Preliminary report on new echinoderm Lagerstätten from the Upper Ordovician of the eastern Anti-Atlas, Morocco

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ABSTRACT: Four distinct echinoderm Lagerstätten have recently been discovered in the Upper Ordovician of the eastern Anti-Atlas, Morocco. They have yielded hundreds of exquisitely preserved specimens. Their taphonomy and associated lithology both suggest rapid, in situ burial. Here we discuss the diverse range of assemblages represented and their significance to the diversity of echinoderms in the Lower Palaeozoic.

The oldest assemblage (Izegguirene Formation, lowermost Caradoc) is dominated by eocrinoids, large ophiuroids, and mitrate stylophorans associated with rare crinoids. It shows strong similarities with slightly older faunas described from the underlying Ouine-Inirne Formation (Llandeillian) in the Central Anti-Atlas. The second assemblage (lower part of the Lower Ktaoua Formation, lower-middle Caradoc) is composed of eocrinoids (Cardiocystites) and small ophiuroids (encrinasterid indet.). The third assemblage was collected in the upper part of the Lower Ktaoua Formation (lowermost Ashgill). This ‘starfish’ bed is dominated by ophiuroids and large solutes, associated with common diploporites and rhombiferans, and rare crinoids and mitrates. Finally, the youngest assemblage (lower part of Upper Tiouririne Formation, lower Ashgill) has yielded abundant remains of edrioasteroids and rhombiferans.

1. INTRODUCTION

Four distinct echinoderm Lagerstätten, yielding hundreds of exquisitely preserved specimens, have recently been discovered in the Upper Ordovician of the eastern Anti-Atlas, Morocco in the El Caïd Rami area (Figure 1). Fossils are preserved as fully articulated individuals with even the most delicate skeletal elements, such as brachioles, arms and aulacophores preserved. This preliminary study briefly overviews the taxonomic diversity of these organisms, their taphonomy and their palaeoecology. This investigation is intended to be a taxonomic survey of all the different echinoderm groups represented. However, more detailed systematic descriptions of the fossils are in progress and will be published elsewhere. Here we discuss the diverse range of assemblages represented and their significance to the diversity of echinoderms in the Lower Palaeozoic and what can be deduced about their palaeoecology and community structure.
2. STRATIGRAPHY AND ENVIRONMENTAL SETTING

Although the various assemblages are all primarily preserved in clastic rich sediments, the formation of these deposits took place in different environments, representing more than one facies type. However, it is clear that these are life assemblages from relatively shallow palaeoenvironments such as distal upper offshore, their preservation probably resulting from rapid, storm influenced burial. The four fossil assemblages are considered Upper Ordovician in age (Figure 2).

This is the first record of *Ascocystites* in the Ordovician of Morocco. This genus was already described in the Middle Ordovician of Brittany (Chauvel 1941, Régnault 1990) and Portugal (Young & Donovan 1993), and in the lower Caradoc of Bohemia (Barrande 1887, Prokop & Petr 1999).

2.1 Repositories

The material referred to in this paper is deposited in the following public institutions: Muséum d'Histoire naturelle de Lyon (ML), Muséum d'Histoire naturelle de Marseille (MHNM), Muséum d'Histoire naturelle de Nantes (MHNN), Muséum d'Histoire naturelle de Toulouse (MHNT) and Museo Paleontológico de la Universidad de Zaragoza, Spain. (MPZ)

3. THE FOSSIL ASSEMBLAGES.

The Ordovician is widely represented in the Palaeozoic outcrops of Morocco, mainly in the Anti-Atlas (Destombes et al. 1985), where fossiliferous rocks appear very rich in echinoderm fossils (Chauvel 1966).

3.1 Assemblage from locality CRF-4 (Bou Nemrou)

The most diverse of the four principal assemblages is found within the Izegguirene Formation at locality CRF-4 (Bou Nemrou), and is earliest Caradoc in age. These massive deposits are dominated by the eocrinoid *Ascocystites* (Figure 3) and large ophiuroids (protasterid nov. gen. nov. sp. Figure 11j).

The asterozoans are entirely composed of members of the class Ophiuroidea. These specimens have ambulacra typical of Ordovician groups represented in most major Lagerstätten. Protasterids, which are also recorded from the Lower Ordovician of the Montagne Noire (Hunter & Vizcaíno 2006) and the Middle Ordovician of Bohemia (Petr 1989) and Brittany (Hunter et al. in press) are the most common asterozoan group, both at Bou Nemrou and in the
next assemblage. The assemblage also exhibit a high diversity of mitrate stylophorans, including *Anatifopsis*, *Aspidocarpus*, and *Eumitrocystella*, as well as rare crinoids. The mitrate assemblage shows strong similarities with slightly older faunas described from the underlying Quine-Inirne Formation (Llandeilian) in the central Anti-Atlas (Chauvel 1971, Cripps 1990, Beisswenger 1994). Within mitrates, the genus *Eumitrocystella* is endemic to the Anti-Atlas, but closely related forms (e.g., *Mitrocystella*) are widespread in peri-Gondwanan regions (Bohemia, France, Spain, Portugal). *Aspidocarpus* is a genus of relatively generalized, primitive mitrocystitid mitrates, that is known from the western margin of Gondwana from the Middle Ordovician (Morocco, and Brittany) to the Caradoc (Brittany, and Bohemia). *Anatifopsis* is a genus of kirkocystid mitrate with a world-wide distribution, known from the Tremadoc to the Ashgill.

3.2 Assemblage from locality CRF-3

This assemblage, which is found in the lower part of the Lower Ktaoua Formation, is presumed to be early-middle Caradoc in age. The echinoderm community is primarily composed of oocrinoids (*Cardiocystites*) (Figure 11a), mitrates (*Eumitrocystella* sp.) and large solutes (*Dendrocystites* sp.), Tizi n'Mouri (CRF-1), eastern Anti-Atlas, Morocco. Upper part of Lower Ktaoua Formation, lower Ashgill. Scale bar: 4cm.

Figure 5. Large solute (*Dendrocystites* sp.) MHNM.15406.33, showing the external mould (left) and the latex cast (right). Tizi n'Mouri (CRF-1), eastern Anti-Atlas, Morocco. Upper part of Lower Ktaoua Formation, lower Ashgill. Scale bars: 4cm (left) & 1cm (right).

3.3 Assemblages from Tarhia region (CRF-1,CRF-2)

In the Tarhia region, two distinct echinoderm assemblages were collected close to the limit between the Lower Ktaoua Formation and the overlying Upper Tiouririne Formation. The presence of the trilobite *Mucronaspis zagoraensis* and biostratigraphic data (Villas et al. 2006) indicate a Pusgillian age for the Tizi n'Mouri assemblage (See Figure 2) The first echinoderm assemblage (locality CRF-1, Tizi n'Mouri) appears in a thin level of yellowish, medium-grained sandstone (quartzitic sandstone). It is mainly composed of the rhombiferan *Homocystites* sp. (Figures 7(right)) and large *Dendrocystites*-like solutes, associated with mitrocystitid mitrates (*Eumitrocystella* sp.) (Figure 4-5). The specimens in these deposits, as in most of the faunas described in this study, appear complete and articulated. They are preserved as natural moulds coated by extremely thin films of limonite. *Homocystites* is a relatively widely distributed rhombiferan (Figure 11c), which was described in the Middle Ordovician of Baltica (Russia; Kesling 1967), the Caradoc of several western Gondwanan regions (Bohemia, Portugal, Spain;
Barrande 1887, Delgado 1908, Gil Cid et al. 1996), and in the Ashgill of Avalonia (Wales; Donovan et al. 1996) and Laurentia (North America, Scotland; Kesling 1967; Paul 1984; Donovan et al. 1996). The large Dendrocystites have short and stout brachioles. As their morphology is clearly distinct from that of the small solutes from the CRF-3 assemblage, the large forms from Tizi n’Mouri very likely belong to another species.

The second assemblage, sampled in locality CRF-2, can be classified as a ‘starfish’ bed (see Goldring & Stephenson, 1972) as it is dominated by a new genus of ophiuroid belonging to the eophiurids (Shackleton, 2005). Like all of the ophiuroids from these assemblages, they require formal taxonomy beyond the scope of this paper, being left in open families until the entire asterozoan fossil record is better understood. This assemblage is also packed with large solutes (Dendrocystites sp.), associated with common diploporites (Asterocystis nov. sp.). It is the first time that Asterocystis is recorded outside of Baltica (see Kesling 1967). The new species of Asterocystis is a diploporan with recumbent ambu-

lacra, bearing weak and slender brachioles. The theca is highly organised and the thecal plates bear numerous covered diploposes (Figure 11b). The rhombiferan Homocystites is common in the Tizi n’Mouri assemblage but rare and poorly preserved in the starfish assemblage (Figure 9).

Figure 6, MHNM.15406.23.1a-b, Ophiuroid (Protaster sp. left) and mitrate (right; Eumitrocystella sp.), locality CRF-3, eastern Anti-Atlas, Morocco. Lower part of Lower Ktaoua Formation, lower-middle Caradoc. Scale bar: 1.5cm (left) & 2cm (right).

Figure 7, Asterocystis sp. (left, MHNT.PAL.20005.0.141.1) and Homocystites sp. (right, MNHM.15406.18.1), localities CRF-I (Tizi n’Mouri) and CRF-2, respectively, eastern Anti-Atlas, Morocco. Upper part of Lower Ktaoua Formation, lower Ashgill. Scale bars: 1cm

3.4 Assemblage from locality CRT (piste de Tinejdad)

The youngest assemblage is from the lower part of Upper Tiouririne Formation (lower Ashgill). It has yielded abundant remains of edrioasteroids (Figure 8) and rhombiferans (Echinosphaerites sp.). This assemblage is preserved in a green, fine-grained sandstone, possibly a greywacke. The trilobite association of Mucronaspis zagoraensis and Kloucekia (Phacopidina) aff. solitaria associated with the echinoderm material indicates a Pusgillian age (Destombes, 1972). Echinosphaerites is a widely distributed fistuliporite rhombiferan, documented in the Middle to Late Ordovician of Baltica, China, Iran, Sibumasu, as well as in various western peri-Gondwanan regions (see Kesling 1967, Bockélie 1981, Parsley 1998, Lefebvre et al. 2005).

Figure 8, Edrioasteroids (MPZ2006/565-569) from the youngest assemblage, lower part of the Upper Tiouririne Formation, lower Ashgill (locality CRT, piste de Tinejdad). Scale bar: 1cm.

Figure 9, Homocystites sp. (MPZ 2006/26-28, 30-31, 42). From the Upper part of Lower Ktaoua Formation. Scale bar: 1.5cm.
PALAEOECOLOGY

The taphonomy of these assemblages is complex, but broadly speaking these are life assemblages which did not undergo considerable transportation. This is evidenced by the fact that both the filter feeding echinoderms and the asterozoans have all of their appendages intact and articulated.

Features such as intact ophiuroid disks, complete articulation of appendages and a weakly disarticulated theca, (attached to the proximal stem), suggest a rapid burial between 2 days to 1 week (Brett et al. 1997), with transport limited to a short distance close to where the animal lived. Complete and articulated arms in all the asterozoans suggest preservation state 2 (Kerr & Twitchett 2004) that is, all skeleton parts, excluding the mouthparts, are articulated. Eocrinoids, mitrates and ophiuroids are also classified as type 1 echinoderms according to the classification of Brett et al. (1997). The mitrates are frequently preserved with their aulacophore in extended position (See figure 11d-f for numerous examples) which is further evidence of rapid burial as the aulacophore typically tends to retract quickly after death.

Along with rhombiferans, diploporans are assigned to type 2 echinoderms according to the taphonomic classification of Brett et al. (1997). Such excellent preservation of all the thin elements fully articulated (for example brachioles and thecal plates) suggests that these diploporans also experienced a relatively rapid burial. There is an obvious alignment of the specimens of Asterocystis indicated by the brachioles arranged like a plume (alignment of the theca with the stem and the brachioles) (for example see Figure 7). This could indicate the influence of unidirectional current in preservation and even in mode of life. Further evidence comes from the ophiuroids and mitrates in the CRF-3 assemblage. It is observed that almost all aulacophores of the mitrates are directed in the same direction; the arms of co-occurring ophiuroids also show a similar unidirectional orientation, all pointing in the same general direction (Figure 10). In Asterocystis, the stem is alternating in its most proximal part and it seems to have an attachment surface in its distal end. The last feature could indicate that the specimens of Asterocystis lived fixed to the substrate. The columnal alternation could have eased movements of the stem in response to the hydrodynamic conditions.

The Asterocystis population seems to comprise juveniles and adults. This differentiation between juveniles/adults (Figure 3) is based on the difference in the total length of the theca (from 2 cm to more than 20 cm), and on the number of thecal plates and brachioles that increases during the growth. The numerous specimens of Homocystites in the CRF-1 (Tizi n’Mouri) assemblage could also be juvenile or immature forms. Evidence comes from their relatively small thecal size, their tiny brachioles, the reduced size and ornamentation of the plates in each circlot. Their large proximal stem could indicate a certain ability to move or to react with the current. The stem in all Homocystites and Ascocystites gradually decreases in diameter until it becomes slender. Moreover, no holdfasts have been observed at the end of the complete stems. Thus, it is suggested a mode of life could be with the stem pushed into the substrate, although it not clear whether the fine-grained sandstones represent the substrate occupied by the echinoderms.

Figure 10, Large slab (MHN.M.15406.23.1a-b) showing ophiuroids and mitrates on the bedding plain with a preferred orientation. CRF-3, eastern Anti-Atlas, Morocco. Lower part of Lower Ktaoua Formation, lower-middle Caradoc. Scale bar: 10cm.

The stem of the Cardiocystites bohemicus (Barrande, 1887) occurring in the CF3 assemblage is very long and constant in diameter, with an apparent synostosial articulation. It seems to be relatively robust and rigid, yet with sufficient flexibility for high amplitude movements. These features seem to indicate that the specimen could filtrate at least 20 cm above the substrate in the water column. The stem could serve as a mooring cable to maintain the theca in the currents. The highly flattened body form of Cardiocystites could be an adaptation to floating in the high currents in shallow water (as expected for other flattened eocrinoids; Nardin In-press).

It is clear that in all the horizons there is trophic tiering with distinct separation between epibenthic feeders (ophiuroids, solutes, and mitrates) found in different associations as the medium to high suspension feeders (eocrinoids rhombiferans, and diploporans). This is particularly apparent in the CRF-3 assemblage, where the gregarious ophiuroid-mitrates assemblage predominates. Gregarious ophiuroid assemblages are commonplace in the fossil record and can be observed today (see Blaber et al. 1987, Fujita & Ohta 1990). The other extreme is the Bou Nemrou assemblage, which, although having a large ophiuroid component, is dominated by eocrinoids, with mitrates also being common here. A notable observation is that communities tend to have two principle components. At Bou Nemrou, there is a clear distinction between the filter feeding eocrinoids and the large ophiuroids, whereas in the CRF-3 assemblage,
mitrates and ophiuroids form the dominating association, while the Tizi n'Mouri assemblages are solute and eocrinoid based communities with ophiuroids occurring in much lower numbers. This mitrate/ophiuroid association in observed throughout the Lower Palaeozoic (see Hunter et al. in press). This trend continues with Bou Nemrou showing a clear distinction between the filter feeding eocrinoids and the large ophiuroids. Apart from the obvious association between taxa these assemblages are notable in that they have many other palaeoecological associations, including the apparent alignment with current conditions (explained above), and the density patterns shown in some of the echinoderms, although it is difficult to document whether this is an actual phenomenon or simply a taphonomic artefact. Most significant is the apparent ontogeny identified in the eocrinoids and the other filter feeding echinoderms, with immature forms even predominating in certain assemblages, e.g. Tizi n'Mouri, with uncommon adults occurring in locality CRF-2. It is clear that each of the assemblages could represent a different palaeo-depth, necessitating a more extensive comparison with other regions and facies of the western peri-Gondwanan margin, where palaeoenvironmental conditions are better established.

The El Caïd Rami assemblages show strong relationships with Middle to Late Ordovician faunas of other areas of the Gondwanan margin, and especially with Bohemia. From an asterozoan point of view these assemblages are significant as they establish that protasterids have a much wider distribution within peri-Gondwana and in particular outside of Bohemia (see Petr 1989). Unfortunately, such palaeogeographic considerations are complicated by the obvious stratigraphic variations found in the faunas. Asterozoan assemblages in the CRF-4 (Bou Nemrou) communities contain protasterids that are recorded from the Lower to the Middle Ordovician (Spencer 1950, 1951). However, the Tarhia assemblages consist entirely of new asterozoans, likely to be endemic to the region. Observations and data from the other echinoderm groups suggest a gradual transition from a late Middle Ordovician-like fauna (Bou Nemrou) not very different from that of the underlying Ouine-Inirne Formation, to a more typical Late Ordovician fauna (Tarhia). The composition of early Ashgill (Pusgillian) assemblages from the Anti-Atlas of Morocco is very different from that of coeval faunas from other peri-Gondwanan regions, which are dominated by rhombiferans with Baltic affinities, and adapted to temperate to warm seawaters. In other Gondwanan regions (e.g., Algeria, Brittany, Carnic Alps, Montagne Noire (France), Sardinia and Spain), forms adapted to cold water (e.g., solutes, mitrates, etc.) are absent or extremely rare in pre-Hirnantian Ashgill deposits.

CONCLUSIONS

The echinoderms are exceptionally preserved and are likely to have been entombed by an obrution deposit.

Many taxa are documented for the first time in the Upper Ordovician of the Anti-Atlas: the eocrinoids Asiocystites and Cardiocystites, the diploporan Asterocystis, the mitrates Anatifopsis, Aspidocarpus, and Eumitrocystella, protasterid and encrinasterid ophiuroids, and the solutes.

The horizons clearly show trophic tiering with epibenthic feeders (ophiuroids and mitrates) and medium to high suspension feeders (eocrinoids, rhombiferans, and diploporans).

Several specific palaeoecological observations can be made; these include faunal associations (e.g. ophiuroids and mitrates), alignment with current conditions, density of fauna and ontogeny.

It is established there is a relationship between El Caïd Rami assemblages and other faunas of the Gondwanan margin and especially Bohemia. A gradual transition can be observed from a Middle Ordovician-like fauna (Bou Nemrou) to a fauna more typical of the Upper Ordovician (CRF-3), which, contrary to the situation in other peri-Gondwanan regions, persists in the early Ashgill (CRF-1, CRF-2, CRT).

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