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The first Ordovician cyclocystoid (Echinodermata) from Gondwana and its morphology, paleoecology, taphonomy, and paleogeography

Mike Reich,[1,2,3] James Sprinkle,[4] Bertrand Lefebvre,[5] Gertrud E. Rössner,[1,2,3] and Samuel Zamora[6]

[1]SNSB – Bavarian State Collection of Palaeontology and Geology, Richard-Wagner-Strasse 10, 80333 München, Germany ⟨m.reich@lrz.uni-muenchen.de⟩, ⟨g.roessner@lrz.uni-muenchen.de⟩
[2]Department of Earth and Environmental Sciences, Division of Palaeontology and Geobiology, Ludwig-Maximilians-Universität München, Richard-Wagner-Strasse 10, 80333 München, Germany ⟨mike.reich@lmu.de⟩
[3]GeoBio-Center, Ludwig-Maximilians-Universität München, Germany
[4]Department of Geological Sciences, Jackson School of Geosciences, University of Texas, 1 University Station C1100, Austin, Texas 78712-0254, USA ⟨echino@jsg.utexas.edu⟩
[5]UMR CNRS 5276 LGLTPE, Université Lyon 1, 2 rue Raphaël Dubois, 69622 Villeurbanne cedex, France ⟨bertrand.lefebvre@univ-lyon1.fr⟩
[6]Instituto Geológico y Minero de Espana, C/Manuel Lasala 44, 9 B, 50006 Zaragoza, Spain ⟨samuel@unizar.es⟩

Abstract.—*Moroccodiscus smithi* represents a new cyclocystoid genus and species based on moldic specimens from the Middle Ordovician Taddrist Formation (Darriwilian) of SE Morocco. This represents the earliest articulated member of the Cyclocystoidea and is the first complete cyclocystoid described from the Ordovician of Gondwana, as well as the first cyclocystoid ever recorded from Africa. The anatomy and morphology of this new species were studied using a combination of conventional paleontological methods and nondestructive X-ray computed tomography. Because *Moroccodiscus* differs from other cyclocystoids, in particular by lacking cupules attached to the marginal ossicles, it is assigned to the new family Moroccodiscidae. This new taxon illustrates the relatively poorly known early diversification of these enigmatic extinct echinoderms and sheds light on the mode of life of cyclocystoids, including injuries to plate circlets during early ontogeny and folding of these disk-like specimens at the time of death. The overall thecal shape was very similar in cyclocystoids and many domal edrioasteroids, probably because they were both sessile or attached, benthic, suspension feeders. However, many oral surface, ambulacral, and marginal ring features had become very different, indicating that these two groups had either converged because of similar life modes or were only distantly related sister groups.

Introduction

Cyclocystoids are a relatively small extinct class of circular, flattened echinoderms that have been known for more than 160 years. Twenty genera and about 40 valid species have been named (Reich and Kutscher, 2010; Sprinkle et al., 2015), from articulated and disarticulated material, ranging from the Middle Ordovician to the early Carboniferous (Heaslip, 1969; Smith and Paul, 1982; Ressmeyer and Frest, 1983; Berg-Madsen, 1987; Fluegeman and Orr, 1990; Haude and Thomas, 1994; Boczarowski, 2001; Sevastopulo, 2002). Most specimens come from Laurentia and Baltica (Lefebvre et al., 2013), but a few are known from Avalonia and Laurussia. Jell and Jell (1999) published the only report of a cyclocystoid plate from Gondwana (Upper Devonian of Australia). However, our new cyclocystoid material described here represents the second report (and first articulated Ordovician material) of this echinoderm group from Gondwana.

Cyclocystoid morphology has been controversial because well-preserved specimens that show all parts of the animal are rare (Paul, 1982), and several different interpretations of their morphology and life mode have been proposed (Salter and Billings, 1858; Foerste, 1920; Sieverts-Doreck, 1951; Kesling, 1963, 1966). In addition, despite the abundance of cyclocystoids in Ordovician strata (Table 1) in comparison to the Silurian–Carboniferous record, our understanding of their origin and phylogeny lags well behind that of many other echinoderm groups. Smith and Paul (1982) produced a comprehensive monograph of the class using a large number of well-preserved museum specimens and established six new genera. We agree with many of their conclusions involving systematics, biostratigraphy, morphology, diversity, phylogeny, and perhaps biogeography, but disagree with their interpretation of orientation and feeding mode.

The recent discovery of a new cyclocystoid (*Moroccodiscus smithi*) from the Middle Ordovician of Morocco shows somewhat different morphology and additional evidence about the likely living orientation of cyclocystoids. Here we describe the eight specimens of this new taxon that have been assembled by the authors, showing different morphology in comparison to all other known cyclocystoid species, genera, and families. *Moroccodiscus smithi* from the Middle Ordovician of Morocco represents the oldest articulated member of the Cyclocystoidea as well as the first record of this group from Africa.

Table 1. Stratigraphic and geographic distribution of Ordovician cyclocystoid taxa (genera and species).

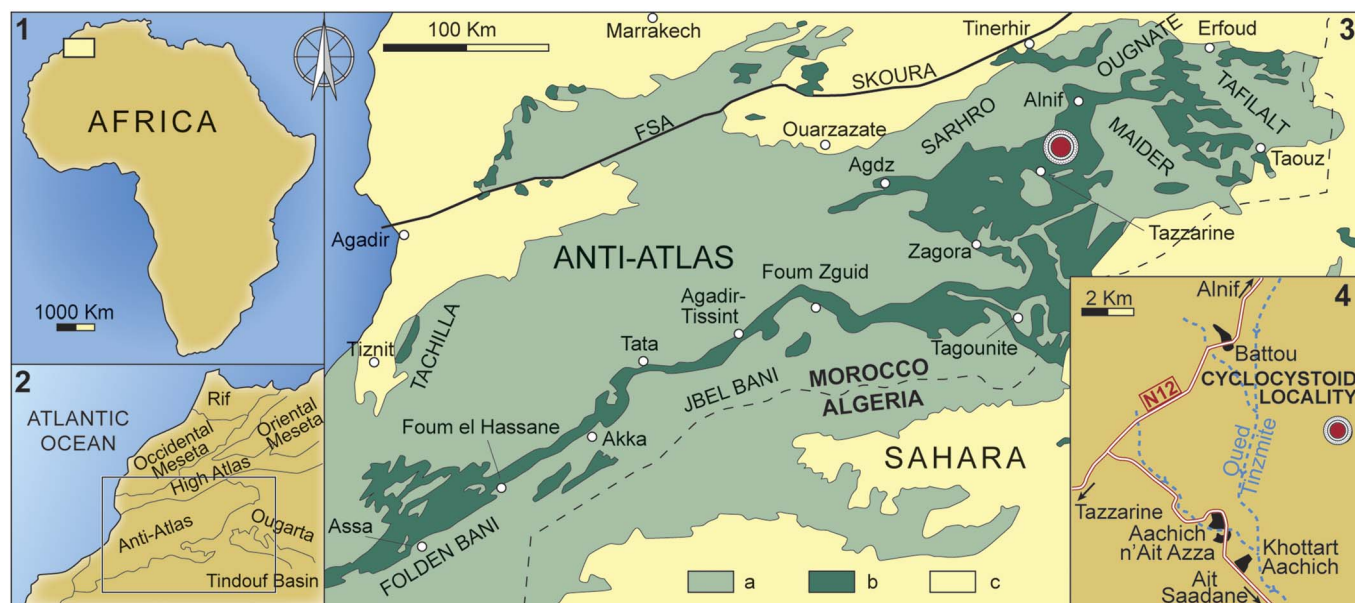| Genus	Species	Age	Location	Country	Paleocontinent
Monocycloides Berg-Madsen, 1987	*Monocycloides oelandicus* Berg-Madsen, 1987	Darriwilian	Öland	Sweden	Baltica
Moroccodiscus Reich, Sprinkle, Lefebvre, and Zamora in Reich et al., 2017 (this paper)	*Moroccodiscus smithi* Reich, Sprinkle, Lefebvre, and Zamora in Reich et al., 2017 (this paper)	Darriwilian	Drâa-Tafilalet	Morocco	Gondwana
Cyclocystoides Salter and Billings, 1858	*Cyclocystoides latus* Smith and Paul, 1982	Sandbian	Ontario	Canada	Laurentia
	Cyclocystoides scammaphoris Smith and Paul, 1982	Sandbian	Illinois	United States	Laurentia
	Cyclocystoides scammaphoris Smith and Paul, 1982	Sandbian	Wisconsin	United States	Laurentia
	Cyclocystoides tholicos Smith and Paul, 1982	Sandbian	Ontario	Canada	Laurentia
	Cyclocystoides sp.	Sandbian	Oklahoma	United States	Laurentia
	'Cyclocystoides' sp.	Sandbian	Ontario	Canada	Laurentia
	Cyclocystoides halli Billings in Salter and Billings, 1858	Katian	Ontario	Canada	Laurentia
	'Cyclocystoides' sp.	Katian	Kentucky	United States	Laurentia
	'Cyclocystoides' sp.	Katian	Wyoming	United States	Laurentia
	Cyclocystoides sp.	Katian	Dalarna	Sweden	Baltica
	'Cyclocystoides' sp.	Katian	Rapla region	Estonia	Baltica
Zygocycloides Smith and Paul, 1982	*Zygocycloides marstoni* (Salter in Smith and Paul, 1982)	Sandbian	Ontario	Canada	Laurentia
	Zygocycloides marstoni (Salter in Smith and Paul, 1982)	Sandbian	Quebec	Canada	Laurentia
	Zygocycloides raymondi (Foerste, 1920)	Sandbian	Ontario	Canada	Laurentia
	Zygocycloides raymondi (Foerste, 1920)	Sandbian	Quebec	Canada	Laurentia
	Zygocycloides sp.	Sandbian	Dalarna	Sweden	Baltica
	Zygocycloides blairi Smith and Wilson, 1995	Katian	Kentucky	United States	Laurentia
	Zygocycloides magnus (Miller and Dyer, 1878)	Katian	Indiana	United States	Laurentia
	Zygocycloides magnus (Miller and Dyer, 1878)	Katian	Ohio	United States	Laurentia
	Zygocycloides marstoni (Salter in Smith and Paul, 1982)	Katian	Ohio	United States	Laurentia
	Zygocycloides marstoni (Salter in Smith and Paul, 1982)	Katian	Brabant	Belgium	Avalonia
	Zygocycloides marstoni (Salter in Smith and Paul, 1982)	Katian	Shropshire	United Kingdom	Avalonia
	Zygocycloides variabilis Smith and Paul, 1982	Katian	Scotland	United Kingdom	Laurentia
	Zygocycloides sp.	Katian	Illinois	United States	Laurentia
Apycnodiscus Smith and Paul, 1982	*Apycnodiscus decussatum* (Begg, 1934)	Katian	Scotland	United Kingdom	Laurentia
	Apycnodiscus salteri (Hall, 1866)	Katian	Michigan	United States	Laurentia
	Apycnodiscus salteri (Hall, 1866)	Katian	New York	United States	Laurentia
Diastocycloides Smith and Paul, 1982	*Diastocycloides nitidus* (Faber, 1886)	Katian	Ohio	United States	Laurentia
Narrawayella Foerste, 1920	*Narrawayella cincinnatiensis* (Miller and Faber, 1892)	Katian	Ohio	United States	Laurentia
Nicholsodiscus Glass, Ausich, and Copper, 2003	*Nicholsodiscus anticostiensis* Glass, Ausich, and Copper, 2003	Katian	Quebec	Canada	Laurentia
Polytryphocycloides Smith and Paul, 1982	*Polytryphocycloides billingsi* (Wilson, 1946)	Katian	Ontario	Canada	Laurentia
	Polytryphocycloides depressus (Billings in Salter and Billings, 1858)	Katian	Ontario	Canada	Laurentia
	Polytryphocycloides depressus (Billings in Salter and Billings, 1858)	Katian	Kentucky	United States	Laurentia
	Polytryphocycloides huronensis (Billings, 1865)	Katian	Ontario	Canada	Laurentia
Scotiadiscus Reich and Smith, 2008	*Scotiadiscus wrighti* (Begg, 1940)	Katian	Scotland	United Kingdom	Laurentia
	Scotiadiscus wrighti (Begg, 1940)	Katian	Oslo region	Norway	Baltica

Figure 1. Geographic and geologic setting of eastern Anti-Atlas Mountains, Morocco, showing type locality of our new cyclocystoid close to the village of Battou. (**1**) Map of Africa. (**2**) Detailed map of northwest Africa showing position of Anti-Atlas Mountains. (**3**) Simplified geological map of Morocco with position of the cyclocystoid locality: (a) Precambrian and Paleozoic rocks; (b) Ordovician rocks; (c) post-Paleozoic cover. (**4**) Detailed geographic map indicating location of the cyclocystoid locality (after Rábano et al., 2014, modified).

Geological setting and stratigraphy

The Ordovician succession is particularly thick and well exposed in the Anti-Atlas Mountains of southern Morocco (Destombes et al., 1985; Fig. 1). It is traditionally subdivided into four main lithostratigraphic units: the Outer Feijas Group; the First Bani Group; the Ktaoua Group; and the Second Bani Group (Choubert, 1942; Choubert and Termier, 1947; Destombes, 1971; Destombes et al., 1985; Marante, 2008).

The Outer Feijas Group includes the Lower and Upper Fezouata formations (Tremadocian–Floian), the Zini Formation (late Floian), and the Tachilla Formation (Darriwilian) (Fig. 2). The Zini Formation corresponds to a diachronistic facies consisting of sandstones and massive quartzites, which is laterally equivalent to part of the Upper Fezouata Formation (Destombes, 1962, 1971; Destombes et al., 1985). The Zini Formation is absent in the western Maïder area (Tazzarine-Alnif area), where the cyclocystoids were collected. The three other units belonging to the Outer Feijas Group are characterized by fine-grained siliciclastic deposits (shales, siltstones), with some thin sandstone interbeds (Destombes, 1962, 1971; Destombes et al., 1985). In the Zagora area (central Anti-Atlas), the Lower and Upper Fezouata formations have yielded exceptionally preserved Burgess Shale-type faunas including anomalocaridids, demosponges, and marrellomorphs (Fezouata Biota; Botting, 2007; Van Roy et al., 2010, 2015; Lefebvre et al., 2016a; Martin et al., 2016).
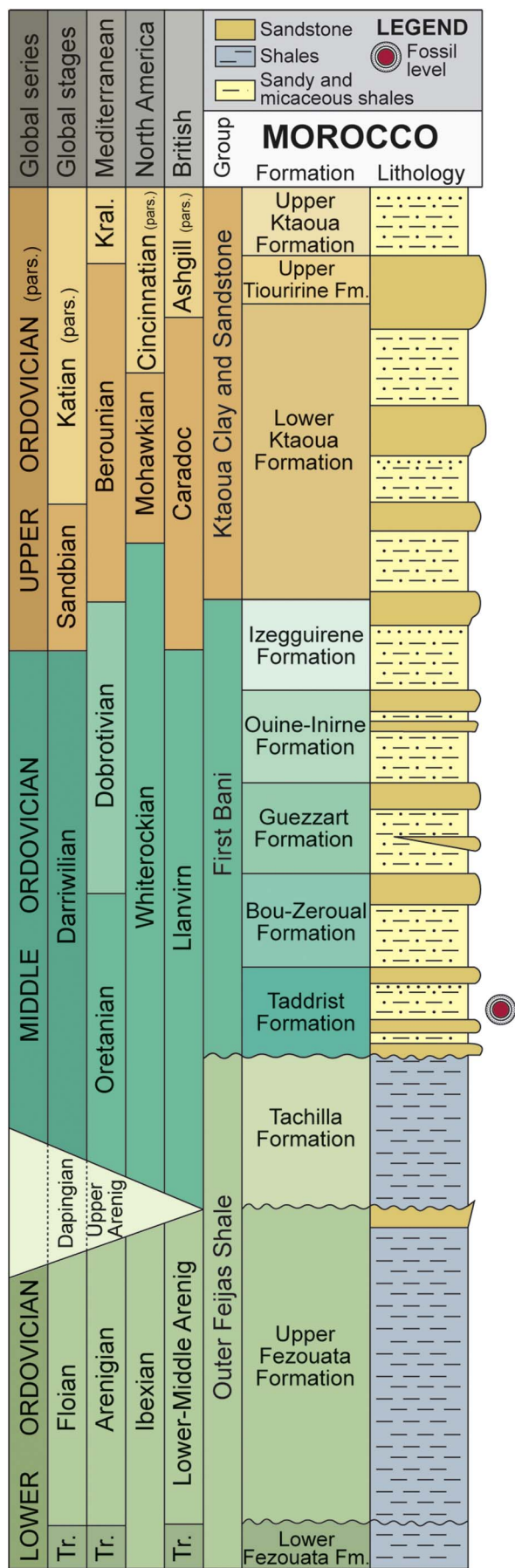
The overlying First Bani Group (Darriwilian–earliest Sandbian) is the thickest, most constant, and most extensive sandstone group in the Anti-Atlas (Choubert, 1942; Destombes, 1971; Destombes et al., 1985). It is subdivided into five sandstone units with interbedded shales: the Taddrist, Bou-Zeroual, Guezzart, Ouine-Inirne, and Izegguirene formations (Fig. 2). The biostratigraphy and fossil taxa recovered from the First Bani Group were both thoroughly reviewed by Gutiérrez-Marco

et al. (2003), while its sedimentology and sequential stratigraphy were investigated by Marante (2008). In the eastern Anti-Atlas, the uppermost part of the First Bani Group has yielded exceptionally preserved assemblages comprising cheloniellid arthropods, eldonioids, and palaeoscolecid worms (Tafilalt Biota; Samuelsson et al., 2001; Alessandrello and Bracchi, 2003; Van Roy, 2006; Lefebvre et al., 2008; Gutiérrez-Marco and Garcia-Bellido, 2015).

The First Bani Group is conformably overlain by the Ktaoua Group (Sandbian–Katian), which is predominantly composed of siltstones, with a variable number of interbedded sandstone units (Destombes, 1962, 1971; Destombes et al., 1985). It is traditionally subdivided into the Lower Ktaoua (early Sandbian–early Katian), Upper Tiouririne (middle Katian), and Upper Ktaoua (late Katian) formations (Fig. 2). Several occurrences of exceptional preservation have been reported from various levels of the Ktaoua Group, including fully articulated specimens of machaeridian annelids (Vinther et al., 2008) and dense beds of exquisitely preserved echinoderms (Hunter et al., 2010; Lefebvre et al., 2010).

In the Anti-Atlas, the Ordovician succession is topped by the sandstones of the Second Bani Group (Hirnantian), which is generally subdivided into the Lower and Upper Second Bani formations (Destombes, 1971; Destombes et al., 1985; Loi et al., 2010). The Lower Second Bani Formation corresponds to shallow shelf deposits lying conformably over the underlying Upper Ktaoua Formation (Destombes et al., 1985; Loi et al., 2010). The Upper Second Bani Formation represents fluvio-glacial sandstones filling large subglacial tunnel valleys, more or less deeply excavated through the underlying deposits of the Ktaoua and First Bani groups (Destombes et al., 1985; Le Héron, 2007; Loi et al., 2010).

Echinoderm remains were first reported in the Ordovician succession of the Anti-Atlas by Ségaud and Termier (1933),

Figure 2. Chronostratigraphical chart for the Ordovician, indicating the level
that provided the studied specimens. Correlations between stratigraphic units in the
Anti-Atlas (after Destombes et al., 1985; Gutiérrez-Marco et al., 2003; Villas et al.,
2006), British regional time scale (Fortey et al., 1995), North American graptolite
zonal sequences (Webby et al., 2004), Mediterranean regional stages (Gutiérrez-
Marco et al., 2003), and global stages are shown (from Sumrall and Zamora, 2011,
modified). Kral = Kralodvorian; Tr. = Tremadocian; pars. = partial.

who mentioned the presence of diploporitans (*Calix sedgwicki*
Rouault, 1851 and *Holocystites*? sp.) in Darriwilian quartzites
from the Jbel Tachilla (western Anti-Atlas). Since this initial
report, abundant and diverse echinoderm faunas have been
described from various parts of the Anti-Atlas and from all
Ordovician formations (Termier and Termier, 1950, 1970;
Choubert et al., 1953; Ubaghs, 1963; Chauvel, 1966, 1969,
1971a, 1971b, 1977, 1978; Chauvel and Régnault, 1986;
Donovan and Savill, 1988; Cripps, 1990; Beisswenger, 1994;
Le Menn and Spjeldnaes, 1996; Ruta, 1999; Gutiérrez-Marco
et al., 2003; Lefebvre and Fatka, 2003; Lefebvre and Botting,
2007; Lefebvre et al., 2007, 2008, 2010, 2016b; Nardin, 2007;
Régnault, 2007; Hunter et al., 2010; Noailles et al., 2010;
Sumrall and Zamora, 2011; Allaire et al., 2015; Martin et al.,
2015; Nardin and Régnault, 2015; Sprinkle et al., 2015;
Zamora et al., 2015).

As a result, the Anti-Atlas of Morocco is the only peri-
Gondwanan region yielding a relatively complete record of
successive echinoderm faunas from the Tremadocian to the
Hirnantian (Lefebvre et al., 2013). It thus provides a unique
record of the diversification of this clade of marine invertebrates
in siliciclastic settings at high, southern paleolatitudes (close to
the South Pole) during the Great Ordovician Biodiversification
Event (Lefebvre, 2007; Lefebvre et al., 2013). Twelve classes or
distinctive groups of echinoderms have been documented so far
in the Ordovician of the Anti-Atlas, including asteroids, cor-
onates, crinoids, cyclocystoids, diploporitans, edrioasteroids,
eocrinoids, ophiuroids, rhombiferans, solutans, somasteroids,
and stylophorans.

The locality yielding the new cyclocystoid lies in the
Taddrist Formation, close to the village of Battou (South of
Alnif, eastern Anti-Atlas) (Figs. 1, 2). This locality was descri-
bed by Rábano et al. (2014), who provided detailed information
about the faunal content and age based on the presence of key
graptolites and trilobites. In this area, the Taddrist Formation has
been excavated predominantly by local collectors and has yiel-
ded a rich faunal assemblage preserved in carbonate concre-
tions. Only three specimens of cyclocystoids were collected by
us directly from the outcrop; the remainder were acquired from
amateur or commercial collectors or bought at fossil shows
(e.g., Sprinkle et al., 2015). Considering that the concretions
from this bed between 38 and 40 m above the base of the
formation have a characteristic aspect, all of them probably
derive from the same or a laterally equivalent outcrop, and
major differences in their stratigraphic position are not likely.
Unfortunately, original top or bottom of our cyclocystoid con-
cretions from this layer has not been recorded by any of the
collectors, perhaps because many concretions were already
weathered out and lying on the surface of this sloping outcrop.

Rábano et al. (2014) suggested that the levels containing
fossiliferous concretions belong to the *Didymograptus murchi-
soni* graptolite Biozone (Gutiérrez-Marco et al., 2003), which

ranges from the late middle Darriwilian (Dw2) to the early late Darriwilian (Dw3) stage slices of the global chronostratigraphic scale (Gutiérrez-Marco et al., 2008; Bergström et al., 2009). However, the Taddrist Formation also yielded palynomorphs typical of the *Laufeldochitina clavata* chitinozoan Biozone (Marante, 2008; Videt et al., 2010). The stratigraphic range of this biozone is generally considered to be restricted to the base of the late Darriwilian (Dw3) stage slice (Videt et al., 2010; Gendry et al., 2013). Consequently, both graptolites and chitinozoans provide congruent stratigraphic data, supporting an early late Darriwilian age (base of Dw3) for the cyclocystoid level (Fig. 2).

The Taddrist Formation is about 80 meters thick in the western Maïder area (Tazzarine-Alnif area; Marante, 2008; Destombes, 2006). This unit was interpreted as the regressive part of a fourth-order sequence (Marante, 2008). The regressive trend was deduced from the transition from fine shales to bioturbated siltstones and finally bioturbated fine sandstones at the top of the Taddrist Formation. Sedimentary structures indicate the influence of distal storms in an otherwise relatively calm, distal setting, on an almost flat and wide continental shelf.

According to Rábano et al. (2014, p. 367), the fossiliferous concretions have yielded the trilobites *Caudillaenus nicolasi* Rábano et al., 2014, *Morgatia*? *rochi* (Destombes, 1972), *Placoparia* (*Coplacoparia*) n. sp., *Colpocoryphe* sp., *Parabarrandia* aff. *crassa* (Barrande, 1872), and an undetermined cheirurid (*Eccoptochile*? sp.). Other non-trilobite fossils include palynomorphs, mollusks (e.g., a cyrtonellid tergomyan, bivalves such as *Praenucula* sp., and orthoconic nautiloids), hyolithids (*Elegantilites* sp.), echinoderms (Diploporita and Asterozoa indet.), conulariids (*Exoconularia* sp.), and rare graptolites (*Didymograptus* sp.). The sandy shales above and below the fossiliferous trench contain abundant trace fossils such as *Teichichnus* isp. and *Palaeophycus* isp. In addition to the new cyclocystoid described herein, a new crinoid species, *Iocrinus africanus*, was recently described by Zamora et al. (2015).

The occurrence of putative remains of cyclocystoids in the early Sandbian Izegguirène Formation (Late Ordovician) of the eastern Anti-Atlas was mentioned by Lefebvre et al. (2008, 2010, 2013). This report was based on a single specimen, then belonging to the private collection of Laurent Lacombe that is now registered and deposited in the University Lyon 1 collections as UCBL-FSL 712001. However, more precise information obtained in late 2013 from Laurent Lacombe and Patrick Catto (who together collected this specimen and another one, UCBL-FSL 712000, in the mid 2000s) did not confirm this age and geographic origin, but pointed out that the two specimens were indeed collected from the same locality (Battou) and level (Taddrist Formation) described in Rábano et al. (2014).

Preservation and taphonomy

Most of the known specimens of this new cyclocystoid were preserved in siderite-encrusted (iron carbonate) concretions (Figs. 3.3–3.15, 4, 5) with a fine clastic internal matrix (siltstone?). The concretions probably formed around the specimens during early diagenesis because of decay of soft tissues and movement of Fe and CO_3 ions through the porous matrix. At least one specimen (Fig. 3.1, 3.2; UCBL-FSL 712001) was found on a slab with similar matrix that may have been a hardground. Both occurrences probably represent repeated storm or slump deposits that buried the specimens alive in a clastic seafloor environment that was near storm wave base on a deep shelf in high-latitude Gondwana.

Many of our cyclocystoid specimens are slightly to moderately damaged, including injuries that occurred during life, damage from catastrophic events that killed, partly or completely buried, and eventually entombed them in their siderite concretions, or damage that occurred during present-day weathering or when the exposed or dug-up concretions were split open. A few specimens, such as our very large holotype (Fig. 3.1, 3.2), are complete and very well preserved, except for some loss of detail because of weathering or later casting on the inferred top mold surface, and some loss of the outer fringe region on the bottom mold that extends to the edge of its smaller slab. Another paratype is nearly complete but may be upside down in its concretion, which apparently occurred at the time of death. Other nearly complete specimens show small or large stunted areas in their marginal rings (Fig. 4.1, 4.2, 4.6, 4.7), probably from nonlethal injuries or predation during life. Others are missing parts of their ossicle ring, frontal plates, and peripheral fringe from breakage when they were killed, or disarticulated plates are strewn over the adjacent mold surface because the carcass was lying partly exposed on the seafloor. Two paratypes are mostly complete and fairly well preserved but folded over in their concretions, with their top and bottom mold layers nearly superimposed (Figs. 3.5, 3.6, 3.12, 3.13, 4.3–4.5), probably because of high currents or seafloor slumps that tumbled and perhaps broke these folded specimens. Many additional specimens in concretions are poorly preserved or incomplete (e.g., Fig. 3.10, 3.11, 3.14, 3.15). This may have occurred at the time of death, during diagenetic concretion growth, during recent weathering, or when the concretions broke up while being split open and not all the mold pieces were recovered.

Materials and methods

Specimens, repositories, and institutional abbreviations.— About 20 specimens of this new cyclocystoid from the Ordovician of SE Morocco are known; this study is based on eight type specimens (and their casts; Fig. 3.1–3.15) now housed at the Collections de Paléontologie, Laboratoire de Géologie, Lyon 1 University, Villeurbanne, France (UCBL-FSL), the Natural History Museum, London, U.K. (NHMUK), the Non-vertebrate Paleontology Laboratory, University of Texas, Austin, USA (NPL), and the Bavarian State Collection of Palaeontology and Geology, Munich, Germany (SNSB-BSPG). These cyclocystoids were collected during several field campaigns (NHMUK-EE 15409, 15413, 16220), donated (UCBL-FSL 712000, 712001; NPL 74385, 74386), or purchased (NPL 62451). The materials we have assembled for this study (holotype, seven paratypes, and additional photographed specimens) are listed with abbreviated stratigraphic locality information.

Specimen #1, UCBL-FSL 712001, top and bottom counterpart molds on slabs (Fig. 3.1, 3.2), region of Taichoute, central Anti-Atlas, Morocco—'First Bani Group,' Darriwilian; coll. Patrick Catto (collected in the mid-2000s; donated November 2013); specimen #2, UCBL-FSL 712000, top and bottom counterpart molds in concretion (Fig. 3.3, 3.4), region of Taichoute, central Anti-Atlas, Morocco—'First Bani Group,' Darriwilian; coll. Patrick Catto (collected in the mid-2000s, donated November 2013; specimen #3, NPL 62451, top and bottom counterpart molds in concretion (Fig. 3.8, 3.9), same trilobite trench locality as mentioned in NHMUK specimens, listed as Oumjrane, NE of Zagora, SE Morocco (30.639525°N, 005.104275°W)—Darriwilian; purchased by James Sprinkle from Moussa Minerals & Fossils at Tucson Fossil Show (February 14, 2014); specimen #4, NPL 74385, top and bottom folded counterpart molds in concretion (Fig. 3.5, 3.6), same trilobite trench locality as mentioned in NHMUK specimens, listed as 4.8 km SE of road N12 at Battou, SE Morocco (30.55223°N, 005.15240°W)—Darriwilian; donated by Kraig Derstler (April 9, 2016), who purchased it online in January 2014; specimen #5, NPL 74386, top and bottom folded counterpart molds in concretion (Fig. 3.12, 3.13), same trilobite trench locality as mentioned in NHMUK specimens, listed as 4.8 km SE of road N12 at Battou, SE Morocco (30.55223°N, 005.15240°W)—Darriwilian; donated by Kraig Derstler (April 9, 2016), who purchased it online in July 2014; specimen #6, NHMUK-EE 15409, top and bottom counterpart molds in concretion (Fig. 3.14–3.15), trench at foot of small hill about 5 km SSE of the village of Bantu, 23 km SW of Alnif, SE Morocco (30.92025°N, 005.25339°W)—Darriwilian; coll. S. Zamora, (September 2013). specimen #7, NHMUK-EE 15413, top and bottom counterpart molds in concretion (Fig. 3.10, 3.11), trench at foot of small hill about 5 km SSE of the village of Bantu, 23 km SW of Alnif, SE Morocco (30.92025°N, 005.25339°W)—Darriwilian; coll. T. Ewin, A.B. Smith, and S. Zamora, (March 2012); specimen #8, NHMUK-EE 16220, mold on surface of unopened concretion (Fig. 3.7), trench at foot of small hill about 5 km SSE of the village of Bantu, 23 km SW of Alnif, SE Morocco (30.92025°N, 005.25339°W)—Darriwilian; coll. S. Zamora (September 2014).

Additional specimens are in private collections or have been shown online (12 total that we know about): specimen in concretion posted on FossilForum website in 2010 by Moroccan collector and noted by Kyle Hartshorn (information sent to J. Sprinkle, June 2015); specimen in concretion purchased at Tucson Fossil Show, February 2013, by private collector after being photographed by Jeremy Savill (information and photo sent to J. Sprinkle, April 2014); two nearly complete and three partial specimens personally owned by Jeremy Savill and purchased between 2010 and 2015 (photos sent to J. Sprinkle, June 2015); partial specimen in concretion shown at the Munich Mineral Show by Moroccan collector (M. Reich, October 2015); two nearly complete and two partial specimens personally owned by Kraig Derstler and purchased between 2012 and 2015 (information given to J. Sprinkle, April 2016).

More than six years ago, an early Moroccan cyclocystoid was found (and shown to MR) deposited in a French private collection (Laurent Lacombe, later transferred to the collection of Patrick Catto); it represents the largest cyclocystoid specimen ever found (UCBL-FSL 712001). This early specimen remained in a private collection for several years until it was made available for scientific investigation and then acquired by the University of Lyon (UCBL-FSL). In the meantime, additional specimens were excavated by a London expedition team (Tim Ewin, Andrew B. Smith, Samuel Zamora; NHMUK) or offered for sale by commercial Moroccan fossil dealers (e.g., NPL).

All specimens are preserved as external molds either on slabs of fine-grained siliciclastic matrix (holotype) or in siderite-encrusted siliciclastic concretions (paratypes and other material). The cyclocystoids described here come from the Middle Ordovician Taddrist Formation of the First Bani Group (Darriwilian); the previously mentioned first specimen found (UCBL-FSL 712001) was erroneously reported as Upper Ordovician (Sandbian) in age (Lefebvre et al., 2008, 2010, 2013).

Photography, casting, and X-ray computed tomography.— Specimens were digitally photographed both dry and whitened with ammonium chloride (Fig. 3.1–3.15). One specimen (holotype) was considered robust enough by its collector for latex and silicon casting of matched-counterpart molds, the standard technique, but this degraded the detail shown by the central disk and the radial ducts through the marginal ossicles.

Other concretionary cyclocystoid molds appeared to be too fragile for this type of casting. Therefore, the best-preserved specimens were investigated and additionally documented by high-resolution X-ray computed tomography at the University of Texas High-Resolution X-ray Computed Tomography Facility (UTCT) or at the Bavarian Natural History Collections (SNSB) in Munich (Figs. 4.1–4.10, 5.1, 5.2).

Scanning at these facilities attempted to differentiate the internal air-filled mold of the cyclocystoid from the enclosing siliciclastic matrix in its reassembled concretion encrusted by siderite. This nondestructive technique has recently been used to scan molds of arthropods and a few echinoderms in a variety of sedimentary rocks and concretions (e.g., Garwood et al., 2009; Legg et al., 2012; Rahman et al., 2012). Specimen 3 was scanned in March 2014 at UTCT with a Zeiss (formerly Xradia, Pleasanton, CA) MicroXCT 400 at 110 kV and 0.09 mA using a 1.0 mm CaF_2 filter for a total of 881 slices at 49.0 μm voxel size; specimens 4 and 5 were scanned in April 2016 at UTCT with an NSI scanner (North Star Imaging, Inc., Rogers, MN) at 150 kV and 0.1 mA with no filter for a total of 977 and 986 slices with 62.6 and 95.6 μm voxel size, respectively. Specimens 1 and 2 were scanned at the Bavarian Natural History Collections

Figure 3. General morphology and preservation of *Moroccodiscus smithi* n. gen. n. sp. from the Darriwilian (Middle Ordovician) of Morocco. (**1, 2**) Holotype UCBL-FSL 712001, top and bottom counterpart molds. (**3, 4**) Paratype UCBL-FSL 712000, top and bottom counterpart molds. (**5, 6**) Paratype NPL 74385, top and bottom counterpart molds. (**7**) Paratype NHMUK-EE 16220, exposed top mold on nearly unbroken concretion. (**8, 9**) Paratype NPL 62451, top and bottom counterpart molds. (**10, 11**) Paratype NHMUK-EE 15413, top and bottom counterpart molds. (**12, 13**) Paratype NPL 74386, top and bottom counterpart molds. (**14, 15**) Paratype NHMUK-EE 15409, top and bottom counterpart molds. All images are photographs of moldic specimens whitened with ammonium chloride sublimate. Scale bar = 10 mm.
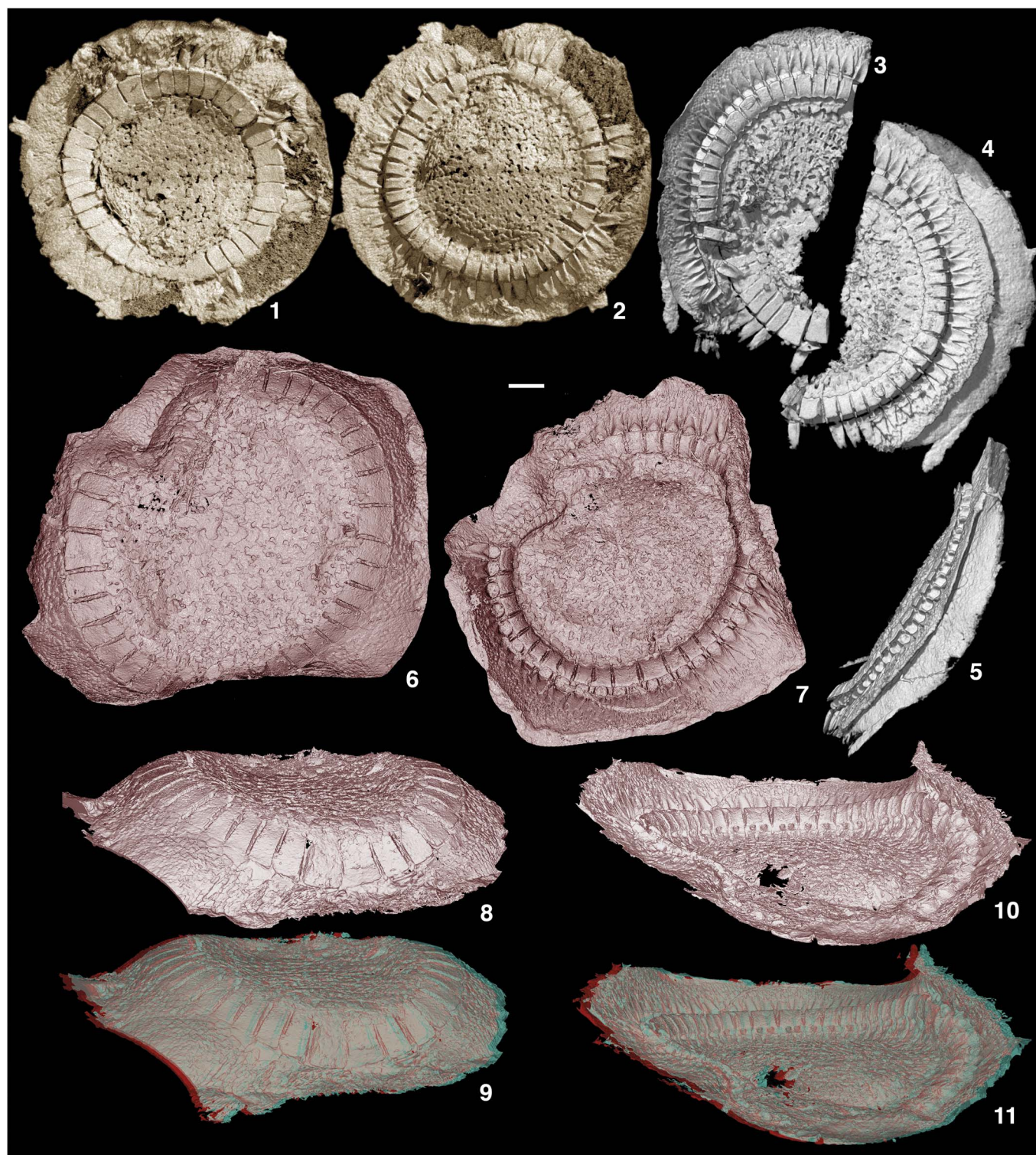
Figure 4. Digitally reconstructed general morphology of *Moroccodiscus smithi* n. gen. n. sp. from the Darriwilian (Middle Ordovician) of Morocco, showing the central disk with pores, the ring of marginal ossicles, the ring of frontal plates, and a wide peripheral skirt. (**1, 2**) Paratype NPL 62451, bottom/top views. (**3–5**) Paratype NPL 74385: (**3, 4**) top/bottom views; (**5**) side view looking toward right edge of 4. (**6–11**) Paratype UCBL-FSL 712000: (**6, 7**) bottom/top views; (**8, 9**) side view looking toward right edge of 6; (**10, 11**) oblique side view looking toward upper edge of 7; (**9, 11**) 3D anaglyph images. Scale bar = 5 mm.

(SNSB) Facility with a phoenix|x-ray nanotom m (GE Sensing & Inspection Technologies GmbH, Wunstorf/Hannover, Germany) at 150 kV and 40 μA (1,400 slices with 42.9 μm voxel size, respectively, and 0.25 mm copper filter), 90 kV and 240 μA (1,720 slices with 23.5 μm voxel size, respectively, and 0.25 mm copper filter) as well as 170 kV and 30 μA (1,400 slices with 27.9 μm voxel size, respectively, and 0.25 mm copper filter).

Visualization and reconstruction were realized with different software applications including ImageJ, SPIERS,
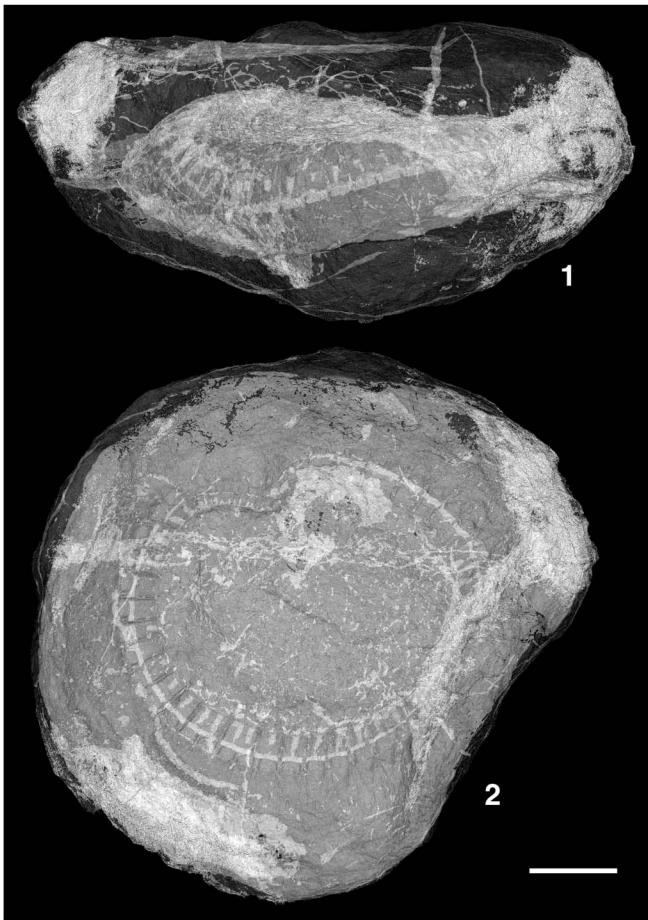
Figure 5. Semitransparent CT digital visualization of a concretion with *Moroccodiscus smithi* n. gen. n. sp. from the Darriwilian (Middle Ordovician) of Morocco. (**1, 2**) Paratype UCBL-FSL 712000, lateral and bottom views. Scale bar = 10 mm.

Avizo Lite v. 9.1, and VGStudio Max 2.2, 3.0 (cf. Rahman et al., 2012; Sutton et al., 2014). Drawings and figures were produced using Adobe Photoshop.

Web-deliverable versions of the animations for NPL paratypes 62451, 74385, and 74386, as well as the original high-resolution X-ray CT data, are available at DigiMorph.org (http://digimorph.org/specimens/Moroccodiscus_smithi/NPL62451/, http://digimorph.org/specimens/Moroccodiscus_smithi/NPL74385/, http://digimorph.org/specimens/Moroccodiscus_smithi/NPL74386/).

Systematic paleontology

The terminology and classification used follows in part Smith and Paul (1982).

Subphylum Echinozoa (Haeckel in) von Zittel, 1895
Class Cyclocystoidea Miller and Gurley, 1895

Remarks.—At present there is still no accepted higher-level ('ordinary') classification of Cyclocystoidea. As a well-defined group of echinoderms, cyclocystoids consisted of a single (cupule-bearing) family—the Cyclocystoididae Miller, 1882—for many years (Smith and Paul, 1982). However, Boczarowski (2001) revised the group by restricting the family Cyclocystoididae to include forms having a ring of 28–45 marginal ossicles and typically two cupules, as well as by proposing the Apycnodiscidae, including cyclocystoids with (16)18–33 marginal ossicles and 1–7 cupules each. We disagree with this systematic assumption (in simple counting of marginal ossicles) and accept (following in part Smith and Paul, 1982) that the absence or presence of cupules (with or without tubercles) and the arrangement of differently perforated marginal ossicles are more useful 'family' characteristics.

Family Moroccodiscidae Reich, Sprinkle, Lefebvre, and Zamora, new family

Type and only genus.—*Moroccodiscus* Reich, Sprinkle, Lefebvre, and Zamora, new genus.

Diagnosis.—Medium to large cyclocystoids lacking cupules attached to the marginal ossicles, and instead having hinged, elongate-trapezoidal frontal plates taking their place, one per radial duct.

Age and occurrence.—Middle Ordovician of Morocco, North Africa.

Discussion.—This Moroccan cyclocystoid appears to represent a new family because it lacks cupules on the outer edge of the marginal ossicles and has elongate-trapezoidal, trough-shaped frontal plates sutured there instead, one per radial duct through the ossicles.

Genus *Moroccodiscus* Reich, Sprinkle, Lefebvre, and Zamora, new genus

Type and only species.—*Moroccodiscus smithi* Reich, Sprinkle, Lefebvre, and Zamora, new species.

Diagnosis.—Medium to large, nearly circular (to subpentagonal) cyclocystoids with poorly defined radiating food grooves on two-layer central disk; marginal ossicles rectangular or trapezoidal, domed, having only one or two radial ducts, typically in a '22111121111' ray pattern in large specimens or '2211111111(1)' ray pattern in smaller specimens, no cupules on outside edge; frontal plates elongate, trough-shaped, one per marginal duct; peripheral skirt wide, beneath, between, and outside frontal plates.

Etymology.—Named for Morocco, where these specimens were found, and combined with the Latin *discus* = disk.

Age and occurrence.—Middle Ordovician of southeastern Morocco, North Africa.

Discussion.—*Moroccodiscus* is clearly distinguished from all other cyclocystoid genera by lacking cupules on the outside edge of the marginal ossicles and by the presence of hinged, elongate-trapezoidal frontal plates instead. All other genera have cupules either with tubercles (*Apycnodiscus*
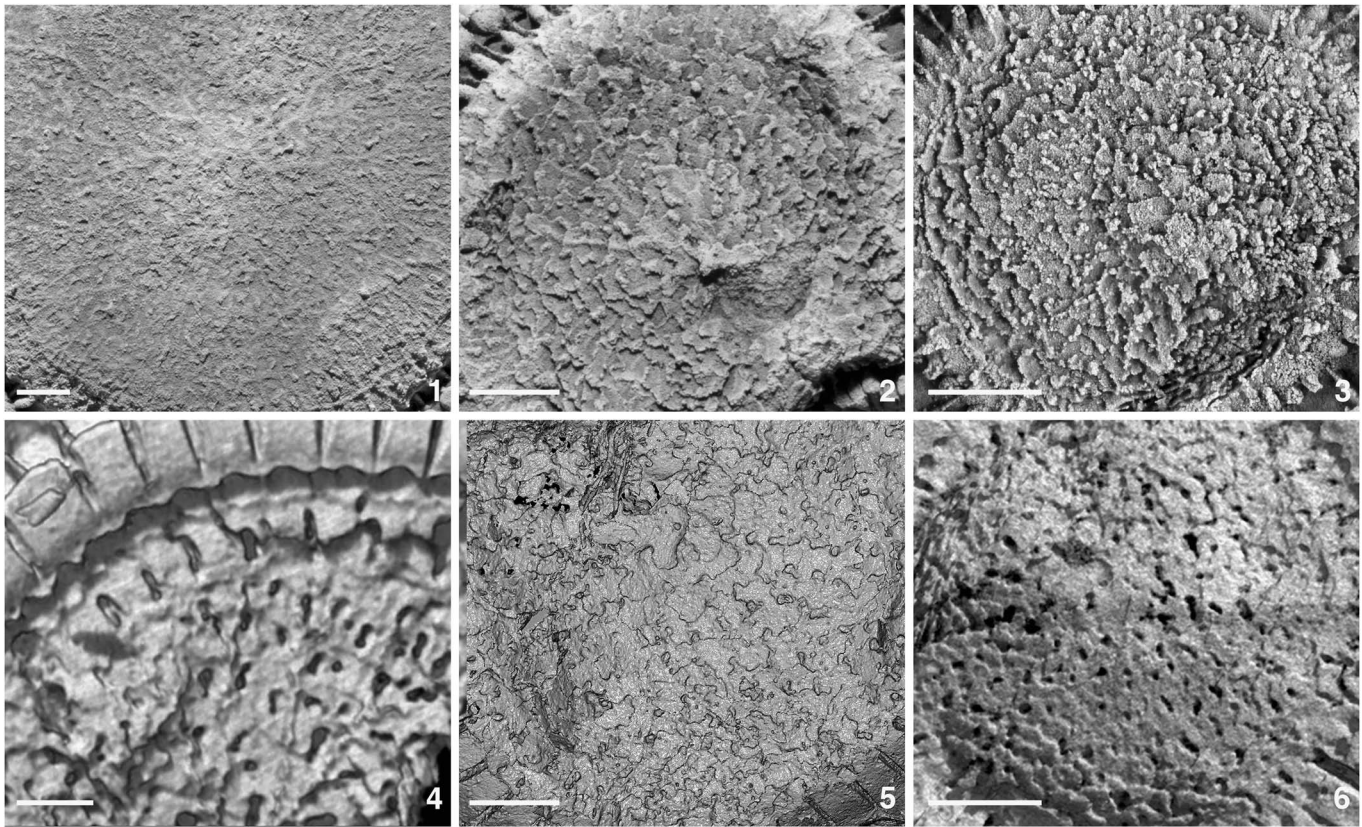
Figure 6. Detailed morphology and preservation of *Moroccodiscus smithi* n. gen. n. sp. showing the central disk (top side) made of small imbricating plates with pores between indistinct ambulacral grooves. (**1**) Holotype UCBL-FSL 712001. (**2, 5**) Paratype UCBL-FSL 712000. (**3, 6**) Paratype NPL 62451. (**4**) Paratype NPL 74385. (**1–3**) Photographs of moldic specimens whitened with ammonium chloride sublimate. (**4–6**) Digitally reconstructed CT images. Scale bars = 5 mm.

Smith and Paul, 1982; *Brutocycloides* Boczarowski, 2001; *Diastocycloides* Smith and Paul, 1982; *Polytryphocycloides* Smith and Paul, 1982; *Scotiadiscus* Reich and Smith, 2008; *Sievertsia* Smith and Paul, 1982; *Zygocycloides* Smith and Paul, 1982), or without tubercles (*Concavocycloides* Boczarowski, 2001; *Cyclocystoides* Salter and Billings, 1858; *Minicycloides* Haude and Thomas, 1994; *Monocycloides* Berg-Madsen, 1987; *Smithocycloides* Boczarowski, 2001).

Two genera (*Narrawayella* Foerste, 1920; *Nicholsodiscus* Glass, Ausich, and Copper, 2003) are only known from specimens showing the non-cupule-bearing side, and a few others (*Apparatocycloides* Boczarowski, 2001; *Chimaerocycloides* Boczarowski, 2001; *Linguacycloides* Boczarowski, 2001; *Neocyclocystoides* Boczarowski, 2001; *Paradoxocycloides* Boczarowski, 2001; *Platycycloides* Boczarowski, 2001) are too poorly diagnosed because these are based only on isolated marginals from acetic/organic acid residues with limited diagnostic value because of preservation.

Moroccodiscus smithi Reich, Sprinkle, Lefebvre, and Zamora, new species
Figures 3–10

2015   New cyclocystoid specimen; Sprinkle et al., figs. 1A–F, 2D.

Holotype.—UCBL-FSL 712001, part and counterpart (casts NHMUK-EE 16221, SNSB-BSPG 2016 I 21, and NPL 83399).

Paratypes.—UCBL-FSL 712000, part and counterpart; NPL 62451, part and counterpart; NPL 74385, part and counterpart; NPL 74386, part and counterpart; NHMUK-EE 15409, part and counterpart; NHMUK-EE 15413, part and counterpart; NHMUK-EE 16220, unopened concretion.

Diagnosis.—Medium-large, nearly circular *Moroccodiscus* with two-layered, thin, central disk, slightly imbricate floor, and cover plates indistinct; 38–54 large, thick, rectangular, domed marginal ossicles with either one or two large radial ducts passing through them, no cupules on distal edge of marginal ossicles that overhangs duct entrance(s); frontal plates elongate-trapezoidal, thinner, trough-shaped, sutured to each marginal ossicle beneath each radial duct; peripheral skirt wide, imbricate, plate size decreasing outward, extending beneath, between, and outside frontal plates.

Age and occurrence.—The type section for *M. smithi* is a long trilobite trench with concretions in sandy and micaceous shale just above second sandstone interval near middle of Taddrist Formation (Darriwilian Stage, Middle Ordovician), ridge above Oued Tinzmite dry washes about 5.8 km SE of small settlement of Battou on route N12, ~23 km SW of town of
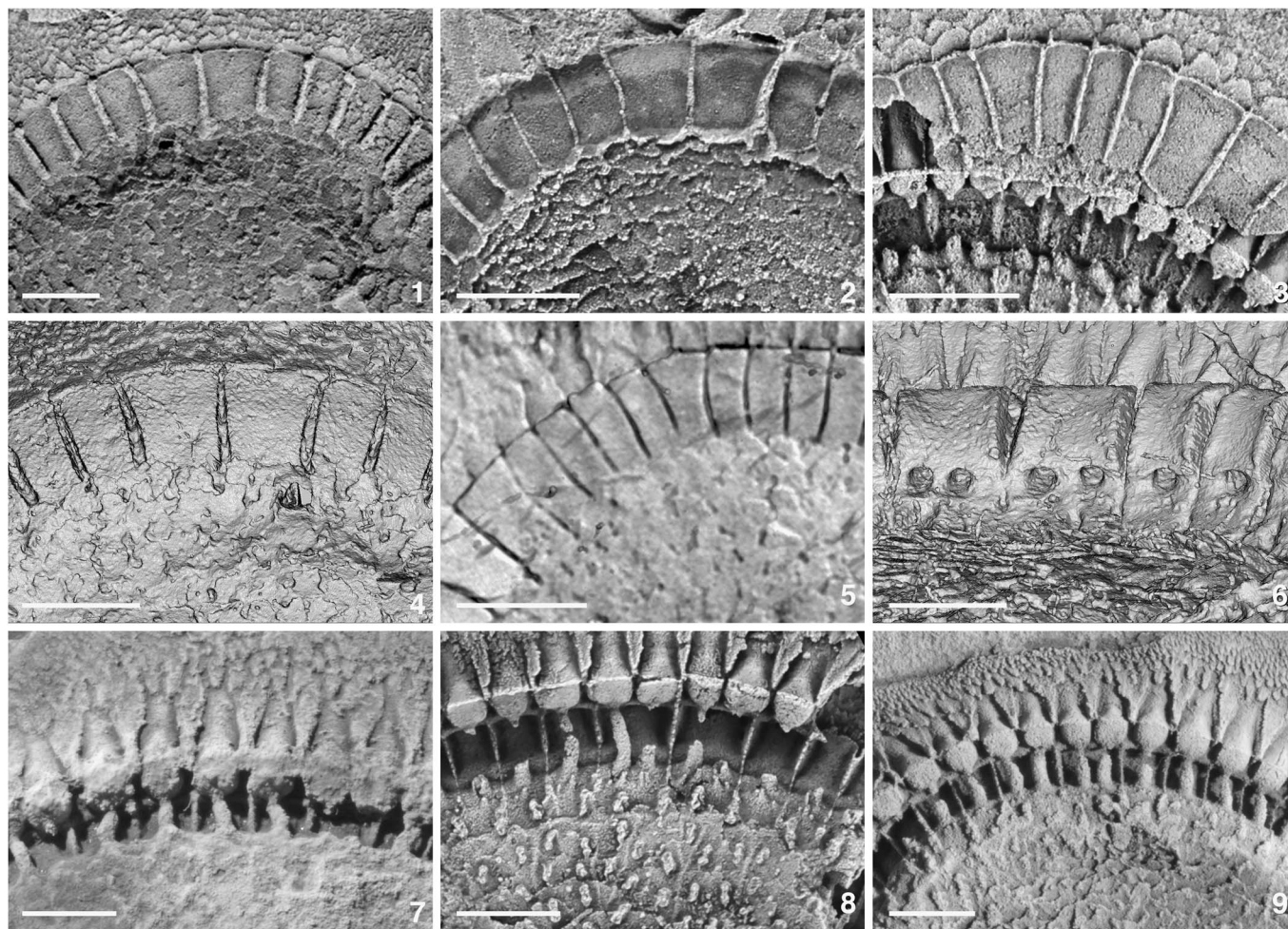
Figure 7. Detailed morphology and preservation of *Moroccodiscus smithi* n. gen. n. sp. showing the marginal ossicles and radial ducts. (**1–5**) rectangular- to trapezoidal-shaped marginal ossicles with one or two radial ducts; the latter ossicles are normally wider and/or trapezoidal. (**1**) Paratype UCBL-FSL 712000; (**2**) paratype NPL 62451; (**3**) paratype NPL 74385; (**4**) paratype UCBL-FSL 712000; (**5**) paratype NPL 74386. (**6**) Both types of marginal ossicles showing the radial duct openings; paratype UCBL-FSL 712000. (**7–9**) Partial marginal rings with steinkern fillings of radial ducts and molds of cupule-like cavities and frontal plates. (**7**) Holotype UCBL-FSL 712001; (**8**) paratype NPL 74386; (**9**) paratype UCBL-FSL 712000. (**1–3, 7–9**) Photographs of moldic specimens whitened with ammonium chloride sublimate. (**4–6**) Digitally reconstructed CT images. Scale bars = 5 mm.

Alnif, eastern Anti-Atlas Mountains, southeastern Morocco, North Africa (see Rábano et al., 2014; Zamora et al., 2015). All known specimens of this cyclocystoid appear to have come from this same thin interval, although the locality has been given several different names by different collectors (30.639525°N, 005.104275°W; 30.92025°N, 005.25339°W; and 30.55223°N, 005.15240°W).

Description.—Most specimens nearly circular, holotype very slightly subpentagonal, axially compressed, many specimens slightly convex on one side, nearly flat or slightly concave on the other side. Most of relief in studied molds located in ring of thick marginal ossicles. Central disk, frontal plates, and peripheral skirt very thin, easily damaged, and more difficult to interpret.

Central disk (Fig. 6): thin, domed, nearly circular area about 61 mm wide in holotype (about 68% of thecal diameter), about 20 mm wide in smaller paratype NPL 62451A (about 50% of diameter); composed of two tightly appressed, thin layers, upper layer of slightly imbricate (toward center), small

(flooring?) plates, each bearing a central, shallow, radiating food groove with elongate pores laterally between plates; lower layer has more rounded pores within polygonal annular plates: two arc-shaped areas near outer margin of disk more disrupted, tilted up, and more clearly imbricate in scans (Fig. 6.1–6.6). Food grooves shallow, difficult to see, in some places marked by plated 'rays' between radiating lines of pores, cover plates on food grooves very small and cryptic, not usually seen; mouth small, usually near center of disk; folded paratype NPL 74386 (Fig. 3.12, 3.13) has small mouth opening partly exposed in fused area (oral frame?) with converging food grooves about one-third its diameter; periproct not seen, possibly lateral.

Marginal ossicles (Figs. 7, 8.1): Holotype having complete circlet of 54 large, rectangular to trapezoidal, thick ossicles with total of 68 radial ducts (Figs. 3.1, 3.2, 7.7, 8.1); smallest paratype NPL 62451 having nearly complete circlet of 33 large ossicles interrupted by about 9 stunted ossicles (Figs. 3.8, 3.9, 4.1, 4.2, 9.7) with total of about 54–55 radial ducts; ossicles with one radial duct nearly rectangular, longer than wide (3.8–3.9 mm long, 2.2 mm wide), nine of these ossicles slightly wider
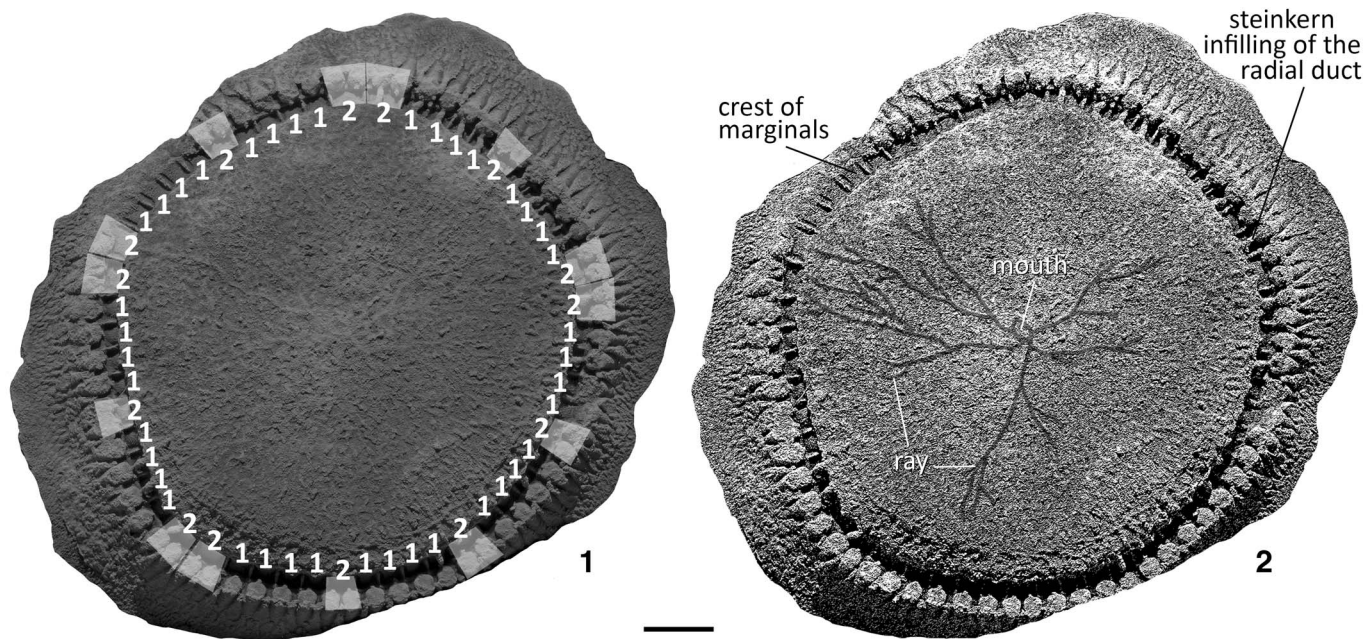
Figure 8. Large holotype (UCBL-FSL 712001) of *Moroccodiscus smithi* n. gen. n. sp. (**1**) Showing marginal ossicle arrangement; position of all double-pore ossicles marked. Note that paired double-pore ossicles all at subpentagonal corners. (**2**) Simplified diagram of the disk, showing the partly preserved pattern of ray branching. Scale bar = 10 mm.

(~3.0 mm wide), with two radial ducts through center, six in pairs, wide, trapezoidal, three unpaired, slightly narrower, trapezoidal; 24 ossicles narrower (~1.8 mm wide, in 5–6 groups of 3–4) with only one radial duct; typical ossicle arrangement in each ray of large holotype and most other specimens is '22111121111' (e.g., Figs. 3.1, 3.2, 8.1), in smaller paratypes '22111111111(1)' (e.g., Figs. 3.3, 3.4, 3.8, 3.9, 4.2, 4.7, 7.9); marginal ossicles gently rounded on top, slightly tilted toward central disk with prominent overhang above duct entrances on distal edge (Fig. 9.1–9.4), separated by thin V-shaped gaps on rounded tops increasing in width distally (e.g., Fig. 7.5, 7.6); ossicles nearly flat on bottom surface with almost no gaps between them; ossicles having medium pustules on top, very small pustules (or stereom) on bottom; few marginal ossicles having slightly curved lateral sutures; one newly inserted ossicle present on paratype NPL 74385 (Fig. 4.4), wedge-shaped top edge does not reach distal edge of ring with gap partly filled by curved edges of adjacent ossicles. No obvious cupules with or without tubercules on distal side of marginal ossicles, which have slightly rounded lower edges sutured to frontals.

Frontal plates (Fig. 9.1–9.5): separate, elongate-trapezoidal, distally tapering, trough-shaped frontal plates attached to lower distal edge of a marginal ossicle (e.g., Fig. 9.1, 9.2, 9.4), each one leading to duct through a marginal (Figs. 7.6, 9.5); about 47 nearly complete frontals present (visible) in holotype UCBL-FSL 712001, 27 present in paratype UCBL-FSL 712000, and 33–34 complete frontals present in paratype NPL 62451; others covered, missing, or in stunted segments; frontals slightly shorter and much thinner than adjacent marginal ossicles, about 3.5 mm long and 1.5 mm wide; laterally bounded (and underlain) by inner edge of imbricate peripheral skirt.

Peripheral skirt (Fig. 9.6–9.8): edge of specimens gradually tapering in thickness, plated below with about 15 diagonal rows

of small to tiny, imbricate, arc-shaped to triangular plates decreasing in size outward, extending between (in V-shaped notches), below, and beyond frontal plates (e.g., Fig. 3.1, 3.4–3.6, 3.8, 3.9). Skirt easily damaged; in small paratype NPL 62451, about one-third of wide skirt missing near where several disrupted frontals present (e.g., Figs. 3.8, 3.9, 4.1, 4.2); plating widest on bottom where skirt about 6–7 mm wide in small paratypes, up to 9.5 mm wide in much larger holotype.

Other features: several plate types (central disk plates, marginal ossicles, frontal plates) show a frosted surface (possibly stereom or tiny pustular ornament) in smoked mold photos or CT scans. The apparent top of the mold is concave and the apparent bottom of the mold is slightly convex as preserved in the original concretion, implying that the original cyclocystoid plating is convex on the top(?) surface and slightly concave on the bottom(?) surface. The central disk with its convex curvature often matches wispy, curved, white lines seen in several concretions (Fig. 10.1, 10.3).

Etymology.—Named for Andrew B. Smith, recently retired from the Natural History Museum, London, who revised the known cyclocystoids for a major monograph in the late 1970s to early 1980s and named many new genera and species (Smith and Paul, 1982; Smith and Wilson, 1995; Reich and Smith, 2008).

Discussion.—The shape and morphology of marginals and frontal plates distinguish this new genus and species from all other known cyclocystoid genera. During ontogeny, the marginal ossicle arrangement apparently changed from 2211111111 (1) (e.g., Figs. 3.3, 3.4, 3.8, 3.9, 4.2, 4.7, 7.9) to 22111121111 (Figs. 3.1, 3.2, 8.1). The detailed arrangement of perforated marginals is clearly understudied in previously described
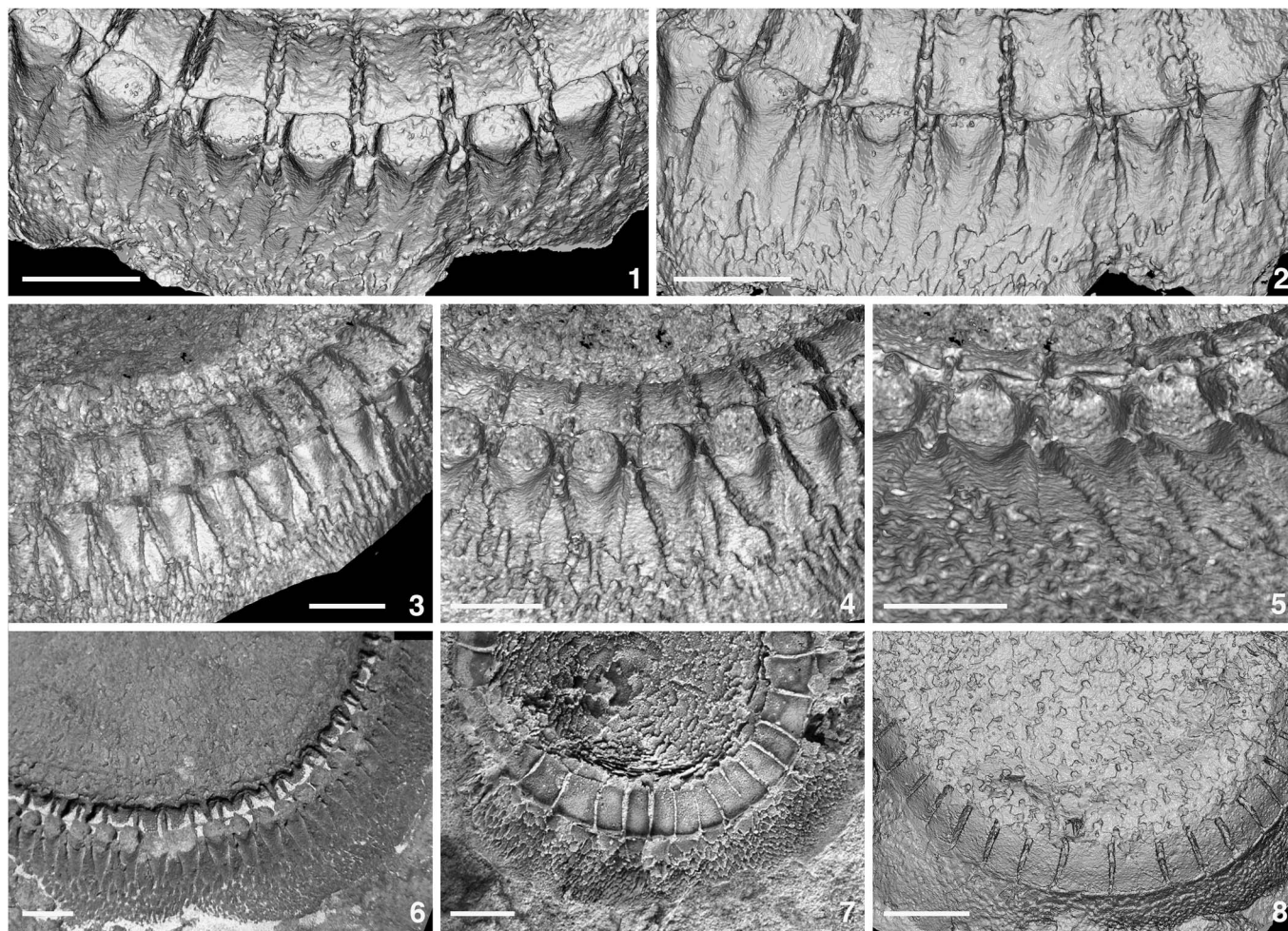
Figure 9. Detailed morphology and preservation of *Moroccodiscus smithi* n. gen. n. sp. showing the frontal plates and the peripheral skirt. (**1–5**) Digitally reconstructed CT images showing the elongate-trapezoidal trough-shaped frontal plates in different views; paratype UCBL-FSL 712000. (**6–8**) Small to tiny, imbricate plates (up to 15 rows) of the wide peripheral skirt in different views: (**6**) moldic holotype UCBL-FSL 712001 top view, not whitened; (**7**) moldic paratype NPL 62451 bottom view, whitened with ammonium chloride sublimate; (**8**) paratype UCBL-FSL 712000 bottom view, digitally reconstructed CT image. Scale bars = 5 mm.

cyclocystoid species but will help in future discussions on higher-level systematics within the Cyclocystoidea.

The elongate, concave frontals sutured to the sloping back edges of the marginal ossicles, mostly under the distal overhang of these large domed plates, the ducts through these plates leading to radiating and distally branching food grooves on the domed central disk, and eventually leading to a central body opening (the mouth?), resembles the upward-facing food-gathering systems of other suspension-feeding echinoderms, such as edrioasteroids. Extending the distal edge of the marginal ossicles into an exposed concave structure and shortening the frontals and perhaps changing their function would produce the cupules found in most other Ordovician cyclocystoids. Some authors, such as Nichols (1969), considered that cupules housed large tube feet, whereas Smith and Paul (1982) believed that these distinct and obviously important skeletal structures were not associated with tube feet. From the partially visible pattern of ray branching in the holotype (UCBL-FSL 712001) and the possible mouth opening near the center of the folded central disk in paratype NPL 74386 of *Moroccodiscus*, we can assume that the mouth is also located near the center of the disk in all specimens of this new species. The interior of the domed central disk has no basal plated surface extending in from the marginal ossicle ring in CT scan cross sections (Fig. 10.1, 10.2). We believe that cyclocystoids were sessile suspension feeders living directly on the seafloor, with the central disk upward and the soft parts protected below it (Sprinkle et al., 2015).

Radial versus interradial orientation in cyclocystoids

Cyclocystoids are nearly radially symmetrical with relatively little irregularity. The mouth appears to have been located in the center of the oral disk in the few specimens where it has been identified, and all the ambulacral grooves, if preserved, apparently lead to this point (Smith and Paul, 1982). The periproct has not been identified in cyclocystoids but, if present, was probably lateral in the posterior interray of the oral disk. The peripheral ossicles, however, do show some irregularity in *Moroccodiscus* and other genera. Because the ambulacra branch dichotomously (Fig. 8.2) during growth away from the central mouth, the marginal ossicles with their pores, cupules, and/or frontal plates
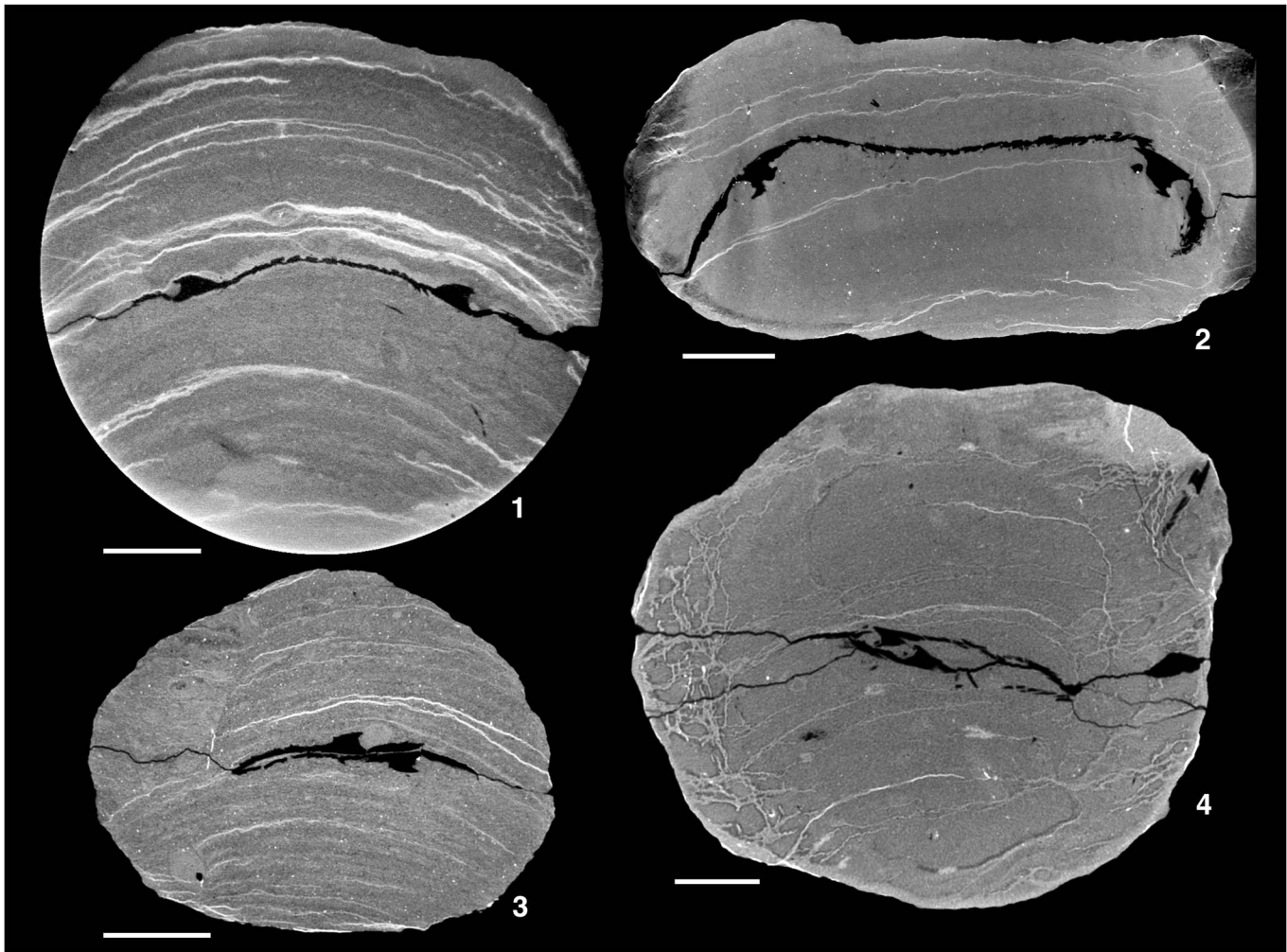
Figure 10. Different slices of X-ray CT-scanned specimens of *Moroccodiscus smithi* n. gen. n. sp., showing various burial features including partial disarticulation, wispy, curved, light-colored, sediment layers in the concretions, and a few light gray burrows. (**1**) Well-articulated complete specimen (paratype NPL 62451; slice 360) showing undisturbed burial with domed central disk, nearly flat marginal ossicles, and slightly raised frontal plates and peripheral fringe, all nearly matching curved, wispy, sediment layers; break into concretion at right. (**2**) Nearly articulated specimen (paratype UCBL-FSL 712000; slice 845) showing undisturbed burial with a nearly flat central disk but highly depressed marginal ossicles, frontal plates, and peripheral fringe (here upside down?) along curved edges of diagenetically growing concretion. (**3**) Folded specimen (paratype NPL 74385; slice 527) in smaller concretion with little siderite showing well-preserved central disk on left and raised tops of marginal ossicles facing outward on right. (**4**) Folded specimen (paratype NPL 74386; slice 590) in large concretion with many cracks and siderite-encrusted areas showing slightly disarticulated central disk on right and raised tops of marginal ossicles facing inward on left. (**3, 4**) Show evidence of more severe seafloor disturbance before burial. Scale bars = 10 mm.

have to increase in number to match the number of ambulacral grooves. *Moroccodiscus* has marginal ossicles arranged in a fairly consistent pattern with one pore through them (most common, 40 total), two pores through a single isolated ossicle (mostly in the larger specimens, usually five total), or two pores through two adjacent ossicles (second most common, usually 10 total) (cf. Figs. 7.1, 7.2, 7.4, 7.6, 8.1). We think the paired double-pore ossicles are most likely interradial and maintain this position, the single-pore ossicles are radial across an ambulacral dichotomous array, and the single double-pore ossicles are added late in ontogeny in the center of this array to support a few more ambulacral branches. In the very large holotype of *Moroccodiscus*, there are 54 marginal ossicles, one less than expected in a specimen with a full complement of adult ossicles; one double-pore ossicle may be missing from this specimen (Fig. 8.1, lower-right side). Up to 10 primary rays may enter the central mouth, even if only five of them are well enough

preserved to be drawn (Fig. 8.2) in this partly weathered specimen. This is a much higher number than previously recorded from other genera (six in *Cyclocystoides* and *Scotiadiscus*, five in *Sievertsia* and *Zygocycloides*, and four in *Apycnodiscus* and *Polytryphocycloides*). By contrast, the relatively small paratype NPL 62451 has only four double-paired two-pore ossicles, perhaps indicating that it had only four ambulacral rays (Fig. 4.1, 4.2), but this may have been affected by the short segment of small stunted plates in the ossicle ring (Fig. 4.2, top).

Growth in cyclocystoids

Like most other fossil and living echinoderms, cyclocystoids can be inferred to have had a free-floating, microscopic larval stage, which was followed by settlement on a suitable substrate and metamorphosis into a tiny, few-plated juvenile version of

the adult body plan. It then probably had a very small oral disk, only five or 10 small, wedge-shaped marginal ossicles, perhaps the same number of frontal plates, and a thin, peripheral fringe. During growth, it then grew the early-formed plates, added new ones between the existing marginal ossicles and frontal plates (we have one example of this [Fig. 4.4], much like a similar example in Smith and Paul, 1982, fig. 12), added new floor(?) plates in rough circlets distal to the existing ambulacral floor plates to lengthen and branch the ambulacra, and added tiny plates to expand the peripheral skirt. We have (or have seen) specimens of this new cyclocystoid ranging from about 30 mm in diameter (incomplete paratype NHMUK-EE 16220), probably a medium-sized juvenile, to around 85 mm in diameter (holotype UCBL-FSL 712001), probably a gerontic adult, with a range of 38 to 54 marginal ossicles, indicating that we are missing most of the juvenile stage. The number of ossicles seems more variable in *Moroccodiscus*, probably because of its large size, compared to other Ordovician genera with a fixed number of cupules and pores (one or two) per ossicle.

Stunted segment in marginal ring

Several specimens (e.g., UCBL-FSL 712000 and NPL 62451) have marginal ossicles (and surrounding plates) in a damaged area stunted and depressed(?) to about half normal size, with central disk plates protruding distally outward (or depressed inward) and peripheral skirt narrower and depressed slightly inward proximally and appreciably inward distally. The damaged area on paratype NPL 62451 is about 5.1 mm wide (about 6.5% of the marginal ossicle ring circumference) and contains several sets of polygonal plates on the flat bottom surface and 12–14 tiny radial ducts extending inward (Fig. 4.2). This implies that about nine or 10 marginal ossicles were affected, most with one pore but a few with two pores. The damaged area probably contained a missing two-pore ossicle on one edge and paired two-pore ossicles near the other edge to agree with adjacent ossicles.

The stunted segment is much larger on paratype UCBL-FSL 712000a, producing a large indent into the usually circular central disk and a smaller indent into the distal peripheral fringe (Fig. 4.7). The stunted segment is at least 16.2 mm wide measured along a curved line (about 15% of the marginal ossicle ring circumference) and includes 17–18 stunted marginal ossicles and frontal plates. Damaged areas such as these with their stunted plates probably indicate previous injuries or non-fatal predation to the margin of the cyclocystoid causing the plates there to either stop growing or regenerate incompletely, but never catching up to normal growth of marginal plates in the adjacent undamaged areas. Similar regeneration features in Paleozoic crinoids, including nipped and regrown arms, regenerated anal tubes, and small plates filling in holes where large cup plates were damaged, have been illustrated by Gahn and Baumiller (2010).

Folded-over specimens

The two Derstler complete paratypes (NPL 74385 and NPL 74386) and one of Savill's partial specimens in his personal collection appear to have the cyclocystoid folded over through the central disk with arcs of the top and bottom surfaces partly or mostly superimposed on what appears to be a half specimen (Figs. 3.5, 3.6, 3.12, 3.13, 4.3–4.5). CT scans of both NPL concretions show most of the central disk membrane folded over with only slight disruption, implying a very flexible central disk, whereas the marginal disk ossicles near the edges of the specimen are snapped apart along sutures and doubled over. Perhaps most interesting is that the foldings in these two specimens have the opposite orientation; smaller paratype NPL 74385 has the domed tops(?) of the marginal ossicles facing outward (Fig. 10.3), whereas larger paratype NPL 74386 has the domed tops(?) of the marginal ossicles facing inward (Fig. 10.4). This probably occurred when living cyclocystoids were subjected to high currents or slumping sediments in storms and were flipped or folded over until the ossicle ring partly broke either before final burial or after burial during compaction of the accumulating sediment. This unusual preservation apparently has not previously been reported in other cyclocystoid genera, judging from figures in Smith and Paul (1982), nor in similarly shaped domal edrioasteroids. Perhaps this resulted from the large size of *Moroccodiscus* versus other cyclocystoids (which weakened and allowed folding of the flattened theca), later changes in cyclocystoid morphology that strengthened the marginal disk and prevented folding in high currents, or the deeper water and fine clastic sediment that rarely formed hardgrounds to which *Moroccodiscus* specimens could tightly adhere. Edrioasteroids are more commonly found attached to skeletonized fossils or to hardgrounds in carbonate settings, and are rarely found detached from their living position and deformed.

Orientation in life and paleoecology

Most earlier authors who named and studied cyclocystoids (Salter and Billings, 1858; Foerste, 1920; Sieverts-Doreck, 1951; Kesling, 1963, 1966; Kolata, 1975) reconstructed them as small-particle suspension feeders living with the flattened ventral side recumbent on or attached to the seafloor. Most later authors (starting with Nichols, 1969, but especially Smith and Paul, 1982, followed by Berg-Madsen, 1987; Rowe, 1988; Glass et al., 2003) reconstructed cyclocystoids as mobile, small-particle deposit feeders with the convex surface down and no large body cavity. Our preliminary report on this new cyclocystoid (Sprinkle et al., 2015) mostly used the morphology of Smith and Paul (1982), but argued that the inferred orientation and life mode used by earlier authors was more likely to be correct.

If cyclocystoids lived convex central disk down (Smith and Paul, 1982), the body space within the cyclocystoid disk would be very small, leaving little room for the digestive system and other soft parts needing protection. For this reason, Smith and Paul (1982) assumed that cyclocystoids had a small, sac-like gut, and much of the digestion and adsorption may have occurred in the permanently covered radial channels. However, the round, flattened shape of this new cyclocystoid, the domed central disk, and the lack of an enclosed body cavity containing the soft parts of the animal indicate to us that cyclocystoids most likely lived with their flat marginal surface downward, sitting
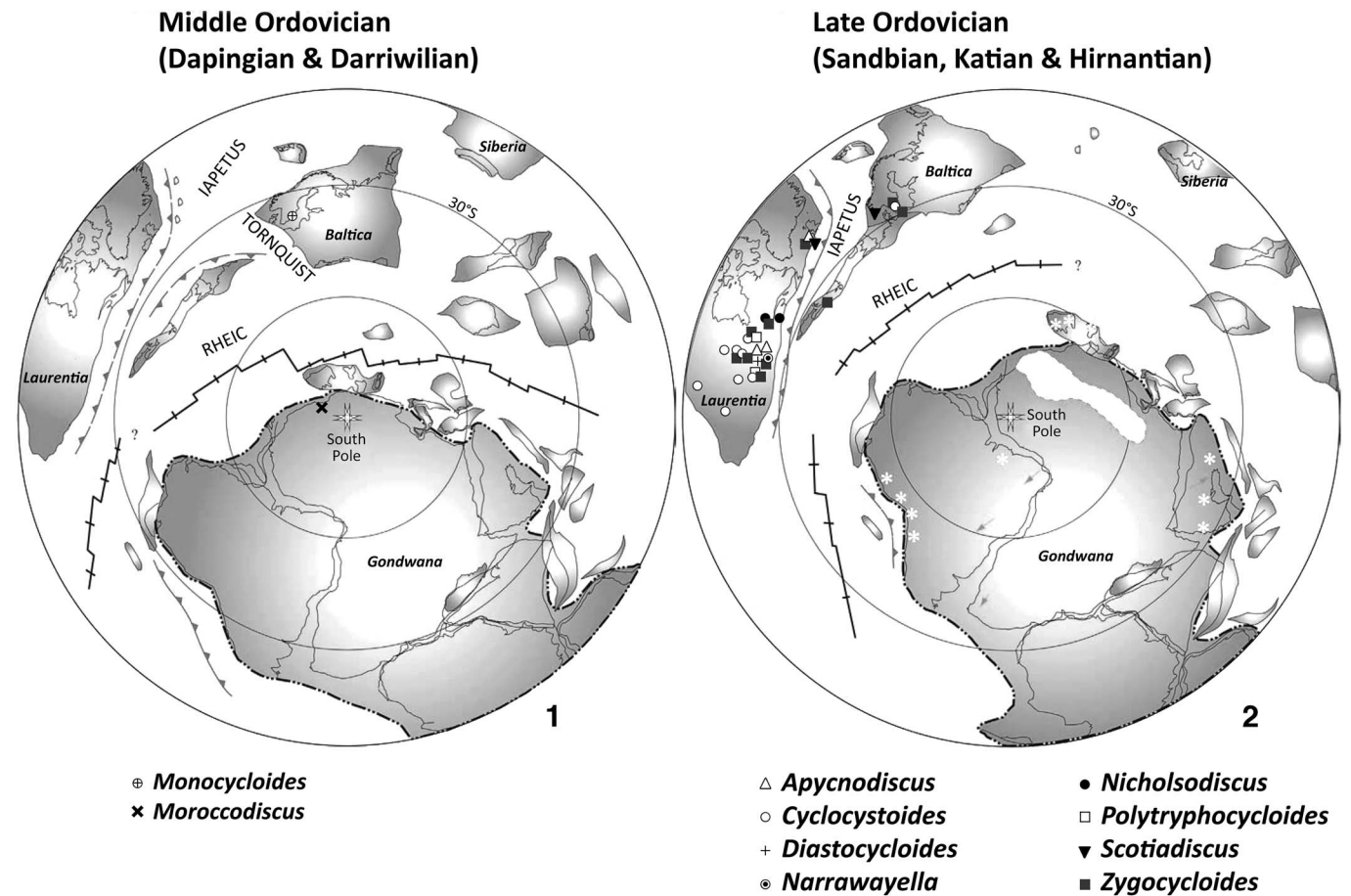
Figure 11. Distribution of the major paleocontinents during the (**1**) Middle and (**2**) Late Ordovician, showing the known geographical distribution of cyclocystoid genera: *Apycnodiscus*, *Cyclocystoides*, *Diastocycloides*, *Monocycloides*, *Moroccodiscus*, *Narrawayella*, *Nicholsodiscus*, *Polytryphocycloides*, *Scotiadiscus*, and *Zygocycloides* (paleogeography from Cocks and Torsvik, 2006; white stars in 2 indicating glacial dropstones, tillites etc.).

on or attached to the seafloor like most post-Cambrian domal edrioasteroids (Guensburg, 1988; Sumrall, 1994). The elongate frontal plates, convex marginal ossicles, and domed central disk with its radiating food grooves were upward-facing regions where food particles were first collected and then transported to a central mouth. The body cavity with these soft parts below the domed central disk sat directly on the seafloor without an underlying plated surface. The flat side of the marginal ring plates and especially the surrounding imbricate peripheral skirt held the cyclocystoid down on the seafloor using the weight of the thick marginal ossicles, perhaps aided by soft-part suction or actual cementation to a stabilized or lithified substrate. Our very large holotype specimen from Morocco is sitting on a yellowish-brown slab that may have been a hardground. Ordovician cyclocystoids are sometimes found on stained carbonate hardgrounds in tropical Laurentia, where cementation was common (e.g., Wilson et al., 1992), and they are predominately found flattened side down (Kolata, 1975; personal communication, T. Guensburg, 2015). However, cyclocystoids are almost never found attached to skeletonized organisms such as brachiopods, trilobites, or conularids, unlike edrioasteroids that commonly attached to these hard substrates (see Sumrall and Zamora, 2011).

Paleogeography and relationship to other cyclocystoids

Moroccodiscus is the oldest known articulated cyclocystoid and only sligtly younger than the oldest cyclocystoid plates (*Monocycloides*; Berg-Madsen, 1987) from the early Darriwilian of Sweden. In contrast to formerly published views (Smith and Paul, 1982), the paleogeographic origins of cyclocystoid echinoderms still remain uncertain and mysterious (Fig. 11) as the previously mentioned oldest (isolated) cyclocystoid material was described from Baltica (Berg-Madsen, 1987), the new form described herein comes from high-latitude Gondwana (Fig. 11.1), but most of the other Ordovician (articulated and disarticulated) cyclocystoids have been reported from Laurentia and Avalonia (Sandbian and Katian; e.g., Kolata, 1975, 1982; Smith and Paul, 1982; Glass et al., 2003; Fig. 11.2, Table 1). The other Ordovician fossil record of cyclocystoids from Baltica is rather poor (Männil, 1983; Reich et al., 2007; Lefebvre et al., 2013; Table 1) and based only on disarticulated material.

Moroccodiscus may be most closely related to *Monocycloides* from Baltica, which is very slightly older, and *Cyclocystoides* from Laurentia and Baltica, which is slightly to much younger, because both of these genera have cupules that

lack tubercles on the marginal ossicles, unlike other Ordovician and most later cyclocystoid genera.

Conclusions

The new cyclocystoid *Moroccodiscus smithi* is described from the middle Taddrist Formation (Darriwilian, Middle Ordovician) in southeastern Morocco from eight type specimens. Most specimens are preserved as molds in split-apart siderite concretions and have been CT scanned (a nondestructive imaging technique) instead of being cast in latex or silicone, which would have damaged fragile structures. *Moroccodiscus* is assigned to the new family Moroccodiscidae because it lacks the cupules on the distal side of the marginal ossicles found in many other cyclocystoids. Food-gathering structures may have been shared between the distal edge of the marginal ossicles and the proximal edge of the elongate frontal plates. *Moroccodiscus* is the first Ordovician cyclocystoid found in Gondwana and is the earliest cyclocystoid known from complete articulated specimens.

Most of our *Moroccodiscus* specimens are either medium to large juveniles or large adult specimens. We do not have any small juveniles from early in ontogeny in our sample. Two of the *Moroccodiscus* specimens have stunted and perhaps damaged areas in their marginal ossicle rings, perhaps indicating an injury or nonlethal predation in early ontogeny. Two other specimens have been preserved folded over in opposite orientations in their concretions, indicating severe storm activity or large-scale slumping of the seafloor was the likely cause of death in these specimens. This type of preservation has not previously been reported in other cyclocystoid (or similarly shaped domal edrioasteroid) occurrences.

The morphology and preservation of *Moroccodiscus* indicate that cyclocystoids were most likely sessile, benthic suspension feeders with the domed side up and a life mode similar to domal edrioasteroids. However, this early cyclocystoid does not seem to be closely related to any known group of edrioasteroids. Cyclocystoids may have originated in Baltica or NW Gondwana in the Middle Ordovician (Darriwilian), but rapidly spread to several other plates (Laurentia and Avalonia) by the Late Ordovician (Sandbian and Katian), where they greatly increased in diversity and abundance.

Acknowledgments

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