1
2 **Late Ordovician solutan echinoderms from the western Tafilalt, Morocco**

3
4 MARTINA NOHEJLOVÁ^{1,2*} & BERTRAND LEFEBVRE¹

5
6 ¹*Univ Lyon, Univ Lyon 1, ENSL, CNRS, LGL-TPE, F-69622, Villeurbanne, France*

7 ²*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;

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

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

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

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

Geological setting and stratigraphy

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

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

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

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

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

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

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

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

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

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 (NH₄Cl)
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

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

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

Subphylum **Blastozoa** Sprinkle, 1973

Class **Soluta** Jaekel, 1901

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

Family **Dendrocystitidae** Bassler, 1938

Genus *Dendrocystites* Barrande, 1887

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

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

Dendrocystites aff. *sedgwicki* Barrande, 1867

Figures 3–6

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Palaeobiogeography, taphonomy and palaeoecology

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

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

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

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

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

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

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

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

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

Acknowledgements

This paper is a contribution to the International Geoscience Programme (IGCP) Project 653 "The Onset of the Great Ordovician Biodiversification" Event and 735 "Rocks and the Rise of Ordovician Life: Filling knowledge gaps in the Early Palaeozoic Biodiversification". The authors are particularly grateful to Roland and Véronique Reboul for field assistance and for

donating many important specimens to public collections. This work also greatly benefited from the field experience of Jacques Destombes, who also provided many important data (notes, maps). Francis Auvray is thanked for providing data on new fossiliferous sites and for donating several specimens of solutans to the palaeontological collections of Lyon 1 University. The authors are also thanking Ali Bachnou, El Medhi Bajedoub, Khadija El Hariri, Christian Gaillard, Ahmid Hafid and Nicolas Olivier for their help in the field (2009–2010). The authors thank Thomas Guensburg, James Sprinkle and Samuel Zamora for their useful and constructive comments, which greatly helped improving the quality of this manuscript. The authors are also grateful to Didier Berthet (Musée des Confluences), Pierre Dalous and Yves Laurent (NHM, Toulouse), Anne Médard and Sylvie Pichard (NHM, Marseille), Khaoula Kouraïss (Marrakesh University), Serge Régnault (NHM, Nantes), Emmanuel Robert (Lyon 1 University) for access to the material deposited in the public collections they are curating. We also wish to thank the editor Aaron W. Hunter (University of Cambridge & The University of Western Australia) for help during field work and his patience during writing this paper.

Funding

The authors are grateful to the LABEX Lyon Institute of Origins (ANR-10-LABX-0066) of the Université de Lyon for its financial support within the program “Investissements d’Avenir” (ANR-11-IDEX-0007) of the French government operated by the National Research Agency (ANR). Field work in the Tafilalt area was funded by the CNRS-CNRST French-Moroccan cooperation project "Les faunes à conservation exceptionnelle de l'Ordovicien de l'Anti-Atlas (Maroc): implications évolutives et écologiques" (2009–2012). This paper is also supported by the Grant Agency of the Czech Republic Project No.18-

14575S and is an outcome of the European Synthesys projects GB-TAF-4565 and CZ-TAF-6049.

References

ÁLVARO, J.J., VENNIN, E., VILLAS, E., DESTOMBES, J. & VIZCAÍNO, D. 2007. Pre-Hirnantian (latest Ordovician) benthic community assemblages: Controls and replacements in a silicilastic-dominated platform of the eastern Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **245**, 20–36.

ÁLVARO, J.J., BENHARREF, M., DESTOMBES, J., GUTIÉRREZ-MARCO, J.C., HUNTER, A.W., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S. this volume. Ordovician stratigraphy and benthic community replacements in the eastern Anti-Atlas, Morocco. *In*: HUNTER, A.W., ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S. (eds) *The Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota, Morocco*. Geological Society, London, Special Publications, **485**.

BABIN, C. & DESTOMBES, J. 1990. Les mollusques bivalves et rostroconches ordoviciens de l'Anti-Atlas marocain: intérêt paléogéographique de leur inventaire. *Géologie Méditerranéenne*, **17**(3), 243–261.

BARRANDE, J. 1887. *Système silurien du centre de la Bohême. 1^{ère} partie: Recherches paléontologiques. Volume 7. Classe des Echinodermes. Ordre des Cystidées*. Gerhard, Leipzig & Řivnáč, Prague, 233 p.

BASSLER, R. S. 1938. Pelmatozoa Palaeozoica (Generum et Genotyporum Index et Bibliographia). *Fossilium Catalogus I Animalia*, **83**, 1–194.

BATHER, F.A. 1913. Caradocian Cystidea from Girvan. *Transactions of the Royal Society of Edinburgh*, **49**, 359–529.

- 549 BOTTING, J.P. this volume. Late Ordovician crinoids from the Anti-Atlas region of Morocco.
 550 *In:* HUNTER, A.W., ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S. (eds) *The*
 551 *Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota, Morocco.*
 552 Geological Society, London, Special Publications, **485**.
- 553 BRETT, C.E., MOFFAT, H.A. & TAYLOR, W. 1997. Echinoderm taphonomy, taphofacies, and
 554 Lagerstätten. *In:* WATERS, J.A. & MAPLES, C.G. (eds), *Geobiology of Echinoderms.*
 555 *Paleontological Society Papers*, **3**, 147–190.
- 556 BRUGUIERE, J.G. 1791. *Tableau Encyclopédique et Méthodique des Trois Règles de la*
 557 *Nature, contenant l'Helminthologie, ou les vers Infusoires, les vers Intestins, les vers*
 558 *Mollusques, etc., Volume 7.* 180 pp. Panckoucke, Paris.
- 559 CASTER, K.E. 1968. Homoiostelea. *In:* MOORE, R.C. (ed.) *Treatise on Invertebrate*
 560 *Paleontology, part 5, Echinodermata 1(2).* Geological Society of America, New York;
 561 University of Kansas, Lawrence, S581–S627.
- 562 CHAUVEL, J. 1966. *Échinodermes de l'Ordovicien du Maroc.* Editions du CNRS, Paris, 120
 563 p.
- 564 CHAUVEL, J. 1977. Note complémentaire sur les cystoïdes rhombifères (Echinodermes) de
 565 l'Ordovicien marocain. *Notes du Service géologique du Maroc*, **38**, 115–139.
- 566 CHAUVEL, J. 1978. Compléments sur les échinodermes du Paléozoïque marocain
 567 (diploporites, éocrinoïdes, édrioastéroïdés). *Notes et Mémoires du Service géologique du*
 568 *Maroc*, **272**, 27–78.
- 569 COLMENAR, J., VILLAS, E. & RASMUSSEN, C.M.Ø. this volume. A synopsis of Late
 570 Ordovician brachiopod diversity in the Anti-Atlas, Morocco. *In:* HUNTER, A.W., ÁLVARO,
 571 J.J., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S. (eds) *The Great Ordovician*
 572 *Biodiversification Event: Insights from the Tafilalt Biota, Morocco.* Geological Society,
 573 London, Special Publications, **485**.

- 574 DALEY, P.E.J. 1992. The anatomy of the solute *Girvanicystis batheri* (?Chordata) from the
575 Upper Ordovician of Scotland and a new species of *Girvanicystis* from the Upper
576 Ordovician of south Wales. *Zoological Journal of the Linnean Society*, **105**, 353–375.
- 577 DALEY, P.E.J. 1995. Anatomy, locomotion and ontogeny of the solute *Castericystis vali* from
578 the Middle Cambrian of Utah. *Geobios*, **28**, 585–615.
- 579 DALEY, P.E.J. 1996. The first solute which is attached as an adult: a Mid-Cambrian fossil
580 from Utah with echinoderm and chordate affinities. *Zoological Journal of the Linnean*
581 *Society*, **117**, 405–440.
- 582 DAVID, B., LEFEBVRE, B., MOOI, R. & PARSLEY, R. 2000. Are homalozoans echinoderms? An
583 answer from the extraxial-axial theory. *Paleobiology*, **26**, 529–555.
- 584 DEHM, R. 1934. Untersuchungen an Cystoideen des rheinischen Unterdevons.
585 *Sitzungsberichte Bayerischen Akademie der Wissenschaften, Mathematisch-*
586 *naturwissenschaftliche Abteilung*, **1934**, 19–43.
- 587 DESTOMBES, J. 1972. Les trilobites du sous-ordre des Phacopina de l'Ordovicien de l'Anti-
588 Atlas (Maroc). *Notes et Mémoires du Service géologique du Maroc*, **240**, 1–113.
- 589 DESTOMBES, J. 2006a. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
590 explicative. Paléozoïque inférieur : Cambrien moyen et supérieur - Ordovicien - Base du
591 Silurien. Feuille Todrha- Maïder. Chapitre D. *Notes & Mémoires du Service géologique du*
592 *Maroc*, **243bis**, 1–58.
- 593 DESTOMBES, J. 2006b. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
594 explicative. Paléozoïque inférieur : Cambrien moyen et supérieur - Ordovicien - Base du
595 Silurien. Feuille Tafilalt – Taouz. Chapitre E. *Notes & Mémoires du Service géologique du*
596 *Maroc*, **244bis**, 1–69.

- 597 DESTOMBES, J., TERMIER, H. & TERMIER, G. 1971. Sur quelques bryozoaires ectoproctes de
598 l'Ordovicien supérieur du Sud marocain. *Notes du Service géologique du Maroc*, **31**, 61–
599 64.
- 600 DOMINGUEZ, P.D., JEFFERIES, R.P.S. & GIL CID, M.D. 2002. An annotated check-list of genera
601 and species of carpoids. *Coloquios de Paleontología*, **53**, 33–68.
- 602 EBBESTAD, J.O., POLECHOVÁ, M., KRÖGER, B. & GUTIÉRREZ-MARCO, J.C. this volume. Late
603 Ordovician molluscs of the central and eastern Anti-Atlas, Morocco. *In*: HUNTER, A.W.,
604 ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S. (eds) *The Great Ordovician*
605 *Biodiversification Event: Insights from the Tafilalt Biota, Morocco*. Geological Society,
606 London, Special Publications, **485**.
- 607 EL MAAZOUZ, B. & HAMOUMI, N. 2007. Différenciation paléogéographique à l'Ordovicien
608 supérieur dans le Tafilalt (Anti-Atlas oriental, Maroc) sous l'interaction de la glaciation et
609 de la tectonique. *Comptes Rendus Geoscience*, **339**, 562–571.
- 610 ERNST, A. this volume. Upper Ordovician bryozoans of Morocco. *In*: HUNTER, A.W.,
611 ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S. (eds) *The Great Ordovician*
612 *Biodiversification Event: Insights from the Tafilalt Biota, Morocco*. Geological Society,
613 London, Special Publications, **485**.
- 614 GIL CID, M.D., DOMÍNGUEZ ALONSO, P.D., SILVÁN POBES, E. & ESCRIBANO RÓDENAS, M.
615 1996. *Bohemiaecystis jefferiesi* n. sp.; primer Cornuta para el Ordovícico español. *Estudios*
616 *Geológicos*, **52**, 313–326.
- 617 GILL, E.D. & CASTER, K.E. 1960. Carpoid echinoderms from the Silurian and Devonian of
618 Australia. *Bulletins of American Paleontology*, **41**, 1–71.
- 619 GORZELAK, P. & SALAMON, M.A. 2013. Experimental tumbling of echinoderms –
620 Taphonomic patterns and implications. *Palaeogeography, Palaeoclimatology,*
621 *Palaeoecology*, **386**, 569–574.

622 GUTIÉRREZ-MARCO, J.C. & GARCÍA-BELLIDO, D.C. 2015. Micrometric detail in
623 palaeoscolecoid worms from Late Ordovician sandstones of the Tafilalt Konservat-
624 Lagerstätte, Morocco. *Gondwana Research*, **28**, 875–881.

625 GUTIÉRREZ-MARCO, J.C. & GARCÍA-BELLIDO, D.C. this volume. The international fossil trade
626 from the Paleozoic of the Anti-Atlas, Morocco. In: HUNTER, A.W., ÁLVARO, J.J.,
627 LEFEBVRE, B., VAN ROY, P. & ZAMORA, S. (eds) *The Great Ordovician Biodiversification*
628 *Event: Insights from the Tafilalt Biota, Morocco*. Geological Society, London, Special
629 Publications, **485**.

630 GUTIÉRREZ-MARCO, J.C., PEREIRA, S., COLMENAR, J., ZAMORA, S. & RÁBANO, I. 2018.
631 Middle Berounian (ca. Sandbian 2–Katian 1) trilobite, brachiopod and echinoderm
632 assemblages from the southern Central Iberian Zone, Spain. In: *The Fossil Week, Abstract*
633 *Book, 5th International Palaeontological Congress, 9-13 July 2018, Paris*. MNHN and
634 Sorbonne University, Paris, 844.

635 GUTIÉRREZ-MARCO, J.C., VAN ROY, P., LEFEBVRE, B., ZAMORA, S., PEREIRA, S. & RÁBANO, I.
636 2020. Le *Tafilalt Biota*: des animaux au corps mou dans des sables de l'Ordovicien
637 supérieur du Maroc. *Géochronique*, **153**, 45–51.

638 GUTIÉRREZ-MARCO, J.C., PEREIRA S., GARCÍA-BELLIDO, D.C. & RÁBANO, I. this volume *a*.
639 Ordovician trilobites from the Tafilalt Lagerstätte: new data and reappraisal of the Bou
640 Nemrou assemblage. In: HUNTER, A.W., ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. &
641 ZAMORA, S. (eds) *The Great Ordovician Biodiversification Event: Insights from the*
642 *Tafilalt Biota, Morocco*. Geological Society, London, Special Publications, **485**.

643 GUTIÉRREZ-MARCO, J.C., MUIR, L.A. & MITCHELL, C.E. this volume *b*. Upper Ordovician
644 planktic and benthic graptolites and a possible hydroid from the Tafilalt Biota,
645 southeastern Morocco. In: HUNTER, A.W., ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. &

- 646 ZAMORA, S. (eds) *The Great Ordovician Biodiversification Event: Insights from the*
647 *Tafilalt Biota, Morocco*. Geological Society, London, Special Publications, **485**.
- 648 HARPER, D.A.T. 1982. The stratigraphy of the Drummuck Group (Ashgill), Girvan.
649 *Geological Journal*, **17**, 251–277.
- 650 HAVLICEK, V. 1971. Brachiopodes de l’Ordovicien du Maroc. *Notes et Mémoires du Service*
651 *géologique du Maroc*, **230**, 1–135.
- 652 HORNÝ, R.J. 1997. Ordovician Tergomya and Gastropoda (Mollusca) of the Anti-Atlas
653 (Morocco). *Sborník Národního Musea v Praze*, **53**, 37–78.
- 654 HUNTER, A.W., LEFEBVRE, B., NARDIN, E., RÉGNAULT, S., VAN ROY, P., & ZAMORA, S. 2010.
655 Preliminary report on new echinoderm Lagerstätten from the Upper Ordovician of the
656 eastern Anti-Atlas, Morocco. *In*: HARRIS, L.G., BÖTTGER, S.A., WALKER, C.W. & LESSER,
657 M.P. (eds) *Echinoderms: Durham*. Balkema, Leiden, 23–30.
- 658 JAEKEL, O. 1901. Ueber Carpoideen, eine neue Klasse von Pelmatozoen. *Zeitschrift der*
659 *Deutschen geologischen Gesellschaft*, **52**, 661–677.
- 660 JEFFERIES, R.P.S. 1990. The solute *Dendrocystoides scoticus* from the Upper Ordovician of
661 Scotland and the ancestry of chordates and echinoderms. *Palaeontology*, **33**, 631–679.
- 662 JEFFERIES, R.P.S. & DALEY, P.E.J. 1996. Calcichordates. *In*: HARPER, D.A.T. & OWEN, A.W.
663 (eds), *Fossils of the Upper Ordovician*. The Palaeontological Association, London, 268–
664 276.
- 665 KERR, T.J.V. & TWITCHETT, R.J. 2004. Experimental decay and disarticulation of *Ophiura*
666 *texturata*: implications for the fossil record of ophiuroids. *In*: HEINZELLER, T. &
667 NEBELSICK, J.H. (eds), *Echinoderms: München*. Balkema, Rotterdam, 439–446.
- 668 KLEIN, J.T. 1734. *Naturalis dispositio Echinodermatum. Accessit lucubrationcula de Aculeis*
669 *Echinorum Marinorum, cum spicilegio de Belemnitis*. Schreiber, Gedani, 79 p.

670 KOLATA, D.R. 1973. *Scalenocystites strimplei*, a new Middle Ordovician belemnocystitid
671 solute from Minnesota. *Journal of Paleontology*, **47**, 969–974.

672 KOLATA, D.R., STRIMPLE, H.L. & LEVERSON, C.O. 1977. Revision of the Ordovician carpoid
673 family Iowacystidae. *Palaeontology*, **20**, 529–557.

674 LEBRUN, P. 2018. *Fossiles du Maroc. Tome 1. Gisements emblématiques du Paléozoïque de*
675 *l'Anti-Atlas*. Editions du Piat, Yssingeaux, 298 p.

676 LEFEBVRE, B. 2007a. Early Palaeozoic palaeobiogeography and palaeoecology of stylophoran
677 echinoderms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **245**, 156–199.

678 LEFEBVRE, B. 2007b. Changes in Late Ordovician (pre-Hirnantian) echinoderm assemblages:
679 palaeoenvironmental and palaeobiogeographical implications. *Acta Palaeontologica*
680 *Sinica*, **46**(suppl.), 241–248.

681 LEFEBVRE, B. & FATKA, O. 2003. Palaeogeographical and palaeoecological aspects of the
682 Cambro-Ordovician radiation of echinoderms in Gondwanan Africa and peri-Gondwanan
683 Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 73–97.

684 LEFEBVRE, B. & LEROSEY-AUBRIL, R. 2018. Laurentian origin of solutan echinoderms: new
685 evidence from the Guzhangian (Cambrian Series 3) Weeks Formation of Utah, USA.
686 *Geological Magazine*, **155**, 1190–1204.

687 LEFEBVRE, B., NARDIN, E., HUNTER, A.W. & RÉGNAULT, S. 2007. Les échinodermes de
688 l'Ordovicien supérieur de l'Anti-Atlas (Maroc): biostratigraphie et paléobiodiversité. *Africa*
689 *Geoscience Review*, **14**, 123–148.

690 LEFEBVRE, B., NOAILLES, F., HUNTER, A.W., NARDIN, E., RÉGNAULT, S., FRANZIN, B., VAN
691 ROY, P. & EL HARIRI, K. 2008. Les niveaux à échinodermes de Bou Nemrou, un gisement
692 à préservation exceptionnelle de l'Ordovicien supérieur du Tafilalt occidental (Maroc).
693 *Mésogée*, **64**, 7–25.

694 LEFEBVRE, B., NOAILLES, F., FRANZIN, B., RÉGNAULT, S., NARDIN, E., HUNTER, A.W.,
695 ZAMORA, S., VAN ROY, P., EL HARIRI, K. & LAZREQ, N. 2010. Les gisements à
696 échinodermes de l'Ordovicien supérieur de l'Anti-Atlas oriental (Maroc): un patrimoine
697 scientifique exceptionnel à préserver. *Bulletin de l'Institut Scientifique, Rabat*, **32**, 1–17.

698 LEFEBVRE, B., DERSTLER, K. & SUMRALL, C.D. 2012. A reinterpretation of the solute
699 *Plasiacystis mobilis* (Echinodermata) from the Middle Ordovician of Bohemia. In: Kroh
700 A. & Reich M. (eds.), *Echinoderm research 2010: Proceedings of the Seventh European*
701 *Conference on Echinoderms, Göttingen, Germany, 2–9 October 2010. Zoosymposia*, **7**,
702 287–306.

703 LEFEBVRE, B., SUMRALL, C.D., SHROAT-LEWIS, R.A., REICH, M., WEBSTER, G.D.,
704 HUNTER, A.W., NARDIN, E., ROZHNOV, S.V., GUENSBURG, T.E., TOUZEAU, A.,
705 NOAILLES, F. & SPRINKLE, J. 2013. Palaeobiogeography of Ordovician Echinoderms. In:
706 Harper, D.A.T. & Servais, T. (eds) *Early Palaeozoic Biogeography and*
707 *Palaeobiogeography*. Geological Society, London, Memoirs, **38**, 165–190.

708 LEFEBVRE, B., ALLAIRE, N., GUENSBURG, T.E., HUNTER, A.W., KOURAÏSS, K., MARTIN,
709 E.L.O., NARDIN, E., NOAILLES, F., PITTET, B., SUMRALL, C.D. & ZAMORA, S. 2016.
710 Palaeoecological aspects of the diversification of echinoderms in the Lower Ordovician of
711 central Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**,
712 97–121.

713 LEFEBVRE, B., GUENSBURG, T.E., MARTIN, E.L.O., MOOI, R., NARDIN, E., NOHEJLOVÁ, M.,
714 SALEH, F., KOURAÏSS, K., EL HARIRI, K. & DAVID, B. 2019. Exceptionally preserved soft
715 parts in fossils from the Lower Ordovician of Morocco clarify stylophoran affinities within
716 basal deuterostomes. *Geobios*, **52**, 27–36.

717 LEFEBVRE B., NOHEJLOVÁ, M., MARTIN, E.L.O., KAŠIČKA, L., ZICHA, O. & GUTIÉRREZ-
718 MARCO, J.C. this volume. New Middle and Late Ordovician cornute stylophorans

719 (Echinodermata) from Morocco and other peri-Gondwanan areas. *In*: HUNTER, A.W.,
 720 ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S. (eds) *The Great Ordovician*
 721 *Biodiversification Event: Insights from the Tafilalt Biota, Morocco*. Geological Society,
 722 London, Special Publications, **485**.

723 MACGABHANN, B.A. 2012. *A solution to Darwin's dilemma: differential taphonomy of*
 724 *Palaeozoic and Ediacaran non-mineralised discoidal fossils*. Unpublished PhD thesis,
 725 Earth and Ocean Sciences, National University of Ireland, Galway, Ireland, 1, 657 p.

726 MEYER, D.L. 1971. Post-mortem disintegration of Recent crinoids and ophiuroids under
 727 natural conditions. *Geological Society of America Abstracts with Programs*, **3**, 645–646.

728 NARDIN, E. 2007. New occurrence of the Ordovician eocrinoid *Cardiocystites*:
 729 Palaeogeographical and palaeoecological implications. *Acta Palaeontologica Polonica*, **52**,
 730 17–26.

731 NARDIN, E., & RÉGNAULT, S. 2015. Palaeoecology of *Ascocystites*-dominated assemblages
 732 (Echinodermata, Blastozoa, Eocrinoidea) from the Upper Ordovician of the Moroccan
 733 Anti-Atlas. *In*: ZAMORA, S. & RÁBANO, I. (eds) *Progress in Echinoderm Palaeobiology*.
 734 *Cuadernos del Museo Geominero*, **19**, 109–114.

735 NARDIN, E., LEFEBVRE, B., DAVID, B. & MOOI, R. 2009. La radiation des échinodermes au
 736 Paléozoïque inférieur, l'exemple des blastozoaires. *Comptes-Rendus Palevol*, **8**, 179–188.

737 NOAILLES-GOBRY F. 2008. *Les solutes (Echinodermata, Blastozoa) de l'Ordovicien*
 738 *supérieur de l'Anti-Atlas oriental (Maroc) : paléoécologie, ontogénie, diversité,*
 739 *affinités et implications paléogéographiques*. Unpublished Master 2 thesis, Université
 740 Lyon 1, Villeurbanne, 45 p.

741 NOAILLES, F., LEFEBVRE, B. & KAŠIČKA, L. 2014. A probable case of heterochrony in the
 742 solutan *Dendrocystites* Barrande, 1887 (Echinodermata: Blastozoa) from the Upper

743 Ordovician of the Prague Basin (Czech Republic) and a revision of the family
 744 Dendrocystitidae Bassler, 1938. *Bulletin of Geosciences*, **89**, 451–476.

745 NOHEJLOVÁ, M., & FATKA, O. 2016. Ontogeny and morphology of Cambrian eocrinoid
 746 *Akadocrinus* (Barrandian area, Czech Republic). *Bulletin of Geosciences*, **91**(1), 141–153.

747 NOHEJLOVÁ, M., LEFEBVRE, B., NARDIN, E., FATKA, O., & BUDIL, P. 2019. New echinoderm
 748 Lagerstätte from the Letná Formation (Sandbian, Upper Ordovician) of Bohemia. *In*:
 749 ROZHNOV, S.V., DGEBUADZE, P.YU. & MIRANTSEV G.V. (eds) *Abstracts of 10th European*
 750 *Conference on Echinoderms*, – Borissiak Paleontological Institute RAS, Moscow, 69.

751 PARSLEY, R.L. 1972. The Belemnocystitidae: solutan homeomorphs of the
 752 Anomalocystitidae. *Journal of Paleontology*, **46**, 341–347.

753 PARSLEY, R.L., 1997. The echinoderm classes Stylophora and Homoiostelea: non
 754 Calcichordata. *In*: WATERS, J.A. & MAPLES, C.G. (eds) *Geobiology of Echinoderms*.
 755 *Paleontological Society Papers*, **3**, 225–248.

756 PARSLEY, R.L. 2009. Morphology, ontogeny, and heterochrony in Lower and Middle
 757 Cambrian gogiids (Eocrinoidea, Echinodermata) from Guizhou Province, China.
 758 *Paleontological Journal*, **43**, 1406–1414.

759 PARSLEY, R.L. 2012. Ontogeny, functional morphology, and comparative morphology of
 760 lower (Stage 4) and basal middle (Stage 5) Cambrian gogiids, Guizhou Province, China.
 761 *Journal of Paleontology*, **86**, 569–583.

762 PARSLEY, R.L., & CASTER, K.E. 1965. North American Soluta (Carpoidea, Echinodermata).
 763 *Bulletins of American Paleontology*, **49**, 109–174.

764 PARSLEY, R.L., & SUMRALL, C.D. 2007. New recumbent echinoderm genera from the Bois
 765 d'Arc Formation: Lower Devonian (Lochkovian) of Coal County, Oklahoma. *Journal of*
 766 *Paleontology*, **81**, 1486–1493.

767 PARSLEY, R.L., ROZHNOV, S.V. & SUMRALL, C.D. 2012. Morphologic and systematic revision
 768 of the solute *Maennilia estonica* (Homoioステlea, Echinodermata) from the Upper
 769 Ordovician of Estonia. *Journal of Paleontology*, **86**, 462–469.

770 PROKOP, R.J., & PETR, V. 2003. *Plasiacystis mobilis*, gen. et sp. n., a strange “carpoid”
 771 (Echinodermata, ?Homoioステlea: Soluta) in the Bohemian Ordovician (Czech Republic).
 772 *Sborník Národního Muzea, Serie B, Přírodní vědy*, **59**, 151–162.

773 RAHMAN, I.A. & LINTZ, H. 2012. *Dehmicystis globulus*, an enigmatic solute (Echinodermata)
 774 from the Lower Devonian Hunsrück Slate, Germany. *Paläontologische Zeitschrift*, **86**, 59–
 775 70.

776 REGNAULT, S. 2007. Occurrence of the genus *Ascocystites* Barrande (Echinodermata,
 777 Blastozoa) in the Upper Ordovician of the Anti-Atlas (Morocco). *Annales de Paléontologie*
 778 **93**, 215–227.

779 ROZHNOV, S.V., & JEFFERIES, R.P.S. (1996). A new stem-chordate solute from the Middle
 780 Ordovician of Estonia. *Geobios*, **29**, 91–109.

781 SERVICE GEOLOGIQUE DU MAROC. 1986. Carte géologique du Maroc : Tafilalt – Taouz.
 782 Echelle 1/200 000. *Notes et Mémoires du Service géologique du Maroc*, **244**.

783 SERVICE GEOLOGIQUE DU MAROC. 1988. Carte géologique du Maroc : Tadrar – Ma'der (Anti-
 784 Atlas oriental, zones axiale et périphérique Nord et Sud). Echelle 1/200 000. *Notes et*
 785 *Mémoires du Service géologique du Maroc*, **243**.

786 SMITH, A.B. 2005. The pre-radial history of echinoderms. *Geological Journal*, **40**, 255–280.

787 SPRINKLE, J. 1973. *Morphology and Evolution of Blastozoan Echinoderms*. Museum of
 788 Comparative Zoology Harvard University, Cambridge (Massachusetts), 283 pp.

789 SPRINKLE, J. & GUENSBURG, T.E. 2004. Crinozoan, blastozoan, echinozoan, asterozoan, and
 790 homalozoan echinoderms. In: WEBBY, B.D., PARIS, F., DROSER, M.L. & PERCIVAL, I.G.

791 (eds) *The Great Ordovician Biodiversification Event*. Columbia University Press, New
 792 York, 266–280.

793 SUMRALL, C.D. & ZAMORA, S. this volume. New Upper Ordovician edrioasteroids from
 794 Morocco. In: HUNTER, A.W., ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S.
 795 (eds) *The Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota,*
 796 *Morocco*. Geological Society, London, Special Publications, **485**.

797 TERMIER, H. & TERMIER, G. 1970. Un échinoderme encroûtant de l'Ashgill (Ordovicien
 798 supérieur) du Tafilalt (Sud marocain): *Herpetocystis destombesi* nov. gen. nov. sp.
 799 *Comptes rendus hebdomadaires des séances de l'Académie des Sciences*, **271**, 1260–1263.

800 THORAL, M. 1935. *Contribution à l'Etude Paléontologique de l'Ordovicien inférieur de la*
 801 *Montagne Noire et Révision Sommaire de la Faune Cambrienne de la Montagne Noire*.
 802 Imprimerie de la Charité, Montpellier, 362 p.

803 UBAGHS, G. 1969. *Les Echinodermes «Carpoides» de l'Ordovicien inférieur de la Montagne*
 804 *Noire (France)*. Editions du CNRS, Cahiers de Paléontologie, 110 p.

805 UBAGHS, G. & ROBISON, R.A. 1985. A new homoiostele and a new eocrinoid from the
 806 Middle Cambrian of Utah. *University of Kansas Paleontological Contributions*, **115**, 1–24.

807 UBAGHS, G. & ROBISON, R.A. 1988. Homalozoan echinoderms of the Wheeler Formation
 808 (Middle Cambrian) of western Utah. *University of Kansas Paleontological Contributions*,
 809 **120**, 1–17.

810 VAN ITEN, H., GUTIÉRREZ-MARCO, J.C., MUIR, L., SIMÕES, M.G. & LEME, M. this volume.
 811 Ordovician conulariids (Scyphozoa) from the Upper Tiouririne Formation (Katian), eastern
 812 Anti-Atlas Mountains, southern Morocco. In: HUNTER, A.W., ÁLVARO, J.J., LEFEBVRE, B.,
 813 VAN ROY, P. & ZAMORA, S. (eds) *The Great Ordovician Biodiversification Event: Insights*
 814 *from the Tafilalt Biota, Morocco*. Geological Society, London, Special Publications, **485**.

815 VAN ROY, P.H.J. 2006. *Non-Trilobite Arthropods from the Ordovician of Morocco*.
816 Unpublished Ph.D. thesis, Ghent University, Ghent, 230 p.

817 VILLAS, E. & COLMENAR, J. this volume. Brachiopods from the Upper Ordovician of Erfoud
818 (eastern Anti-Atlas, Morocco) and the stratigraphic correlation of the bryozoan-rich Khabt-
819 el Hajar Formation. *In*: HUNTER, A.W., ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. &
820 ZAMORA, S. (eds) *The Great Ordovician Biodiversification Event: Insights from the*
821 *Tafilalt Biota, Morocco*. Geological Society, London, Special Publications, **485**.

822 VINTHER, J., VAN ROY, P. & BRIGGS, D.E.G. 2008. Machaeridians are Palaeozoic armoured
823 annelids. *Nature*, **451**, 185–188.

824 ZAMORA, S. & SUMRALL, C.D. this volume. The first report of coronates (echinodermata)
825 from Africa. *In*: HUNTER, A.W., ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S.
826 (eds) *The Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota,*
827 *Morocco*. Geological Society, London, Special Publications, **485**.

828 ZAMORA, S., DARROCH, S.A.F. & RAHMAN, I.A. 2013a. Taphonomy and ontogeny of early
829 pelmatozoan echinoderms: a case study of a mass mortality assemblage of *Gogia* from the
830 Cambrian of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **377**,
831 62–72.

832 ZAMORA, S., ZHU, X. & LEFEBVRE, B. 2013b. A new Furongian (Cambrian) Echinoderm-
833 Lagerstätte from the Sandu Formation (South China). *Cahiers de Biologie Marine*, **54**,
834 565–569.

835 ZAMORA, S., NARDIN, E., ESTEVE, J., & GUTIERREZ-MARCO, J.C. this volume. New
836 rhombiferan blastozoans (Echinodermata) from the Late Ordovician of Morocco. *In*:
837 HUNTER, A.W., ÁLVARO, J.J., LEFEBVRE, B., VAN ROY, P. & ZAMORA, S. (eds) *The Great*
838 *Ordovician Biodiversification Event: Insights from the Tafilalt Biota, Morocco*. Geological
839 Society, London, Special Publications, **485**.

ZHU, X.J., PENG, S., ZAMORA, S., LEFEBVRE, B. & CHEN, G. 2016. Furongian (upper Cambrian) Guole Konservat-Lagerstätte from South China. *Acta Geologica Sinica*, **90**, 801–808.

Figure captions

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

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

Fig. 3. *Dendrocystites* aff. *sedgwicki* Barrande, 1867 from the Upper Ordovician Lower Ktaoua Formation (Anti-Atlas, Morocco). (a) Three large ('gerontic morphotype') specimens; ML20.269424, Tizi n'Mourghi (ECR-F1). (b) Accumulation of medium-sized ('adult morphotype') specimens; AA.JTK.OS.1, Jbel Taklimt (ECR-F9). All photographs are from latex casts whitened with NH₄Cl. Scale bar represents 1 cm.

Fig. 4. Small ('juvenile morphotype') specimens of *Dendrocystites* aff. *sedgwicki* Barrande, 1867 from the Upper Ordovician Lower Ktaoua Formation (Anti-Atlas, Morocco). (a) Specimen with rounded theca; MHNN.P.045601, Piste de Jorf (ECR-F3). (b) Specimen with 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 NH₄Cl. 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 NH₄Cl. 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 NH₄Cl.
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 NH₄Cl. Scale bar represents 1 cm.

881