Basin, Czech Republic (Lefebvre *et al.* 2012) suggest that, in Darriwilian times,  
420 dendrocystitids were already diverse and more widely distributed palaeogeographically than  
421 previously expected (i.e. in Avalonia, Baltica and high-latitude peri-Gondwanan regions).

422 In the taphonomic classification of echinoderms proposed by Brett *et al.* (1997), solutans  
423 belong to type 1 forms, i.e. taxa with a delicate endoskeleton made of weakly sutured plates.

424 Decay experiments made on Recent type 1 echinoderms (e.g. ophiuroids) suggest that, within  
425 days or a few weeks after death, their endoskeleton is totally disarticulated into isolated plates  
426 (Meyer 1971; Kerr & Twitchett 2004). Consequently, the preservation of fully articulated,  
427 complete specimens of *Dendrocystites* in the Upper Ordovician of the western Tafilalt area  
428 requires their rapid burial by obrution (e.g. storm-generated, turbiditic) deposits. In several  
429 localities, and in particular in Tizi n'Mourghi (ECR-F1), where most specimens were found,  
430 solutans are densely packed, and pressed against each other, and frequently aligned in the  
431 same direction (Fig. 3). This unidirectional preservation, which is also observed in other  
432 Moroccan starfish beds (see Nardin & Régnault 2015; Zamora *et al.* this volume), suggests  
433 that solutans were most likely transported a short distance by unidirectional, laminar bottom  
434 currents, before their definitive burial (Lefebvre *et al.* 2008, 2010; Hunter *et al.* 2010).

435 In the eastern Anti-Atlas, Late Ordovician echinoderm Lagerstätten (including most of  
436 those yielding *Dendrocystites*) are restricted to a relatively narrow area, more or less N-S  
437 oriented and straddling the western Tafilalt over several tens of kilometers. This trend  
438 matches very closely the distribution of conglomerates and slumps, located along a distensive  
439 fault system structured and active during the Sandbian–Katian time interval in this area (see  
440 e.g. Destombes 2006b; El Maazouz & Hamoumi 2007). Additional biostratigraphic and  
441 sedimentological investigations are necessary to determine if the Tafilalt echinoderm  
442 Lagerstätten result from the burial of para-autochthonous communities by storm deposits or  
443 from the downslope transport of shallow assemblages by turbiditic flows. Taphonomic  
444 experiments demonstrate that living or freshly killed type 1 echinoderms can endure severe  
445 hydrodynamic conditions (e.g. turbidites) with no disarticulation (Kerr & Twitchett 2004;  
446 Gorzelak & Salamon 2013). The Lady Burn Starfish Beds (South Thraive Formation) in the  
447 Upper Ordovician of Scotland is a well-known example of turbidite-generated echinoderm  
448 Lagerstätte (see e.g. Harper 1982; Jefferies 1990). Although they were transported downslope

449 by gravity currents, thousands of complete, fully-articulated type 1 echinoderms, including  
450 abundant specimens of the two solutans *Dendrocystoides scoticus* and *Girvanicystis batheri*  
451 were collected in this starfish bed (Bather 1913; Jefferies 1990; Daley 1992; Jefferies &  
452 Daley 1996).

453       Regardless whether they were buried *in-situ* by storm deposits or transported downslope by  
454 turbidites, Late Ordovician Moroccan solutans were originally living in shallow  
455 environmental conditions at or above storm wave base. The high density of individuals on  
456 some slabs suggests a very likely gregarious mode of life, in low-diversity echinoderm dense  
457 beds (Lefebvre *et al.* 2007, 2010; Hunter *et al.* 2010). In the western Tafilalt, solutans are  
458 frequently found associated with ophiuroids, glyptocystitid rhombiferans (e.g. *Homocystites*),  
459 stylophorans, and sometimes, with crinoids and edrioasteroids. In the Upper Ordovician of  
460 Bohemia and the Central Iberian Zone, *Dendrocystites* occurs in shallow environmental  
461 conditions and associated with echinoderm faunal elements both very similar to those  
462 documented in the western Tafilalt area. For example, the recently discovered Chrustenice  
463 echinoderm Lagerstätte (Sandbian, Letná Formation) yielded slabs covered by abundant,  
464 densely packed, current-oriented, fully articulated specimens of *Dendrocystites* (Fig. 7),  
465 associated with crinoids, edrioasteroids, ophiuroids, glyptocystitid rhombiferans  
466 (*Homocystites*) and stylophorans (Nohejlová *et al.* 2019). Similarly, *Dendrocystites* was  
467 collected at Viso del Marquès (southern Central Iberian Zone) in shallow, storm-generated,  
468 fine black shales with intraformational pebbles of the Cantera Shale, associated with crinoids,  
469 glyptocystitid rhombiferans (*Homocystites*) and stylophorans (Gil Cid *et al.* 1996; Gutiérrez-  
470 Marco *et al.* 2018; Lefebvre *et al.* this volume). Consequently, all known occurrences of  
471 *Dendrocystites* are restricted to relatively shallow, storm-influenced environmental settings.

472       The life orientation of solutans is still disputed and it has major implications for their mode  
473 of life (see e.g. Rahman & Lintz 2012; Noailles *et al.* 2014). If solutans were living with their

474 ambulacral groove facing away from the substrate (stylophoran-like orientation; see Lefebvre  
475 *et al.* 2019), then this would support a suspension-feeding mode of life (Bather 1913; Gill &  
476 Caster 1960; Parsley 1972; Parsley *et al.* 2012; Rahman & Lintz 2012). In contrast, if their  
477 ambulacral food groove was directed towards the substrate (pleurocystitid-like orientation;  
478 see Sumrall 2000), then solutans were very likely detritus-feeders (see e.g. Kolata 1973;  
479 Jefferies 1990; Daley 1995; Lefebvre *et al.* 2012; Noailles *et al.* 2014). Although, both life  
480 orientations are possible, rare examples of epibiotic echinoderms (edrioasteroids, eocrinoids)  
481 attached to solutans tend to support the view that solutans were detritus, rather than  
482 suspension-feeders (see Daley 1995; Lefebvre *et al.* 2012; Noailles *et al.* 2014). Similarly to  
483 pleurocystitid rhombiferans, solutans would then probably use their stout brachiole to sweep  
484 the substrate and feed on the organic matter concentrated on the sea floor. Nevertheless, the  
485 solutans from the Upper Ordovician of Morocco do not provide any evidence for this debate:  
486 all specimens were transported, at least a short distance, before burial, so that individuals  
487 showing both life orientations are often preserved side by side on a same slab. Moreover, no  
488 epibionts have been observed so far attached to specimens of *Dendrocystites* aff. *sedgwicki*. In  
489 the Upper Ordovician of the Prague Basin, several new, yet undescribed examples of  
490 edrioasteroids attached to the thecal surface of *Dendrocystites* could bring strengthens the  
491 brachiole downward orientation model (Nohejlová *et al.* 2019).

492

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843

#### 844 **Figure captions**

845

846 **Fig. 1.** (a) Simplified geological map of the Moroccan Anti-Atlas, showing the distribution of  
847 Ordovician rocks. (b) Simplified geological map of the region between Erfoud and Alnif (i.e.  
848 area covered by the two 1:200.000 geological maps of Todrha-Maïder and Tafilalt-Taouz)  
849 showing the position of solutan localities and the distribution of Ordovician rocks.

850

851 **Fig. 2.** Range and distribution of Late Ordovician solutan echinoderms from the western  
852 Tafilalt area, Morocco. The stratigraphy is based on Álvaro *et al.* (this volume).

853

854 **Fig. 3.** *Dendrocystites* aff. *sedgwicki* Barrande, 1867 from the Upper Ordovician Lower  
855 Ktaoua Formation (Anti-Atlas, Morocco). (a) Three large ('gerontic morphotype') specimens;  
856 ML20.269424, Tizi n'Mourghi (ECR-F1). (b) Accumulation of medium-sized ('adult  
857 morphotype') specimens; AA.JTK.OS.1, Jbel Taklimt (ECR-F9). All photographs are from  
858 latex casts whitened with NH<sub>4</sub>Cl. Scale bar represents 1 cm.

859

860 **Fig. 4.** Small ('juvenile morphotype') specimens of *Dendrocystites* aff. *sedgwicki* Barrande,  
861 1867 from the Upper Ordovician Lower Ktaoua Formation (Anti-Atlas, Morocco). (a)  
862 Specimen with rounded theca; MHNN.P.045601, Piste de Jorf (ECR-F3). (b) Specimen with  
863 cordiform theca; MHNN.P.045611, Piste de Jorf (ECR-F3). (c) Specimen with cordiform

864 theca; ML20.269428, Tizi n'Mourghi (ECR-F1). All photographs are from latex casts  
865 whitened with NH<sub>4</sub>Cl. Scale bar represents 1 cm.

866

867 **Fig. 5.** Medium-sized ('adult morphotype') specimens of *Dendrocystites* aff. *sedgwicki*  
868 Barrande, 1867 from the Upper Ordovician Lower Ktaoua Formation (Anti-Atlas, Morocco);  
869 all from Tizi n'Mourghi (ECR-F1). (a) ML20.269425. (b) ML20.269429. (c) ML20.269442.

870 All photographs are from latex casts whitened with NH<sub>4</sub>Cl. Scale bar represents 1 cm.

871

872 **Fig. 6.** Large ('gerontic morphotype') specimens of *Dendrocystites* aff. *sedgwicki* Barrande,  
873 1867 from the Upper Ordovician Lower Ktaoua Formation (Anti-Atlas, Morocco); all from  
874 Tizi n'Mourghi (ECR-F1). (a) ML20.269420. (b) ML20.269435. (c) ML20.269419. (d)  
875 ML20.269440. (e) ML20.269450. All photographs are from latex casts whitened with NH<sub>4</sub>Cl.

876 Scale bar represents 1 cm.

877

878 **Fig. 7.** *Dendrocystites barrandei* Bather, 1913 and *Homocystites* sp. from the Upper  
879 Ordovician Letná Formation (Sandbian, Barrandian Area). The photograph is from latex cast  
880 whitened with NH<sub>4</sub>Cl. Scale bar represents 1 cm.

881