ABSTRACT

Complete, articulated crinoids from the Ordovician peri-Gondwanan margin are rare. Here, we describe a new species, *Iocrinus africanus* sp. nov., from the Darriwilian-age Taddrist Formation of Morocco. The anatomy of this species was studied using a combination of traditional palaeontological methods and non-destructive X-ray micro-tomography (micro-CT). This revealed critical features of the column, distal arms, and aboral cup, which were hidden in the surrounding rock and would have been inaccessible without the application of micro-CT. *Iocrinus africanus* sp. nov. is characterized by the presence of seven to thirteen tertibrachials, three in-line bifurcations per ray, and an anal sac that is predominantly unplated or very lightly plated. *Iocrinus* is a common genus in North America (Laurentia) and has also been reported from the United Kingdom (Avalonia) and Oman (middle east Gondwana). Together with *Merocrinus*, it represents one of the few geographically widespread crinoids during the Ordovician and serves to demonstrate that faunal exchanges between Laurentia and Gondwana occurred at this time. This study highlights the advantages of using both conventional and cutting-edge techniques (~~i.e.~~ such as micro-CT) to describe the morphology of new fossil specimens.

Subjects: Paleontology, Taxonomy

Keywords: ~~Crinoidea,~~ Paleozoic, ~~Ordovician, Morocco,~~ Micro-CT, Paleogeography

NEVER repeat words from the title as key words

INTRODUCTION

Ordovician crinoids from West peri-Gondwana (North Africa and Southwestern and Central Europe) are relatively rare, with only a few species reported from Spain, France, Italy, Morocco, Portugal, and the Czech Republic (Ubaghs, 1969; ~~Ubaghs,~~ 1983; Prokop & Petr, 1999; Ausich, Gil Cid & Domínguez Alonso, 2002; Ausich, Sá & Gutiérrez-Marco, 2007; Correia & Loureiro, 2009; Zamora, Colmenar & Ausich, 2014; Sumrall *et al.*, 2015). Crinoids from Morocco include an incomplete specimen assigned to *Ramseyocrinus* sp. by Donovan and Savill (1988) from the Upper Fezouata Formation, which is Floian (Early ~~Lower~~ Ordovician) in age (*sensu* Ausich, Sá & Gutiérrez-Marco, 2007), and several well-preserved complete specimens of *Rosfacrinus robustus* Le Menn and Spjeldnaes, 1996 from the Upper Tiouririne Formation (Lefebvre *et al.*, 2007), which is ~~dated as~~ Katian (~~Upper~~ Late Ordovician). 'Lower' is not an 'age'

Most of the crinoid genera from the Ordovician of peri-Gondwana are endemic, and this hampers our ability to understand the migration patterns of crinoids during this important time interval, in which several echinoderm classes reached major peaks in diversity (Guensburg & Sprinkle, 2000; Sprinkle & Guensburg, 2004; Nardin & Lefebvre, 2010; Lefebvre *et al.*, 2013). Until now, the only exception was *Merocrinus*, which has been reported from England (Avalonia), Spain (peri-Gondwana), and North America (Laurentia) (Ausich, Gil Cid & Domínguez Alonso, 2002). Herein, we report a new species of *Iocrinus* from the Ordovician of Morocco, thereby extending the range of this genus with certainty to encompass West peri-Gondwana (in addition to Avalonia and Laurentia; Donovan *et al.*, 2011) and confirming its cosmopolitan distribution. *Iocrinus africanus* sp. nov. is described based on a single well-preserved specimen, which was collected from south Alnif (eastern Anti-Atlas, Morocco) and is preserved in a concretion found in the Taddrist Formation, which is Darriwilian in age (Rábano, Gutiérrez-Marco & García-Bellido, 2014). ~~In this paper, we study~~ The new crinoid was studied using both traditional techniques and X-ray micro-tomography (micro-CT). This allows us to describe the morphology of *Iocrinus africanus* sp. nov. in great detail and serves as a basis for comparison with other species of *Iocrinus*.

Geological Setting and Stratigraphy

Ordovician outcrops are very well developed and exposed in the Anti-Atlas Mountains of Morocco (Destombes, Hollard & Willefert, 1985). Many units yield well-preserved specimens of echinoderms, a number of which are currently under study (e.g., Hunter *et al*., 2010; Van Roy *et al*., 2010, in press; Sumrall & Zamora, 2011; Martin *et al*., in press), and these faunas occur throughout sections from the Lower to Upper Ordovician. Numerous clades of echinoderms have been documented in these faunas, including stylophorans, solutes, blastozoans, crinoids, asteroids, edrioasteroids, and cyclocystoids.

The Ordovician succession in the Anti-Atlas region is divided into the following lithostratigraphic units: the Outer Feijas Shale Group, the First Bani Sandstone Group, the Ktaoua Clay and Sandstone Group, and the Second Bani Sandstone Group (Choubert, 1943; Choubert & Termier, 1947; Destombes, Hollard & Willefert, 1985). The Outer Feijas Shale Group includes the Lower and Upper Fezouta formations (Tremadocian–Floian) and the Tachilla Formation (Darriwilian) (Fig. 1). These units are characterized by siltstones that are ~~very~~ rich in graptolites, with some thin sandstone interbeds, and contain exceptionally preserved Burgess Shale-type faunas in places (Van Roy *et al*., 2010, in press; Martin *et al*., in press). The overlying First Bani Group spans the Darriwilian to Sandbian and is subdivided into five formations (Taddrist ~~Formation~~, Bou-Zeroual ~~Formation~~, Guezzart ~~Formation~~, Ouine-Inirne ~~Formation~~, and Izegguirene Formation) that are chiefly comprised of sandstones with interbedded shales. This group is the thickest, most constant, and most extensive sandstone group in the Anti-Atlas Mountains (Destombes, Hollard & Willefert, 1985). The fossil taxa recovered from the First Bani Group were reviewed by Gutiérrez-Marco *et al.* (2003), and there are no reports of crinoids from this time interval.

The First Bani Group is overlain by the Ktaoua Clay and Sandstone Group (Sandbian–Katian), which is comprised of siltstones interbedded with two or three sandstones units, depending on the exact position within the Anti-Atlas Mountains. It is divided into three units: the Sandbian to Katian Lower Ktaoua Formation, the Katian Upper Tiouririne Formation, and the Katian Upper Ktaoua Formation. The Ordovician ends with the Second Bani group, which is Hirnantian in age (not shown in Fig. 1).

The new locality yielding *Iocrinus africanus* sp. nov. lies in the Taddrist Formation, Now in the First Bani Group, close to the village of Battou (south Alnif, eastern Anti-Atlas) (Figs. 1, 2). This locality was recently described by Rábano, Gutiérrez-Marco, and García-Bellido (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 yielded a rich faunal assemblage preserved in carbonate concretions (Fig. 3). Rábano, Gutiérrez-Marco, and García-Bellido (2014) suggested that the levels containing fossiliferous concretions belong to the *Didymograptus murchisoni* ~~graptolite~~ Biozone ? (Gutiérrez-Marco *et al.*, 2003), which is roughly equivalent to the upper Darriwilian 2/basal Darriwilian 3 stage slices of the global chronostratigraphic scale (Gutiérrez-Marco, Sá & Rábano, 2008; Bergström *et al.*, 2009). According to Rábano, Gutiérrez-Marco, and García-Bellido (2014), the fossiliferous concretions have yielded the trilobites *Caudillaenus nicolasi* Rábano, Gutiérrez-Marco, and García-Bellido, 2014, *Morgatia*? *rochi* (Destombes, 1972), *Placoparia* (*Coplacoparia*) sp. nov., *Colpocoryphe* sp., *Parabarrandia* aff. *crassa* (Barrande, 1872), and an undetermined cheirurid (*Eccoptochile*? sp.). Other non-trilobite fossils include molluscs (e.g., a cyrtonellid tergomyan, bivalves such as *Praenucula* sp., and orthoconicnautiloids), hyoliths (*Elegantilites* sp.), echinoderms (Diploporita and Asterozoa indet.), conularids (*Exoconularia* sp.), and rare graptolites (*Didymograptus* sp.). In addition to the crinoid described herein, new cyclocystoids, the first ever reported from Africa, were recently presented from this locality and await formal description (Sprinkle, Reich & Lefebvre, 2015).

Be Metric!

MATERIAL AND METHODS

The studied specimen is preserved in a yellowish carbonate concretion that is approximately ~~7 cm~~ 70 mm in length and ~~4.5 cm~~ 45 mm in width. The crinoid is preserved as a natural mould and includes the complete theca, articulated arms, and part of the column. The specimen is housed in the Museo Geominero (Madrid, Spain) under the repository number MGM 6754.

A latex cast of the specimen was prepared to study the morphology of the animal (Fig. 4). In addition, the specimen was imaged using micro-CT and digitally reconstructed to characterize the fossil in three dimensions (Fig. 5). The specimen was scanned on a Nikon XT H 225 cabinet scanner at the Natural History Museum, London with a 0.5 mm thick copper filter, 215 kV voltage, 177 µA current, and 3142 projections (each with an exposure time of 708 ms). Tomographic reconstruction was performed in Nikon CT Pro software using filtered back projection, giving a tomographic dataset with a voxel size of 37 µm. This dataset was then visualized with the free SPIERS software suite (Sutton *et al.*, 2012); an inverted linear threshold was applied to the dataset, and the pixels that could be unambiguously identified as representing the crinoid were manually assigned to a separate region-of-interest. Isosurfaces were rendered to give an interactive three-dimensional model of the fossil, which was subjected to weak smoothing and island removal to reduce noise. Micro-CT slices, segmented images, and the interactive 3-D model (in VAXML format) are provided as supplemental information (Data S1, S2).

used on p. 10, l.204

Webster (1974)

Terminology

The terminology used below follows Moore (1962), Ubaghs (1978), and Ausich *et al.* (1999); the classification follows Ausich (1998). Note, the terminology used for the aboral plates differs from that of Ausich, Gil Cid, and Domínguez Alonso (2002).

Nomenclatural acts

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:act:D091338E-643F-4D5A-8A08-7D7D190DBC2E. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

RESULTS

Systematic paleontology

h Class CRINOIDEA J.S. Miller, 1821

Subclass DISPARIDA Moore and Laudon, 1943

Order MYELODACTYLIDA Ausich, 1998

Family IOCRINIDAE Moore and Laudon, 1943

Genus *Iocrinus* Hall, 1866

Type species

Heterocrinus (*Iocrinus*) *polyxo* Hall, 1866 = *Heterocrinus subcrassus* Meek and Worthen, 1865. ?

Iocrinus africanus sp. nov.

urn:lsid:zoobank.org:act:D091338E-643F-4D5A-8A08-7D7D190DBC2E

Holotype

MGM 6754, a nearly complete, articulated specimen (not retaining the attachment structure and dististele) preserved as a mould in a carbonate concretion (Figs. 4, 5; Data S1, S2).

Type locality and age

Close to the village of Battou, south Alnif, eastern Anti-Atlas, Morocco (Fig. 2); Taddrist Formation, Darriwilian (Middle Ordovician).

Etymology

Named in reference to the African continent.

Diagnosis

Basal plate height approximately 37 percent of radial plate height; radial plates 1.25 times higher than wide; single, broad transverse ridge between adjacent radial plates; primibrachials 1.5 times wider than high; three to five primibrachials; four to five secundibrachials; seven to thirteen tertibrachials; three in-line bifurcations per ray; anal sac unplated or very lightly plated (except for the robust column of plates from the C-ray superradial); proximal columnals pentastellate.

'Very' is grossly overused by geologists - I delete it here because no locrinus has a large crown.

Description

9 Crown ~~very~~ small in size. Aboral cup medium bowl-shaped; smooth plate surfaces; radial and basal plates sharply convex.

Basal circlet 27 percent of aboral cup height; five basal plates, approximately ~~2~~ two times wider than high, much smaller than radial plates. Radial circlet 73 percent of aboral cup height; radial plates five, maximum height approximately 1.25 times higher than maximum width; maximum width of radial plate at mid-height, radials narrow sharply proximally, maximum width more than 10 times proximal width; maximum width 1.6 times distal width. Radial facets peneplenary, approximately as deep as wide. A, B, D, E radial plates simple, C radial compound; C inferradial approximately same size as simple radials; C superradial much smaller than C inferradial, wider than high, distal heterotomous division with anal plates to left and C-ray arm to right.

All anal plates above aboral cup; column of 16 stout anal sac plates preserved from the left facet on the C-ray superradial, plates very convex, successive plates with bend yielding a sinuous appearance for this column of plates; each plate higher than wide, otherwise very similar to shape of brachials. Other anal sac plates disarticulated and collapsed within the crown, presumably sac plates were lightly calcified or uncalcified, except for the column of plates from the C superradial.

Arms robust, primaxil varies from third to fifth primibrachial (45553; ABCDE), secundaxil fourth or fifth secundibrachial; where known, tertaxil positioned on the seventh or thirteenth tertibrachial; as many as 16 unbranched quartibrachials on a branch

is it complete, incomplete or don't know?

of the A-ray arm. Brachials strongly convex aborally with flattened lateral, abambulacral extensions, rectangular uniserial, deep ambulcacral groove, more proximal brachials approximately 1.7 times wider than high. Brachial facet with two, merging aboral ligament fossae. Primaxial approximately the same size as non-axillary primibrachials; remaining brachials diminish in size distally.

Column strongly pentastellate, holomeric, heteromorphic, proximal column N3231323;

nodals higher than priminternodals at seg(s)

obvious heteromorphic pattern lacking in mesistele, large portion of columnal facets presumably a petaloid articulation (but details not preserved). Preserved column higher than crown height and preserved in an open coil.

Remarks

Characters differentiating genera within the Iocrinidae are listed in Ausich, Rozhnov, and Kammer (2015). The combination of visible basal plates, three to five primibrachials, no fixed interradial plates, pentalobate/pentastellate columnal shape, holomeric column construction, and a petaloid facet clearly align the new crinoid described herein with the genus *Iocrinus*. Another feature that identifies the specimen as belonging to *Iocrinus* is the preservation of the column in an open coil. This is similar to *Iocrinus subcrassus*, which is thought to have had a holdfast that could coil around erect objects (Brett, Deline & McLaughlin, 2008; Meyer & Davis, 2009).

mention Kelly's MS thesis?

Donovan et al. (2011) placed the British taxa with a conical, smooth cup and pentagonal proxistele in Margoiocrinus Donovan.

Species-level characters within *Iocrinus* include: the height of the basal plates, the height of the radial plates, radial plate height versus width, presence and character of the transverse ridge between adjacent radial plates, primibrachial shape, number of primibrachials, number of secundibrachials, number of tertibrachials, maximum number of in-line bifurcations in a ray, anal sac plating, and the shape of the proximal columnal (Table 1). *Iocrinus africanus* sp. nov. is distinguished from other *Iocrinus* species based on the shape of the radial plates, the number of tertibrachials, the number of bifurcations in-line per ray, and the lack of or very light plating of most of the anal sac.

Donovan *et al.* (2011) reported the only other putative *Iocrinus* known from Gondwana, *I.* sp. cf. *I. subcrassus* from the Middle Ordovician of Oman. Assuming that this taxon does belong to *Iocrinus*, which cannot be confirmed without further information about the CD-interray and C-ray morphologies, the new Moroccan species differs from the Donovan *et al.* (2011) specimen as follows. *Iocrinus africanus* sp. nov. has a basal plate height approximately 37 percent of radial plate height; a broad transverse ridge; primibrachials 1.5 times wider than high; four to five secundibrachials; and three in-line bifurcations per ray. In contrast, *I.* sp. cf. *I. subcrassus* has a basal plate height approximately 50 percent of radial plate height; a narrow transverse ridge; primibrachials slightly higher than wide; seven secundibrachials; and as many as seven in-line bifurcations per ray.

Taxonomic assignments within the Iocrinidae have received some attention in the last three decades (Warn, 1982; Guensburg, 1984; Donovan, 1985, 1989; Ausich, Rozhnov & Kammer, 2015); with the new species described herein, a total of eight species and one subspecies are currently recognized for *Iocrinus* (Webster & Webster, 2014). These include the Laurentian species: *I. crassus* (Meek and Worthen, 1865); *I. similis* (Billings, 1865); *I. subcrassus* (Meek and

What of Iocrinus shelvensis Ramsbottom, 1961? Although it is a Margiocrinus.

Worthen, 1865); *I. subcrassus torontoensis* Fritz, 1925; and *I. trentonensis* Walcott, 1884; and the Avalonian species: *I. llandegleyi* Botting, 2003; *I. pauli* Donovan and Gale, 1989; and *I. whitteryi* Ramsbottom, 1961 (Table 2). Additional *Iocrinus* identifications left in open nomenclature are known from Avalonia, Laurentia, and Gondwana (for the previous potential Gondwanan occurrence, see Donovan *et al.*, 2011). *I.* ocrinus *africanus* sp. nov. is Darriwilian in age, and thus it is among the oldest members of the genus (Table 2). In terms of morphology, it is equally dissimilar to species from both Laurentia and Avalonia. The occurrence of *I. africanus* sp. nov. in Morocco confirms the presence of *Iocrinus* in Gondwana and demonstrates that *Iocrinus*, together with *Merocrinus*, is the most geographically widespread Ordovician crinoid genus.

Do NOT start a sentence with an abbreviation

The use of micro-CT was essential for describing the morphology of *Iocrinus africanus* sp. nov. in full. The posterior interray is buried below the surface of the concretion and is hence not visible in the latex casts (Fig. 4); however, the posterior interray and the C-ray can be clearly seen in the micro-CT scans (Fig. 5; Data S1, S2). Without an understanding of these characters, it would not have been possible to confidently assign the specimen to the genus *Iocrinus*.

PALEOBIOGEOGRAPHICAL IMPLICATIONS

The Middle to Late Ordovician was characterized by high degrees of endemism in crinoids (Paul, 1976; Lefebvre *et al.*, 2013), and *Iocrinus* and *Merocrinus* are the only geographically widespread genera from this period (Fig. 6). Both genera first appeared in Gondwana and/or Avalonia during the Darriwillian. *Merocrinus* first occurred in Laurentia during the Sandbian, and *Iocrinus* first occurred in Laurentia during the Katian. Therefore, the known geographical distribution of these genera indicates that their migration to Laurentia was asynchronous. *Iocrinus* is a disparid crinoid,

Supplemental Information

Supplemental information for this article can be found online at the following links:

S1: https://fluff.bris.ac.uk/fluff/u3/ir12122/2mItdZD36sXtqlZhYzXQtQTES/

S2: https://fluff.bris.ac.uk/fluff/u1/ir12122/4y_W6sShmkjAFWN_tWCeYwTEH/

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FIGURE CAPTIONS

Figure 1. Chronostratigraphical chart for the Ordovician, indicating the levels that provided the studied specimen. Correlations between stratigraphical units in the Anti-Atlas (after Destombes, Hollard & Willefert, 1985; Gutiérrez-Marco *et al.*, 2003; Villas *et al.*, 2006), the British regional time scale (Fortey *et al.*, 1995), North American graptolite zonal sequences (Webby *et al.*, 2004), Mediterranean regional stages (Gutierrez-Marco *et al.*, 2003), and global stages are shown. Modified from Sumrall and Zamora (2011). Abbreviations: Kral., Kralodvorian; pars., partial; Tr., Tremadocian.

Figure 2. Geographical and geological setting of the eastern Anti-Atlas Mountains, Morocco, showing the type locality (indicated by a star) close to the village of Battou. After Rábano *et al.*

(2014).

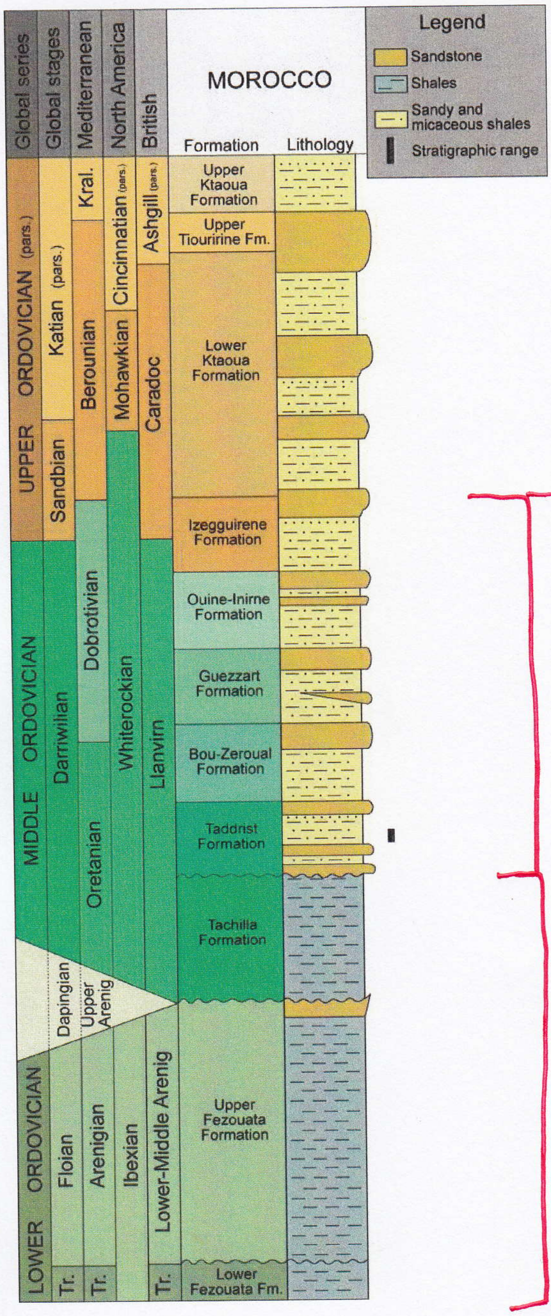
Figure 3. Field photographs showing the Taddrist Formation and the levels yielding fossiliferous concretions. (A) [describe]. (B) [describe]

Figure 4. *Iocrinus africanus* sp. nov. (MGM 6754) from the Darriwilian (Middle Ordovician) of Morocco. A, B. General morphology including the complete theca showing the E-ray (A) and BC-interray (B), the proximal column, and part of the arms. C. Detail of the theca showing the E-ray. D. Detail of the theca showing the A-ray. E. Detail of the theca showing the D-ray. All images are photographs of latex casts of the specimen whitened with ammonium chloride sublimate.

Figure 5. *Iocrinus africanus* sp. nov. (MGM 6754) from the Darriwilian (Middle Ordovician) of Morocco. Digital reconstructions of the specimen. A. General morphology showing the AE-interray. B. Detail of the theca showing the C-ray. C. Detail of the theca showing the BC-interray. D. Detail of the theca showing the D-ray. E. Detail of the column showing pentastellate shape and holomeric construction. F. Detail of the proximal arms showing the E-ray. G. Column in an open coil. Abbreviations: A–E, ambulacra.

Figure 6. Distribution of the major paleocontinents during the Middle Ordovician, showing the known geographical distribution of *Iocrinus* and *Merocrinus*. Modified from Cocks and Torsvik (2006).

FIGURE 1



~~[illegible]~~ Ktaoua Clay and Sandstone Group

First Bani Group

Outer Feijas Shale Group