New occurrence of the Ordovician eocrinoid *Cardiocystites*: Palaeogeographical and palaeoecological implications

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Flattened eocrinoids are very rare in the fossil record, notably because of their fragility. Recent investigations in the Anti-Atlas (Morocco) have provided one of the oldest known specimens of *Cardiocystites* from the Upper Ordovician (early–middle Sandbian). This discovery increases the number of eocrinoid genera known in Morocco. This new material is the fifth published specimen of the genus *Cardiocystites.* It is well preserved, thus allowing morphological details, such as the location of the anal pyramid and the plane of thecal flattening, to be observed. Palaeoecological reconstruction can be deduced or confirmed from these new details. The respiration of *Cardiocystites* now seems due to the combination of both epidermal gaseous exchange and cloacal pumping. Stem length and synostosial articulation indicate that the stem might have been used as a mooring line allowing the theca to float in the currents. The flattening of the *Cardiocystites* theca seems to be an adaptation to high energy hydrodynamic conditions and cold waters. Occurrences of *Cardiocystites bohemicus* in Morocco, in the early–middle Sandbian, and in Bohemia, in the early Katian, indicate that the genus probably originated in the west Gondwanan margin. Migration could explain the occurrence of *Cardiocystites* in this area and also in Avalonia in the late Sandbian. The global sea-level rise and the presence of cool water circulation from west Gondwana to Avalonia and Laurentia in the early Sandbian favour such a hypothesis.

Key words: Blastozoa, Eocrinoidea, taxonomy, palaeoecology, palaeobiogeography, Ordovician, Gondwana, Morocco.

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Introduction

Echinoderms are one of the main components of the Palaeozoic fauna. Moroccan rocks reveal abundant Ordovician outcrops, which contain numerous echinoderm fossils. Early Moroccan studies mentioned two diploporan genera from the Ordovician of Anti-Atlas and Moyen-Atlas (Bigot and Dubois 1931, 1933; Ségaud and Termier 1933). In spite of many later works which reveal a diversified echinoderm fauna (see Chauvel 1966a, b, 1969a, b, 1971a, b, 1977, 1978; Choubert and Termier 1947; Destombes 1962, 1963; Termier and Termier 1948, 1950), this fauna remains relatively unknown as these works mainly concern stratigraphic surveys with few palaeontological descriptions. The Moroccan Ordovician echinoderm fauna is well diversified, now composed of nine groups (asteroids, crinoids, diploporans, eocrinoids, edrioasteroids, ophiuroids, rhombiferans, solutes, and stylophorans). However, only two eocrinoid genera have been studied from the Ordovician of Morocco: (1) *Rhopalocystis* Ubaghs, 1963 from the upper Tremadoc in the Zagora region (central Anti-Atlas), and (2) *Balantiocystis* Chauvel, 1966 from the upper Arenig in the Tan Tan region (western Anti-Atlas).

The new section of El Caïd Rami (eastern Anti-Atlas; Fig. 1) yielded numerous specimens of various genera previously unknown in Morocco: asteroids, crinoids, eocrinoids, rhombiferans, and solutes. This material also extends the stratigraphic range of some stylophoran genera. The new eocrinoid fauna contains numerous specimens attributed to the genus *Ascocystites* Barrande, 1887 (see Régnault 2006) and one specimen of *Cardiocystites* Barrande, 1887. The latter genus is described under two species: (1) *Cardiocystites bohemicus* Barrande, 1887, first found in Bohemia in the Zahořany Formation in the upper Berounian (lower Katian, time slice 6a) (Fig. 2); (2) *Cardiocystites pleuricostatus* Dean and Smith, 1998, described in Avalonia (Wales) in the Smeathen Wood Beds (Burrellian, late Sandbian, time slice 5b) (Fig. 2). This genus was known from only four specimens until the discovery of the new Moroccan specimen which is particularly well preserved, with a very long stem and a complete calyx with articulated brachioles. Its description provides more information about the major morphological characteristics and palaeoecology of *Cardiocystites*. Its stratigraphic and geographical locations allow the origin and palaeogeographical affinities of the genus *Cardiocystites* to be examined.

Institutional abbreviation.—MHNM, Muséum d'Histoire Naturelle de Marseille, France.

Geological and geographical settings

The study area is a fossiliferous outcrop located in the eastern flank of the Oued El Caïd Rami, about 41 km south-west of Erfoud, in the eastern part of the Anti-Atlas, Morocco (Fig. 1).

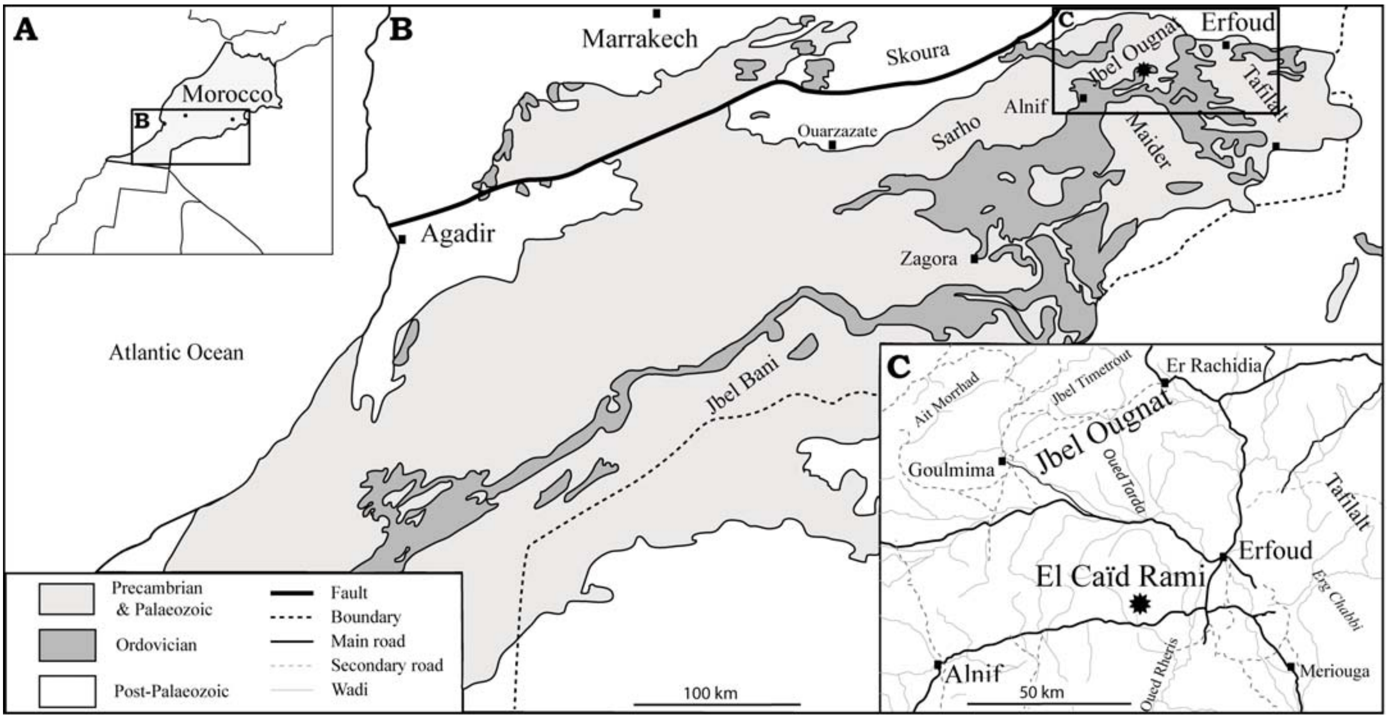

Fig. 1. Location of the collecting site. **A**. General map of Morocco. **B**. Geological sketch-map of Anti-Atlas (after Destombes et al. 1985; modified). **C**. Geographical location of the studied section (black star).

This flank is composed of a thick siliciclastic rock succession, dated from the Middle to Upper Ordovician. Its lower part is composed of shales bearing lenticular sandstones (upper Fezouata Formation) overlain by the shales of the Tachilla Formation. The upper part is composed of fine- to middle-grained quartzitic sandstones (First Bani group; transition between the Middle and Upper Ordovician), overlain by arenaceous argillites comprising some lenticular beds of fine- to middle-grained sandstones (lower Ktaoua Formation; Upper Ordovician).

The material was collected from beds of micaceous middle-grained sandstones alternating with large argillite beds. Erosive grooves at the top of the sandstone beds indicate relatively high energy hydrodynamic conditions. These fossiliferous horizons have been related to the base of the lower Ktaoua Formation (Destombes et al. 1985), corresponding to the early Caradoc (early–middle Sandbian, time slice 5a; Fig. 2) (Webby et al. 2004; Bergström et al. 2006).

Systematic palaeontology

Sub-phylum Blastozoa Sprinkle, 1973

Class Eocrinoidea Jaekel, 1918

Genus *Cardiocystites* Barrande, 1887

Type species: *Cardiocystites bohemicus* Barrande, 1887: 120, pl. 31: 10–12 from the Zahořany Formation (Caradoc) of Zahořany (Bohemia).

Remarks.—The presence of *Cardiocystites* is rare in the fossil record. Currently only four specimens have been described. This genus and the most of the other eocrinoids are built of numerous thin skeletal elements, weakly articulated, which could be preserved only under special environmental conditions like rapid burial *in situ* (e.g., obrution event) or cool temperatures and low-energy conditions (Type 1 echinoderms in Brett et al. 1997). The need for such specific preservation conditions could explain the rarity of *Cardiocystites* fossils.

Cardiocystites has a flattened heart-shaped calyx, composed of thick rounded marginal plates enclosing large thin central plates. The adoral part carries five free-standing ambulacra, which bear numerous brachioles. A long columnal-bearing stem is attached aborally in four paired basals. *Cardiocystites* is characterised by these unusual features, which do not co-occur in other genera. The presence of all these characteristics in the new Moroccan specimen justifies its assignment to the genus *Cardiocystites*.

Distribution.—Upper Ordovician (Sandbian and Katian) of the Czech Republic, Morocco (Anti-Atlas) and England (Shropshire).

Cardiocystites bohemicus Barrande, 1887

Material.—One specimen with part and counterpart (MHNM. 15406.13.1/2); Upper Ordovician, Morocco, Oued El Caïd Rami.

Description.—The single specimen described below is particularly well preserved. The stem is especially long, about 14.6 cm and the numerous brachioles are articulated with the theca, of which both sides are preserved (Fig. 3). The

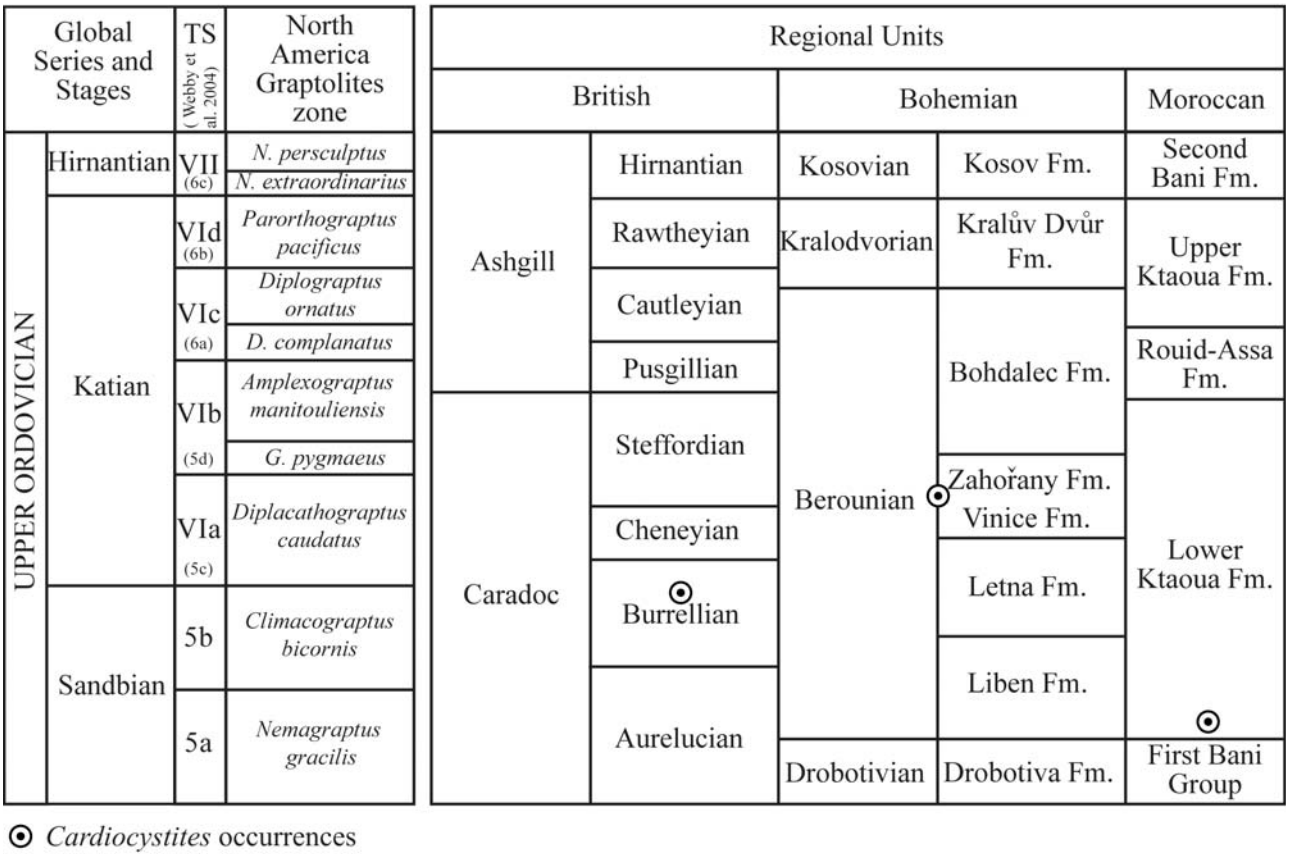

Fig. 2. Correlation chart between main stratigraphic subdivisions proposed for the Upper Ordovician by the International Subcommission on Ordovician Stratigraphy (ISOS; modified from Webby et al. 2004; Bergström et al. 2006), North Gondwanan graptolite biozones (after Vannier et al. 2003; Webby et al. 2004; Finney 2005), lithostratigraphic units defined in the Anti-Atlas (after Destombes et al. 1985; Gutiérrez-Marco et al. 2003; Vecoli and Le Hérissé 2004), British regional time scale (after Webby et al. 2004; Finney 2005), and Bohemian regional time scale (after Prokop and Petr 1999; Vannier et al. 2003; Vecoli and Le Hérissé 2004). Abbreviations: G., *Geniculograptus*; D., *Dicellograptus*; N., *Normalograptus.*

heart-shaped flattened theca is composed of differentiated plates. The maximum width is around 11.3 mm and the maximum length (measured perpendicularly to the width) is around 11.6 mm.

Thecal plating comprises an outer series of frame plates and an internal series of polygonal central plates. The thecal frame is composed of six thick elongate marginal plates. The antanal and anal pairs of the aboral marginal plates serve as basals for the attachment of the stem. The facet for the stem is circular. All four aboral marginal plates are relatively straight and parallelepipedal, thin (0.4 mm) and elongate (6.8 mm). The two adoral marginals are cylindrical and curved, ornamented with transverse folds, moderately thick (0.8 mm) and elongate (8.8 mm).

The central plates are polygonal and adjacent, large and very thin (<0.2 mm). The central area of the anal face is composed of four plates, and the central area of the antanal face has only three plates. On the anal face, the rectangular central plates are sub-equal in size and the aboral plates are trapezoidal and triangular. On the antanal face, the rectangular central plates coincide with the same plates of the other side, whereas the third plate, which is triangular, is equivalent to the two aboral triangular plates of the anal face. The ornamentation of the central plates is restricted to two longitudinal ridges which are unequal in size, the most central being the longest. Their positions coincide on each side of the theca. These ridges run from the aboral zone and diverge slightly towards the adoral mound. The ridges are slightly realigned by the plate sutures as they cross the theca (Figs. 4, 5). There is no opening to the exterior for respiratory function.

The anal pyramid is located at the junction between the most adoral marginal plate and the adoral mound (Fig. 3B_2). Five triangular plates cover the periproct, forming a circular structure (about 0.7 mm in diameter). The anal region is composed of the anal pyramid surrounded by around 15 small polygonal adjacent plates in a clearly differentiated area about 1 mm in diameter (Fig. 5).

The ambulacral system spreads from a central mound, at the connection between the two adoral marginal plates. The flat-topped mound is composed of seven small rectangular oral plates (Fig. 4). The mouth is presumably located at the point of ambulacral convergence (Fig. 3A_2). The oral zone is composed of five regular free-standing ambulacra. All ambulacra are equal in length, conical with a relatively thick proximal part (around 1.2 mm in diameter). They are relatively short (one third of the theca width, around 3.6 mm).

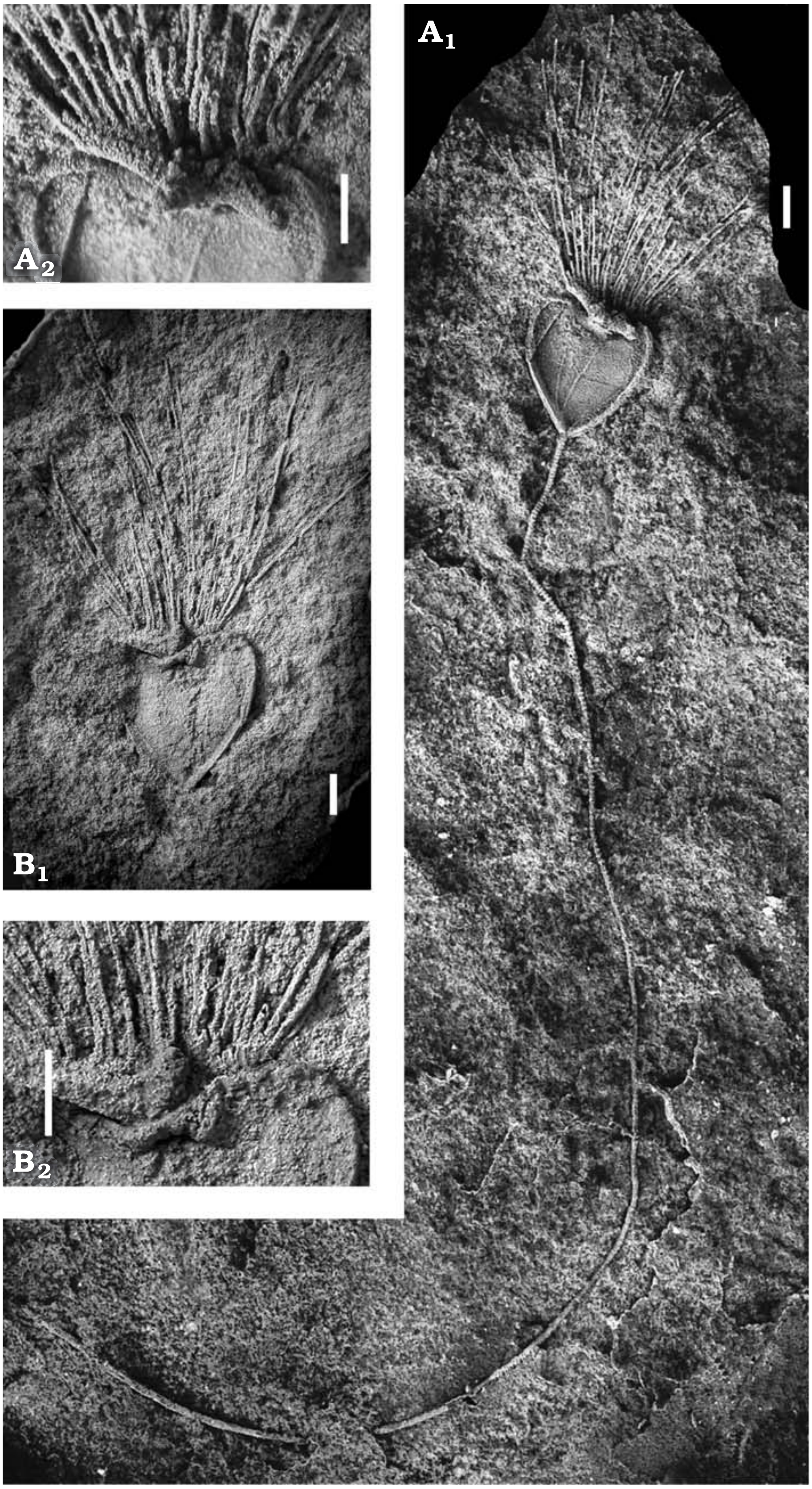

Fig. 3. Global morphology of the *Cardiocystites bohemicus* Barrande, 1887 eocrinoid featuring developed ambulacra and the well-preserved stem inserted into the theca (Upper Ordovician, Morocco, Oued El Caïd Rami). **A**. MHNM. 15406.13.1; A_1, photograph of the antanal face showing brachioles, the theca and the well-preserved stem; A_2, enlargement showing erect ambulacra and brachioles. **B**. MHNM. 15406.13.2; B_1, photograph of the anal face; B_2, enlargement showing the anal pyramid. Scale bars 5 mm.

Each ambulacrum is biserially plated, with ten pairs of plates plus a terminal azygous plate. The ambulacral plates are biconvex, flattened in their central area overlain by raised edges (Fig. 4). The proximal plates are larger and more regularly trapezoidal than the distal ones, probably to ease the flexing of the ambulacra.

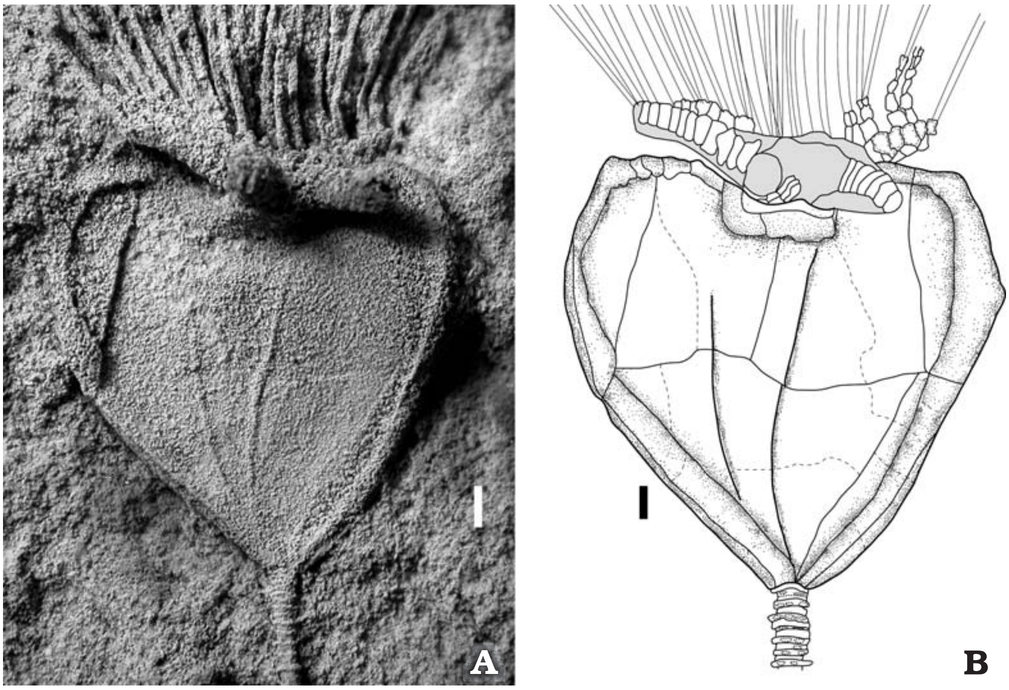

Fig. 4. Antanal face of the eocrinoid *Cardiocystites bohemicus* Barrande, 1887 (MHNM.15406.13.1); Upper Ordovician, Morocco, Oued El Caïd Rami. **A**. Photograph of latex cast showing brachioles and stem articulated to the theca. **B**. Camera lucida drawing. Brachioles are not detailed because of their thinness. Scale bars 1 mm.

Brachioles are numerous (at least 27 are visible on the antanal side), straight, thin and relatively long (at least twice as long as the maximum thecal length; Fig. $3B_1$). They come off both sides of the ambulacra. Each brachiole is mounted on one ambulacral plate, implying a maximum number about twenty-one per ambulacrum (Fig. 4).They are biserial with a larger plate at the base. Brachiolar cover plates are rectangular, short and straight.

The stem is inserted in a circular facet, at the junction between the antanal and anal aboral marginal plates. It is slender, very long (more than 14.6 cm), and composed of at least 600 columnals. Diameter and thickness were measured on the first 120 columnals and sporadically in the distal part. Columnals are cylindrical, averaging around 0.3 ±0.13 mm in thickness and around 0.6 ±0.11 mm in diameter. The diameter is relatively uniform along the stem, whereas the thickness decreases distally. Sutures between the columnals appear straight and smooth, and could indicate a synostosial articulation. Shape of the columnals differs due to proximal to distal taper (Fig. $3A_1$). The proximal part of the stem is heteromorphic, with alternating high nodals (ornamented with small spines) and small internodals. The central part of the stem still shows the alternation between the nodals and internodals, but nodal ornamentation changes to transverse ridges. A succession of columnals identical in size and ornamentation, with reduced transverse ridges, composes the most preserved distal part of the stem. Its distal end is missing.

Comparison.—The specimen possesses all the major features of the Bohemian species *Cardiocystites bohemicus*. It differs from the two Bohemian specimens in having a smaller theca and less irregularity in the alternation between nodals and internodals. However, these small differences could be attributed to intraspecific variability or different growth stages. The Moroccan specimen resembles to *C. pleuricostatus* by shape of the ambulacral plates but it clearly differs by (1) the thecal size, larger in *C. pleuricostatus*; (2) the thecal plating, in *C. pleuricostatus*, one basal is divided in 3 parts; and (3) the ornamentation, which is well developed with numerous ridges perpendicular to the sutures of the plates.

Morphological implications

Plane of thecal flattening.—Echinoderms contain many clades, which have independently developed thecal flattening, mostly in response to their mode of life or palaeoenvironmental conditions. They include, for example, asteroids, ophiuroids, and solutes, which show only flattened morphologies, and rhombiferans and eocrinoids, in which thecae can be flattened or globular. Thecal flattening and the reasons for it are still poorly known. It is generally not considered as a single homologous character state transformation (Sumrall 1997; Sumrall et al. 2001).

The definition of thecal flattening types is based on the relative positions of the mouth and the periproct. Some flattened echinoderm clades (e.g., asteroids, ophiuroids, and edrioasteroids) are flattened in a “dorso-ventral” plane, which is perpendicular to the polar axis of the theca. Eocrinoids are the only group to show anterior-posterior and lateral types of flattening. The “anterior-posterior” type (*sensu* Sumrall et al.

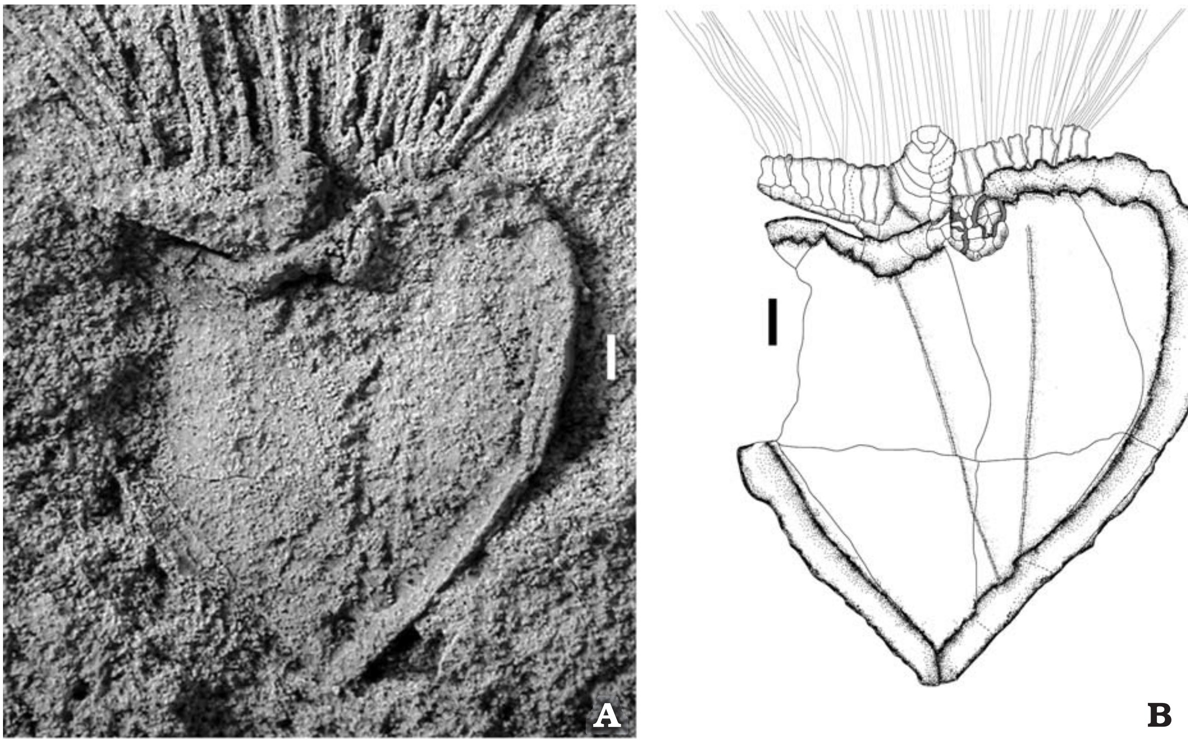

Fig. 5. Anal face of the eocrinoid *Cardiocystites bohemicus* Barrande, 1887 (MHNM.15406.13.2); Upper Ordovician, Morocco, Oued El Caïd Rami. **A**. Photograph of latex cast showing anal pyramid and brachioles articulated to the theca. **B**. Camera lucida drawing. Brachioles are not detailed because of their thinness. Scale bars 1 mm.

2001) is defined as when thecal compression is in a plane parallel to the polar axis, and when the periproct is located in the central area (*Haimacystis* Sumrall, Sprinkle, and Guensburg, 2001; *Lingulocystis* Thoral, 1935). This type of thecal flattening also occurs in flattened rhombiferans (e.g., *Pleurocystites* Billings, 1854; *Amecystis* Ulrich and Kirk, 1921). The "lateral" type can be defined as when the thecal compression is parallel to the polar axis and when the periproct is located in one or two lateral plates in the marginal frame (e.g., *Mandalacystis* Lewis, Sprinkle, Bailey, Moffit, and Parsley, 1987; *Rhipidocystis* Jaekel, 1901). This type of flattening also occurs in stylophorans.

Cardiocystites shows a compression plane parallel to the polar axis. The anal pyramid was previously unknown. This structure, shown by the Moroccan specimen is situated at the junction of the marginal frame and the central area at the top centre of this area. The anal region seems more related to the central plates than the marginal ones, notably because of the position of the surrounding small platelets. This configuration could indicate an "anterior-posterior" flattening, which is at variance with the previous hypothesis (Sprinkle 1973; Dean and Smith 1998; Sumrall et al. 2001).

Palaeoecological implications

Respiration.—No respiratory structures have been observed on the thecal plates. Numerous respiratory hypotheses were proposed for echinoderms without respiratory structures (e.g., *Amecystis* in Broadhead and Strimple 1975): (1) modification of the water vascular system through the development of podia or tube feet associated with pores located on the ambulacra (mostly in living echinoderms); (2) cutaneous or epidermal respiration. The diffusion of oxygen and carbon dioxide could have been more efficient through a thin epidermis; and (3) cloacal pumping, commonly associated with the anus. The mechanism of sea-water pumping through the anal opening allows the diffusion of oxygen and carbon dioxide between cloacal sea water and the water vascular system. The last two modes of respiration have been presumed in other flattened eocrinoids (e.g., *Lingulocystis* in Broadhead and Strimple 1975). Epidermal respiration was suggested in *Cardiocystites* because of thecal flattening, the thinness of the plates, and the lack of periproct characteristics (Dean and Smith 1998).

The thecal plates of the Moroccan specimen are very thin (<0.15 mm) and potentially offer a large surface for gaseous exchanges. The small size of the anal pyramid, its location and the absence of flexible and large plated structure seem to argue against the hypothesis of the cloacal pumping as respiratory mechanism in *Cardiocystites*. This configuration supports respiratory exchanges by the thin epidermis.

Mode of life.—Thecal flattening is generally interpreted as a response to a recumbent mode of life (e.g., rhombiferans, stylophorans) because both thecal sides are differentiated in their plating and the two ambulacra are oriented parallel to the flattening plane and to the substrate. Both thecal faces in flattened eocrinoids have identical plating, and ambulacra are sometimes four or five in number and relatively well-developed (e.g., *Cardiocystites*, *Rhipidocystis*). The presence of these two features seems to contradict the interpretation of a recumbent mode of life. In the case of eocrinoids, thecal flattening could be an adaptation to a quite different mode of life.

The stem of the Moroccan specimen is very long and uniform in diameter, with a possible 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 stem did not merely support the thecal weight but that it could also serve as a mooring cable to maintain the theca in the currents. Because of the length of the stem the specimen could filter at least 20 cm above the substrate. Unfortunately, the distal end of the stem is absent. Similar hypotheses of stem use have already been mentioned for other genera with comparable synostosial stems (see *Lingulocystis* in Ubaghs 1960 and in Vizcaïno et al. 2001; *Mandalacystis* in Lewis et al. 1987). Previous sedimentological studies have observed that the presence of *Lingulocystis* seems to be correlated with relatively shallow water and high energy hydrodynamic conditions (Vizcaïno et al. 2001).

The sedimentological indications of El Caïd Rami indicate a muddy to sandy substrate, deposited in energetic shallow water corresponding to a proximal platform environment (at the base of a tempestite storm deposit with the presence of plane laminations with erosive grooves, proximal upper offshore). The polar paleogeographical location indicates relatively cold water (Wilde 1991).

The highly flattened body form of *Cardiocystites* could be an adaptation to hang passively in high currents in shallow water (as expected for *Lingulocystis*), with relative stability brought by: (1) the attachment to the substrate provided by a long flexible stem and (2) the weight of the well-developed ambulacral system, facilitating a hydrodynamic drag.

Palaeobiogeographical significance

Cardiocystites bohemicus was first found in Bohemia in the Zahořany Formation corresponding to the upper Berounian (lower Katian; Fig. 2) and then in the west Gondwanan margin (Morocco) in the lower Ktaoua Formation corresponding to the early Caradoc (early–middle Sandbian; Fig. 2).

Cardiocystites pleuricostatus was described from Avalonia (Wales) in the Smeathen Wood Beds (Burrellian, late Sandbian; Fig. 2). The microcontinent Avalonia drifted away from the west Gondwanan margin in the uppermost Arenig or in the basal Llanvirn (Middle Ordovician), to reach palaeolatitudes comparable with Baltica during the early Upper Ordovician (Cocks et al. 1997; Cocks and Torsvik 2002). However, the palaeogeographical location of Bohemia is still a controversial subject: (1) numerous authors consider Bohemia to belong to the peri-Gondwanan area (see Ausich et al. 2002), ranging hypothetically from 70-65°S (Cocks and Torsvik 2002), or 50°S (Paris and Robardet 1990) to 40°S (Young 1990), and (2) Bohemia is also considered to be a distinct terrane, which is relatively far from the Gondwanan margin, at around 30°S (Havlíček et al. 1994; Villas et al. 1999).

Specimens of *Cardiocystite bohemicus* were discovered in Morocco in the early–middle Sandbian and in Bohemia in the early Katian. Other groups display the same pattern of dual distributions in Morocco and in Bohemia in the lower part of the Upper Ordovician: e.g., the brachiopod genera *Tafilaltia* Havlíček, 1970 and *Tissintia* Havlíček, 1970 or the diploporan species *Codiacystis bohemica* (Barrande, 1887) and *Aristocystites bohemicus* Barrande, 1887 (Cocks 2000; Gutiérrez-Marco et al. 2003; Prokop and Petr 1999). These occurrences argue for the peri-Gondwanan position of Bohemia, according to the first hypothesis described above, at least during the Sandbian stage.

At present the first recorded appearance of *C. bohemicus* is diachronous between West Gondwana (early–middle Sandbian) and Bohemia (early Katian). The stratigraphic positions of the first appearances of other faunas suggest the same phenomenon between these two regions for the same geological period (from the late Darriwilian to the early–middle Katian): e.g., the ostracods *Piretopsis* (*Cerninella*) cf. *bohemica* (Barrande, 1855); the brachiopods *Brandysia cf. benigna* Havlíček, 1965, and *Jezercia* Havlíček and Mergl, 1982, the trilobite *Zeliszkella* (*Z.*) Delo, 1935; the echinoderms *Aristocystites bohemicus* Barrande, 1887 and *Ascocystites drabowiensis* Barrande, 1887 (Gutiérrez-Marco et al. 1999; Prokop and Petr 1999; Lefebvre and Fatka 2003).

Currently the occurrence of the genus *Cardiocystites* is restricted to the peri-Gondwanan area and Avalonia (called South European Province, *sensu* Paul 1976) during the lower part of the Upper Ordovician (Fig. 6). A very comparable pattern can be observed for the trilobite species *Degamella princeps princeps* (Barrande, 1972) or the brachiopod genera *Tafilaltia* and *Tissintia* that are very characteristic of the high-latitude Mediterranean Province of western Gondwana (e.g., Morocco, early Sandbian; Bohemia, early Katian; see Havlíček et al. 1994). They are also known from Wales (Avalonia, late Sandbian; Cocks and Torsvik 2002). One curious aspect of these distributions is that the faunas from the South European Province are separated into two regions, one with a palaeolatitude of approximately 40°S and another located at 70°S (Fig. 4).

Specimens of *Cardiocystites* (*C. bohemicus*) are present on the Gondwanan margin before the drift of Avalonia. The known stratigraphic occurrences could indicate the appearance of *Cardiocystites* in the Mediterranean Province (*C. bohemicus*).The presence of *C. pleuricostatus* in Avalonia could be explained by faunal migration to lower palaeolatitudes. This migration seems to coincide with the major transgressive event during the early Katian. This transgression, which started in the early Sandbian and progressed until

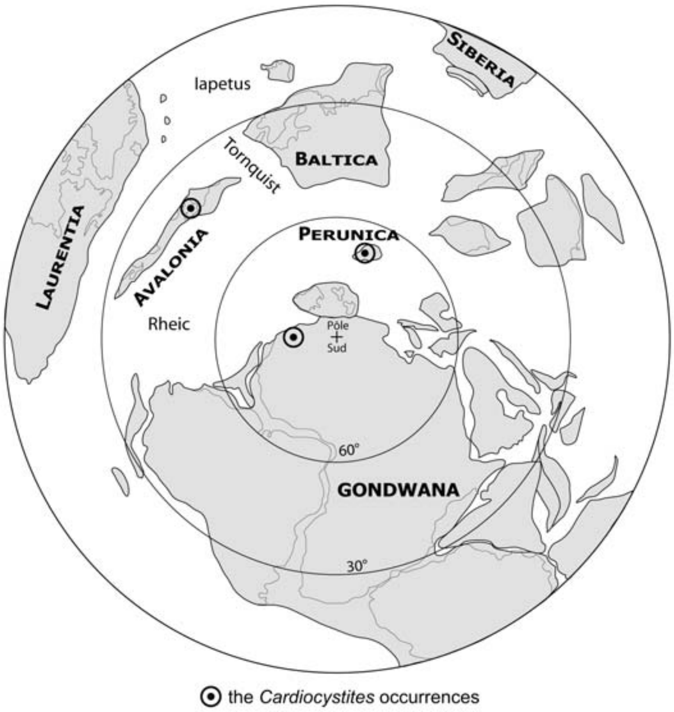

Fig. 6. Palaeogeographical reconstruction of the continent position for the Sandbian (Upper Ordovician); modified from Cocks and Torsvik 2004.

the well-established Hirnantian sea-level fall, is globally recognised (or e.g., Baltica, Laurentia, and Gondwana) (Villas et al. 2002). Moreover, the main event of the Taconic orogeny coupled with the regional flexural subsidence of the south Laurentia margin allowed cooler intermediate polar water circulation, causing upwelling phenomena across the eastern margin of Laurentia and downwelling phenomena across the west Gondwanan margin (Patzkowski and Holland 1993; Patzkowski et al. 1997; Villas et al. 2002; Pope and Steffen 2003; Herrmann et al. 2004). This last hypothesis has been put forward to explain the distribution of some stylophoran genera in the early Sandbian of Morocco and in the early Katian of Shropshire (Lefebvre 2007).

Conclusion

The specimen described herein is of interest because *Cardiocystites* has a very poor fossil record. It is the oldest representative of this genus and the first flattened eocrinoid fossil from the Ordovician of Morocco. Its completeness and relatively good preservation also confirms the significant characteristics of *C. bohemicus* and the main differences between the two known species *C. bohemicus* and *C. pleuricostatus*. This specimen demonstrates the very long stem and the location of the anal pyramid. This last detail might support the hypothesis of an "anterior-posterior" flattening plane (*sensu* Sumrall et al. 1997) and suggests admit epidermal mechanism of respiratory exchange. The combination of the morphological observations (a flexible but robust long stem, a small flattened theca, and a plume of numerous brachioles) and the sedimentological information (siliciclastic deposits with erosive grooves) seems to indicate that thecal flattening in this case could have been an adaptation to high-energy, cool, and shallow water. The occurrences of *C. bohemicus* in Morocco (early–middle Sandbian) and in Bohemia (early Katian) suggest the origination of the genus *Cardiocystites* in the west Gondwanan margin (or Mediterranean Province, *sensu* Havlíček et al. 1994) at the base of the Upper Ordovician. This specimen provides an additional argument for the faunal migration in the early Upper Ordovician from the west Gondwanan margin to Avalonia or Laurentia. The cool water circulation associated with the global eustatic rise might have helped the genus to spread to Avalonia using larval dispersion.

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