

Stylophorans in middle Arenig shallow water siliciclastics: *Vizcainocarpus* from the Imfout Syncline in Morocco's western Meseta

Ronald L. Parsley¹ – Juan Carlos Gutiérrez-Marco²

¹ Tulane University, Department of Earth and Environmental Sciences, New Orleans, LA 70118, USA. E-mail: parsley@tulane.edu

² Facultad de Ciencias Geológicas, Instituto de Geología Económica (CSIC-UCM), E-280040 Madrid, España. E-mail: jcgrapto@geo.ucm.es

Abstract. Numerous specimens of the ankyroid *Vizcainocarpus naimae* sp. nov. (Stylophora, Echinodermata) have been found in middle Arenigian shallow-water, inner shelf, fine to medium grained siliciclastics of the Oum-er-Rbia Formation, located in the Imfout Syncline in Morocco's western Meseta. Their occurrence in this sedimentary/ecological setting is atypical because ankyroids are most common in deeper water calcisiltites and limestones. Aspects of orientation and feeding habits in the debate over stylophorans as echinoderms or calcichordates (ongoing since the 1960s) appear to be largely resolved by data derived from these specimens. The aulacophores of most specimens face into the prevailing sediment-depositing current and appear to have draped over the adjacent sand wave. There is no evidence that they were orientated in the calcichordate mode with the convex side of the theca facing down and aulacophore extending into the substrate, as proposed by Jefferies (1973, 1986, 2001) and Sutcliffe et al. (2000).

Key words: Echinodermata, stylophorans, *Vizcainocarpus*, middle Arenig, Imfout Syncline, Morocco

Introduction

The orientation and feeding mode of stylophoran echinoderms, especially ankyroids (Parsley 1998), has been a source of speculation and interpretation for many years. Stylophorans are asymmetrical to (nearly) bilaterally symmetrical animals that consist of a theca and an elongated appendage. They show no evidence of the pentamerism typical of most echinoderm groups. Their skeletal plates are constructed of typical echinodermal stereom. Ankyroid thecae are typically elongate, convex dorsally, and planar to slightly concave on the ventral surface. Stylophoran appendages are divided into three distinct areas: the (commonly) tetramerous proximal aulacophore, the stylocone (cornutes, without anchoring projections) or styloid (ankyroids, with anchoring blades or spike-like projections), and the distal aulacophore composed of uniserial ossicles and paired cover plates over each segment.

Before Ubaghs (1961) demonstrated that the long appendage is in fact a feeding structure (aulacophore) and not a stem, it was generally accepted that stylophorans stretched out and fed along the bottom, with the mouth opening located at the opposite end of the theca from the appendage. This orifice is now commonly taken to be the anal opening. However, see Bather (1913) for his proposed mode of cothurnopore feeding in the cornute genus *Corthunocystis*.

Ubaghs (1961, 1967) demonstrated the likelihood that a water vascular system extended the length of the aulacophore (making the structure an arm). Reassignment of the stem to a feeding structure is based on his observations of the water vascular system impressed onto the tops of the distal aulacophore's uniserial ossicles. Paired cover plates arch over the tops of the ossicles and water vascular system. The impressions consist of a longitudinal groove for

the axial water canal and side connections leading to shallow depressions which are interpreted to be the ampullar pits. This discovery established that the aulacophore end was anterior, reversing the previous morphological orientation, and established the dorsal/ventral orientation of the theca. The food groove and cover plates are dorsal.

When stylophorans are subject to close morphological, taphonomic, and experimental scrutiny, the taxonomic assignment to the Echinodermata and basic morphological orientation proposed by Ubaghs appears to be confirmed.

Several other alternative morphological orientation/life-modes have been suggested for ankyroids but their acceptance has been limited. Jefferies (1968) proposed a totally new classification for stylophorans and placed them in a new subphylum: the Calcichordata. Calcichordate orientation reverses anterior/posterior and dorsal/ventral proposed by Ubaghs (1961). Morphological analysis and preservational evidence (see Ubaghs 1969, Parsley 1988, 1991, Kolata et al. 1991, Lefebvre and David 2001) are such that this zoological assignment and its morphological interpretation are both unlikely.

A second alternative morphological orientation/life-mode, especially supported in several papers by Kolata and various co-authors (but especially see Kolata et al. 1991, p. 847 for synoptic discussion), contends that ankyroids are infaunal and that both mouth and anus are located in the transverse slit, opening in the end of the theca opposite from the non-feeding appendage. Their argument is simple and parsimonious, but there is little morphological or preservational evidence to support it. A detailed morphological study of the aulacophore, clearly indicating it is a feeding structure, and evidence presented herein, cast considerable doubt on this life-mode interpretation.

Stylophoran range and general paleoecology

Stylophorans range from Middle Cambrian to Lower Pennsylvanian (Kolata et al. 1991). They are found commonly in deeper water (middle or outer shelf) calcisiltite sediments that are commonly slightly to moderately dysaerobic. When ankyroids are found in shallower water (inner shelf) they are commonly found in limestones or interbedded shaley units with high organic content. Ankyroids, in particular, are rare in well-aerated, high-energy arenites and are not common in shallow water sedimentary conditions.

Stylophoran feeding posture

Aulacophore function was discussed by Ubahgs (1979), who suggested that stylophorans were microphagous, and fed by extending the distal aulacophore upwards from the styloid to a near vertical position in the water column. His interpretation is, in fact, partly based on the preservational tendency for the ankyroid aulacophore to be curved “scorpion-like” over the dorsal thecal surface. This scorpion-like curvature is now commonly interpreted as the *post mortem* constriction of tendons/muscles, and it can be compared broadly with *post mortem* ligament/muscle flexure in the necks of dead saurischian dinosaurs that curve posteriorly over the back of the animal.

Other evidence for feeding in the water column came from Parsley (1981) and Fisher (1993) who reported on Ordovician enopleuroid ankyroids living under brachiopod shells but extending their aulacophores out from under them. Specimens living in this semi-cryptic environment presented compelling evidence that the aulacophore, extending out from under a brachiopod shell, is indeed a feeding structure, and that the paired plates articulating with the large aulacophore icicles are (dorsal facing) cover plates.

In a study centred primarily on stylophoran functional morphology, Parsley (1988) opined that the aulacophore broadly bowed upwards as it stretched out over the substrate. This bowing would constrict the bases of the tightly articulated cover plates and force them open. Such a feeding mode would work best if the aulacophore was facing into the current (see also Lefebvre 2003).

Parsley (1991) conducted a series of flume studies testing 1 : 1 scale models of enoplourid ankyroid stylophorans in currents of greatly varying velocities. Results clearly demonstrated that the elevated aulacophore held vertically or reflexed back over the theca (as suggested by Ubahgs) imparts a distinct instability to the animal, and in currents of less than 10 cm/sec the animal would tumble or flip over in the water column. In the same series of experiments, models on a (fine-grained) sand surface and facing into the current, with the modelled aulacophore stretched straight out, or slightly convexity arched over the sediment, were stable in currents from +10 to +30 cm/sec. At higher velocities (+25 cm/sec) the models sat stably on an irregularly rippled surface.

Geological setting

All of the studied material comes from a single sandstone bed which is located in the uppermost part of the Oum-er-Rbia Formation (Gigout 1942, Allix 1978, Rais-Assa 1984). It crops out near the axis of the Imfout Syncline. The syncline is a relatively simple north-northwest trending fold to the north of the Rehamna Massif, on the Northwestern or External Zone of the Hercynian belt in the coastal block of Morocco's western Meseta (Piqué et al. 1991, 1993, Figs 1 and 2).

The Oum-er-Rbia Formation was originally part of an early Paleozoic, shallow water, epicontinental platform spanning western and Central Morocco; the slope was in eastern Morocco. This area, plus the sediments of the Anti-Atlas Mountains, constituted what was then part of the northern Gondwana platform (Piqué et al. 1993). In the Imfout Syncline the Mid-Ordovician sediments (especially the Oum-er-Rbia Formation) were deposited on the mid-shelf, above storm base, and hummocky, cross stratified, tempestites are common (Hamoumi 1988, 1996).

The Ordovician succession in the Imfout Syncline was defined by Gigout (1942, 1951). Most sediments in the syncline are composed of coarse- to fine-grained siliciclastics of terrigenous origin, and display a very low grade of metamorphism. The Oum-er-Rbia Formation is a sequence of 500 to 600 metres of green argillaceous shales with intercalations of thin sandstones and noduliferous beds. It has been placed in the middle Arenig on the basis of rare but definitive occurrences of graptolites, trilobites, articulate brachiopods and echinoderms from equivalent outcrops in the coastal Meseta (Yovanovitch 1933, Gigout 1951, 1954, Destombes et al. 1985). Underlying this Ordovician sequence is the Middle Cambrian El Hank Formation.

The overlying Imfout Formation is found in the axis of the syncline and is composed of 300 metres of sandstones. Its age is less certain, and has been dated as Llandeilo *sensu lato* (Gigout 1942, 1951, 1965), middle Arenig to Llanvirn (Gigout 1956a, 1956b), early to middle Arenig (Destombes 1971), or Arenig to Llandeilo (Destombes et al. 1985).

Biostratigraphy

The ankyroids studied herein occur in a thin sandstone bed in the upper part of the Oum-er-Rbia Formation that lies 23 metres below the base of the overlying Imfout Formation (Fig. 2). The ankyroids form a nearly monospecific assemblage in a wide (about two metres), thin lens (about one cm thick), occurring near the top of a horizontally laminated sandstone bed slightly over 25 cm in thickness (Fig. 3). Only fragments of linguloids co-occur with the ankyroids.

The ankyroids are assignable to a single species, *Vizcainocarpus naimae* sp. nov. Most specimens are preserved as moulds, and sand grains coarsely imprint the latex casts made from them. Almost all specimens are thecae that range from 4 to 8 mm in length, and commonly most of the proximal aulacophore is still attached. While the orien-

tation of the specimens appears to be biologic, the narrow range of size (no small juveniles or large adults) suggests to us that some hydrodynamic sorting has occurred. Some specimens are complete to the end of the styloid and several specimens have part to almost all of the distal aulacophore coarsely preserved.

Ankyroids in shallow water siliciclastics

Here we report on a recent discovery of Lower Ordovician (Arenig) ankyroids that lived most atypically in, and are persevered in, shallow water, high energy siliciclastic deposits of the Oum-er-Rbia Formation in Morocco's western Meseta. The material studied consists of three small slabs with numerous ankyroid specimens, and approximately thirty additional individual specimens on small slabs, totalling about 100 specimens. The total area of the surface is about one-half of a metre square. This is a notable discovery because stylophorans are very rarely closely gregarious (in the sense that they are found with less than centimetre spacing). This many individuals, in close proximity and on an essentially isochronous surface, allows for moderately rigorous conclusions concerning their life habits. Evidence for burial horizons is present in the form of low current ripples observed on several of the larger slabs.

Bedding structures show that the ankyroids lived above fair-weather base levels. The taphonomy of the specimens demonstrates that some of the animals were tumbled in a rigorous current and were quickly buried in a jumbled orientation. Most specimens, however, are preserved with the proximal aulacophore pointed into the direction of the prevailing current as indicated by the low sand waves that define the bedding planes. On the best preserved untrimmed slab, all specimens ($n = 28$) have their proximal (aulacophore) ends oriented closely perpendicular to the ridges of the sand waves. They deviate from the perpendicular to the sand waves in a narrow arc from 0 to ± 40 degrees, and most deviate on the order of ± 20 degrees (see the rose diagram, Fig. 4). It is quite possible that these animals lived in a pronounced tidal environment and may have frequently reset their (rheophylic) orientation. This is suggested by a few specimens (5 of the 28) on a younger bed less than two millimetres higher than the lower bed that are arranged about 180 degrees to the underlying set. Such a reversal in orientation may indicate habitation in a tidal regime. If this interpretation is correct, then all of the specimens resting on the ventral face of the theca are rheophylically oriented. Several specimens are not sitting on their ventral faces and may be current aligned. Because of the uniformly oriented thecae sitting in the sand wave troughs, it is highly unlikely that their uniformity of position is due to sedimentary sorting. They appear to be preserved in normal feeding position.

The proximal aulacophore is angled upwards relative to the horizontal plane of the theca. This high angle extension of the proximal aulacophore was part of the feeding posture, as aligned specimens were draping the distal end of

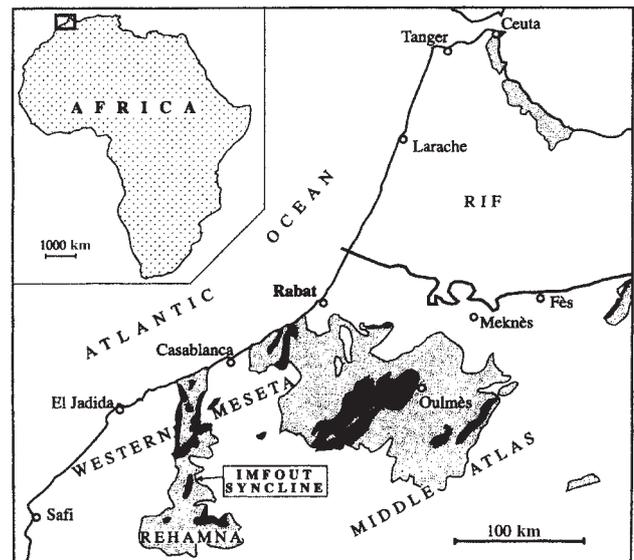


Figure 1. Regional geological sketch map showing extent of Pre-Mesozoic outcrops (stippled), Ordovician rocks (in black), and the Imfout Syncline in Morocco's western Meseta.

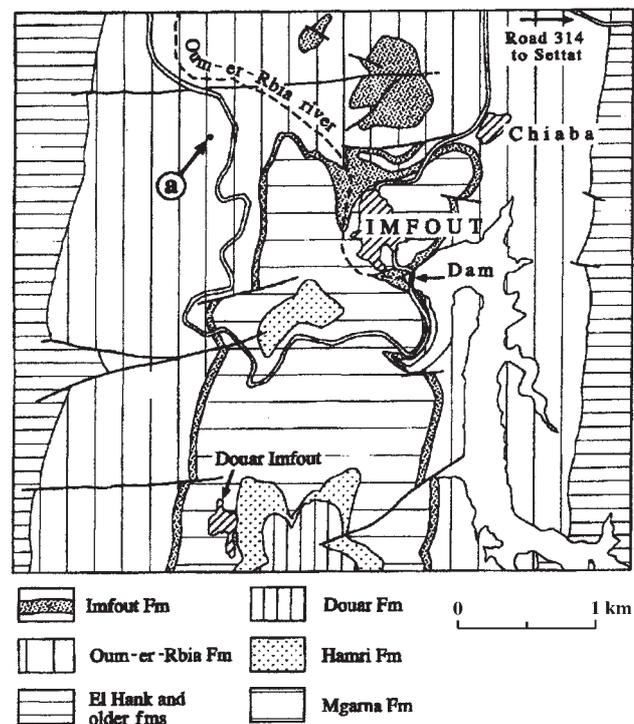


Figure 2. Geological map of the Northern Imfout Syncline, Morocco, showing the locality (a) where *Vizcainocarpus* specimens were collected.

the aulacophore over the adjacent sand wave (Fig. 5C). Their stability on the scoured resting surfaces would appear to be somewhat precarious, but considering the animals low hydrodynamic profile, denticulate "skirt" around the ventrolateral edges of the marginals, and the pronounced spikes on both styloid and proximal distal aulacophore ossicles (Fig. 5G), the organisms could anchor in sediments with fairly rapid bottom currents (> 25 cm/sec; based on flume studies, Parsley 1991).



Figure 3. Field photograph of the type locality and horizon in the Oum-er-Rbia Formation (middle Arenigian), where *Vizcainocarpus naimae* specimens were collected.

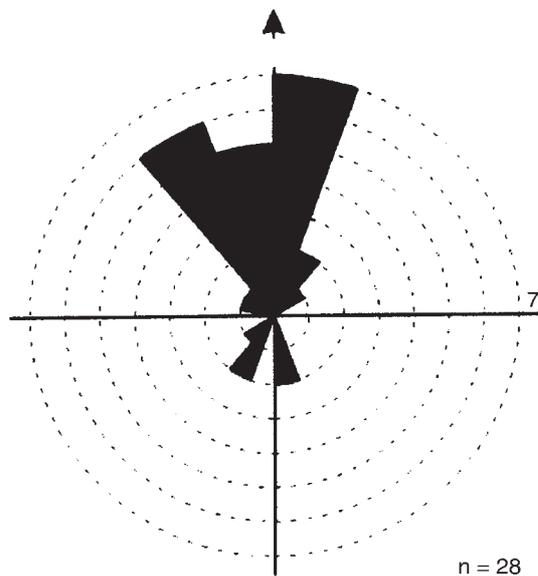


Figure 4. Rose diagram showing the orientation of specimens to paleocurrent. A total of 28 specimens were measured on a single slab. Of the 28 specimens, 23 are facing into the direction of the paleocurrent, five are facing in the opposite direction (we interpret as realignment to counter flow?). All but two of the specimens are oriented with the convex face/cover plates of the aulacophore facing upwards.

Discussion

Specimens on the burial horizon align to current as evinced by the numerous aligned specimens. The evidence strongly indicates that the proximal aulacophore was draped over the up-slope of the adjacent sand wave or ripple and the distal aulacophore extended down slope on the other side of the wave crest. The cusps on the styloid and proximal half of the distal aulacophore and the ventrolateral stereom “skirt” on the thecal marginals provide sufficient anchoring to keep the animal in place even with the vigorous deposition pattern of ripple-forming currents. The rheophylic orientation and feeding mode of ankyroids proposed by Parsley (1988, 1991) and Lefebvre (2003) both appear to be confirmed. Interestingly, the ability

of *Vizcainocarpus* to feed and maintain its orientation in such a high-energy regime (current velocities > 25 cm/sec) conforms closely to the conditions modelled in Parsley’s (1991) flume studies.

Because of the ongoing debate over the taxonomy (as either echinoderms or calcichordates) and functional morphology of stylophorans, the data discussed here is important. There is no evidence to support the calcichordate orientation and mode of locomotion proposed by Jefferies (1973, 1986, 2001) and Sutcliffe et al. (2000), in which the convex (normally upper) face of the theca is directed into the substrate and the aulacophore (stem or tail in this case) extends down into the sediment, and by repeated insertion and pulling drags the animal along, aulacophore end first. Such excessive motion for very little forward progress in return would be highly inefficient (see Ruta 1999, Lefebvre and David 2001, Lefebvre 2003 for further rebuttal). In Parsley’s (1991) flume experiments, model specimens with the aulacophore extended into the sediment and flat surface of the theca facing up, were quickly buried by shifting sediment. Presumably in the calcichordate orientation each cycle of extraction of the “stem” or “tail” (aulacophore in echinoderm usage), and its reinsertion into the sediment, would have raised the upper (flat) surface of the theca out of the substrate and allowed prevailing bottom currents to flush away the overlying sediment.

The specialized adaptive features present on this species (marginal “skirt”, prominent styloid blades, and pronounced ossicle projections on the distal aulacophore) argue that this is its normal setting. In spite of this rather extreme example of an ankyroid living in an atypical high energy habitat, it seems quite likely that the overwhelming majority of ankyroids, which lived in quieter conditions, faced their aulacophores into the prevailing currents and extended it flat along the bottom or arched it slightly (see Lefebvre 2003).

Systematic paleontology

Class Stylophora Gill and Caster 1960

Discussion: Stylophorans are present throughout the Ordovician of Morocco, and have been variously reported as single specimens to occurrences of over 100 specimens. There is a tendency for species of Lower and Lower Middle Ordovician age to show similarity and close affiliation with those of the Montagne Noire, France. Stylophorans were first noted in Morocco by Gigout (1954) as a single cornute specimen of *Phyllocystis blayaci* Thoral from the Imfout Syncline in the western Meseta. Subsequent stylophoran finds (Ordovician) come from the Anti-Atlas Mountains (pre-Saharan border), where at least nine genera have been described by Chauvel (1966, 1971), Cripps (1990), Beisswenger (1994), and Ruta (2000), and range from Arenig to Ashgill. The material discussed herein is the second locality in the Imfout Syncline (in the Jema of Ouled Abbou region) to produce Ordovician stylophorans.

Order Ankyroida Parsley 1998

Emended diagnosis: Stylophorans with essentially bilaterally symmetrically arranged marginal plates. Marginals vary in coverage of dorsal and ventral faces. Somatic plates vary from tessellated pavements to regularized plate patterns. Commonly without a zygale, but when present the distal element is somatic in origin and is homologous with the central somatic ("CS") plate of more advanced genera. Articulating spines commonly (if not always) articulate with M4/M'4 and are homologous to marginals M5/M'5. Respiratory pore structures are absent. Styloid with spikes, flanges, or multicusp projections. Cover plates on distal aulacophore are commonly short and tightly articulated (modified from Parsley 1998).

Genus *Vizcainocarpus* Ruta, 1997

1997 *Vizcainocarpus* Ruta, pp. 366–376.

2000 *Vizcainocarpus rutai* Lefebvre, pp. 900–902.

Type species: *Vizcainocarpus dentiger* Ruta, 1997

Description: Ankyroid with symmetrical teardrop-shaped theca; gently convex on dorsal face, planer to slightly concave on the ventral face; ten marginal thecal plates (M1/M'1–M5/M'5) that are slightly wider on the ventral surface than the dorsal; tall transverse strut (nearly as tall as the marginals) extends from M'1 to M5 and is composed of an extension of M'1 and the CS plate. Ventrally-lateral margins of marginals project outwards to form a skirt-like margin with dentacle-like cusps. Aulacophore opening formed by M1 and M'1 ventrally and most of the lateral surface; LA and RA form the upper lateral and dorsal part. Somatic spaces between marginals and strut on ventral face occupied by small tessellated platelets; on the upper face somatic platelets are larger and diminish gradually in size distally. Dorsal platelets are bossed in three or four ill-defined rows adjacent to the adorals, all dorsal platelets are composed of coarse stereom similar in mesh size and pattern to the adjacent marginals. Proximal aulacophore tetramerous, six to eight segments, two or three distal segments distorted by partial envelopment around styloid, deeply inserted into the cup formed by M1/M'1 and cup angled upwards about > 45 degrees from horizontal. Styloid has two sharp spike-like projections. Distal aulacophore about the same length as the theca, with proximal ossicles projected into aulacophore-like spikes; cover plates apparently rather short and tightly articulated with the ossicles.

Discussion: Until the discovery of the Imfout material, *Vizcainocarpus* was known from only three specimens. The holotype species, *V. dentiger* Ruta, 1997 is represented by a single specimen, a mould inside a siliceous nodule from the Lower Arenig of the Montagne Noire in Southern France. The latex casts of the specimen, which consist of the theca, proximal aulacophore, and a few segments of the distal aulacophore, display the extant morphology rather well. A second species, *V. rutai* Lefebvre

2000, from the Tremadoc of Shropshire, is known from two incomplete and rather poorly preserved thecae. In contrast, over 100 specimens of *V. naimae* sp. nov. are known from the Imfout Syncline. Because of the coarse preservation and loss of plates through solution we can add only a few aspects to basic generic morphology, such as differing specific relationships of the CS plate to the marginal plate frame, and additional data on the distal aulacophore. Latex casts were made of the moulds and their fidelity is quite high considering the coarseness of preservation.

Vizcainocarpus naimae sp. nov.

Figs 5–7

Holotype: Holotype specimen is MGM 2202 (Fig. 5A).

Paratypes: MGM 2200a, b and MGM 2203–2206.

Type horizon: In the Oum-er-Rbia Formation, 23 metres below the base of the overlying Imfout Formation

Type locality: One and one half kilometres WNW of Imfout, about one quarter kilometre west of highway No. 128.

Derivation of name: The name is from Dr. Naïma Hamoumi of the University of Mohamed V in Rabat, Morocco, who has studied widely the Ordovician rocks of that country.

Diagnosis: *Vizcainocarpus* ranging from sub oval to teardrop in shape. Transverse strut tall and narrow. Adorals LA and RA short, aulacophore embayment between them pronounced. Dorsal somatic platelets are small, relatively smooth, and unbossed.

Description: Theca is composed of five pairs of marginal plates; M1/M'1 to M5/M'5: the transverse strut is composed of an extension of M'1 and the CS plate, which is derived from M5 and has not migrated in either direction along the inner margin of the right hand marginals. The strut appears to be narrower than in the type species. As in the other species the distal most marginal plate M'5 wraps around the distal end of the theca and provides an anchoring site for the anal opening and surrounding anal pyramid platelets. Along the ventrolateral margin of the lateral marginals the edge projects ventrolaterally to produce an irregular marginally denticulate "skirt". Dorsal somatic plates are small and apparently form a tessellated surface. The slightly curved surface apparently completely covered the relatively tall strut. Finger-like anal valve plates are located at the distal end of the dorsal surface but are commonly poorly preserved, and anal valve extent and morphology are yet to be determined.

The ventral surface in our material is not well preserved. It is gently concave and the marginal plates, including M1/M'1, are fairly uniformly broad. Somatic surfaces between marginals and transverse strut are paved with tessellated surfaces composed of small platelets. Proximally, adjacent to M1 and M'1 in the tessellated fields, there may be a pair of oval lateripores. Several specimens suggest their presence, but they may be simply a product of preservation.

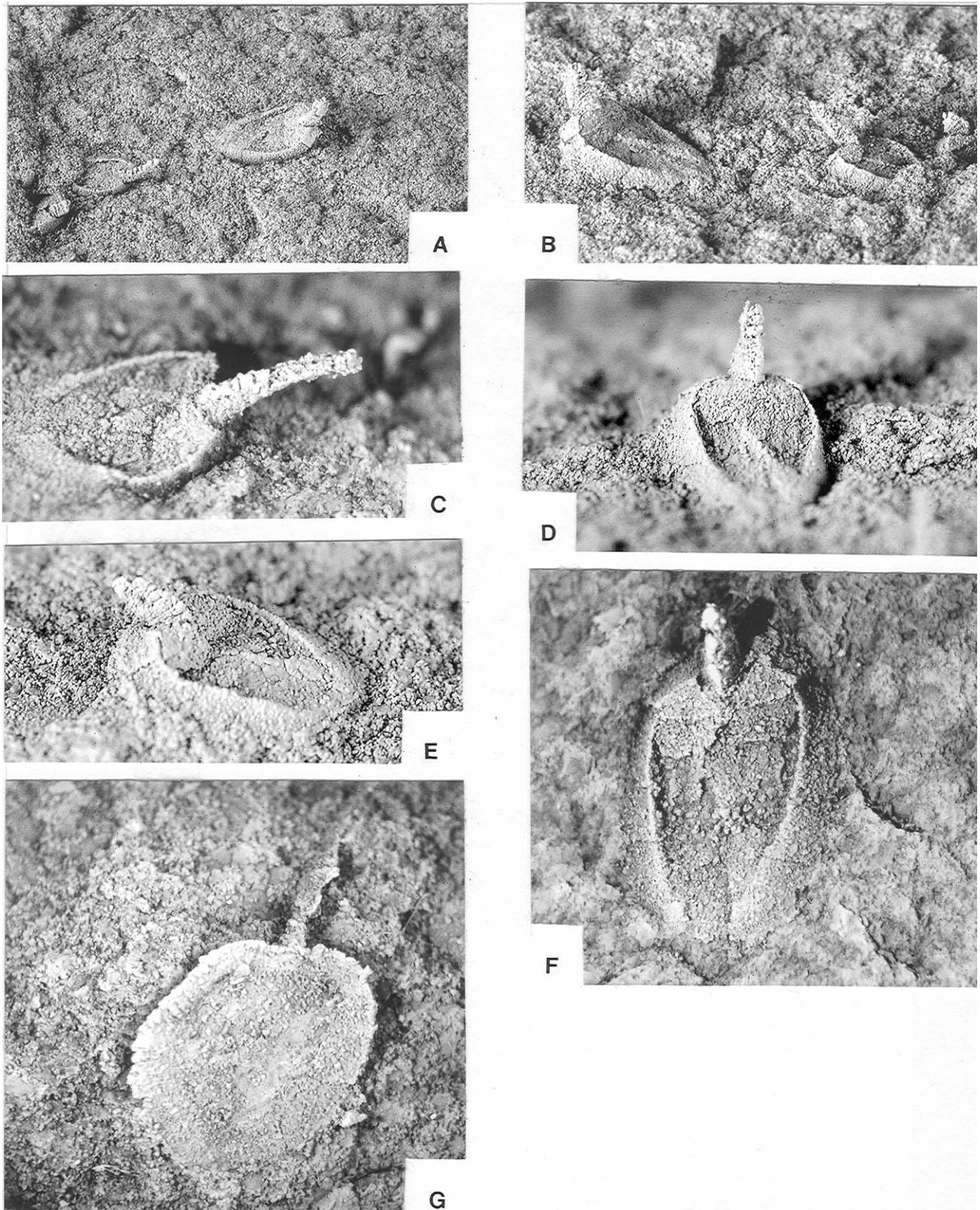


Figure 5. Latex casts of *Vizcainocarpus naimae* sp. nov. Casts are whitened with a sublimate of NH_4Cl . Magnification of all specimens $\times 4.6$. Specimens have the prefix MGM and are housed in the Geomining Museum of the Spanish Geological Survey, Madrid.
 A – pair of current aligned specimens facing elevated proximal aulacophores into paleocurrent direction. Paratype, MGM 2200a, b. B – pair of current aligned specimens with proximal aulacophores facing into paleocurrent direction. Paratype, MGM 2201a, b. C – specimen with part of the distal aulacophore attached and presumably in feeding orientation. Holotype, MGM 2202. D – specimen facing into paleocurrent direction. Ventral transverse strut prominent. Paratype, MGM 2203. E – upper surface of theca with adaulacophorals, well preserved and somatic plates draped over the transverse strut. Paratype, MGM 2204. F – upper surface of theca with marginals and somatics fairly well preserved. Paratype, MGM 2205. G – ventral face of theca with curved aulacophore attached. Note remnants of styloid blades. Paratype, MGM 2206.

At least six tetramerous segments make up the proximal aulacophore; the two distal segments are somewhat deformed by the insertion of the styloid. The styloid is flat sided but projects laterally in alignment with the two spike-like projections on its ventral side. Cover plates on its upper surface appear to be tightly articulated. The proximal four to six ossicles of the distal aulacophore have ventrally projected spikes, similar to the styloid; the remaining six to 10+ ossicles are more rounded on their ventral face. Cover plates are rather short and appear to be tightly articulated.

Discussion: Several characters separate the type species *V. dentiger* Ruta, 1997 from *V. naimae* that are clearly not associated with mode of preservation. In the type species M1/M'1 plates are very broad, considerably more so than in *V. naimae* where M1/M'1 is about the same width on the ventral face as the M2 and M3 paired marginals. On the dorsal face two differing characters are present. First, in *V. naimae* the adoral plates are shorter than in *V. dentiger*; second, in *V. dentiger* the proximal somatic plates on the dorsal face are thick, composed of coarse stereom, and are bossed by low horn-like projections. In *V. naimae* these somatic plates are relatively thin and smooth.

Our reconstruction (Fig. 7) shows that there are ten marginal plates M1 to M5 on the right side; M'1 to M'4 on the left and extending onto the rounded posterior formed by M'5. In respect to distribution of marginals, it is quite similar to the reconstructions of Lefebvre (2000) in which he 1. corrects Ruta's (1997) construction of *V. dentiger* (Lower Arenig of the Montagne Noir, France), and 2. reconstructs the major thecal plates in the species *V. rutai* Lefebvre (Tremadoc of Shropshire, England).

The CS plate on our material is sutured and aligned with M5 just as it is in the cornute ancestral condition, where the distal extension of the strut across the ventral face is in fact an extension of M5. We take the position of CS relative to M5 to be a primitive character because, in other coeval and near coeval genera, the strut-like CS plate can be aligned, or partly so, with marginals adjacent to M5. Separating the CS plate from the M5 marginal is one of the definitive steps in the derivation of ankyroids from cornutes (Parsley 1998). Alignment of the CS plate in *V. dentiger* and in *V. rutai* is slightly different, as in these species its midline aligns with the suture between M4 and M5 and sutures with both of them (see Lefebvre 2000).

Ruta (1997) interpreted a cavity between the right adoral (RA) and M1 plates as a hydropore. Even though the preservation in our material is rather coarse, there is no evidence for a hydropore associated with the RA plate on any of the specimens where this part of the theca can be observed. We suggest that the genus does not have a hydropore associated with the RA plate and the "hydropore opening" on Ruta's holotype may be a fracture.

The total length of the aulacophore, which is preserved in our material, is slightly longer than the theca, and the strong denticulate pattern of the distal aulacophores' ventral ossicles, observed by Ruta (1997), is also observed in the Moroccan material. These styloid-like, ventrally directed, anchoring spines on the ossicles persist to about the mid

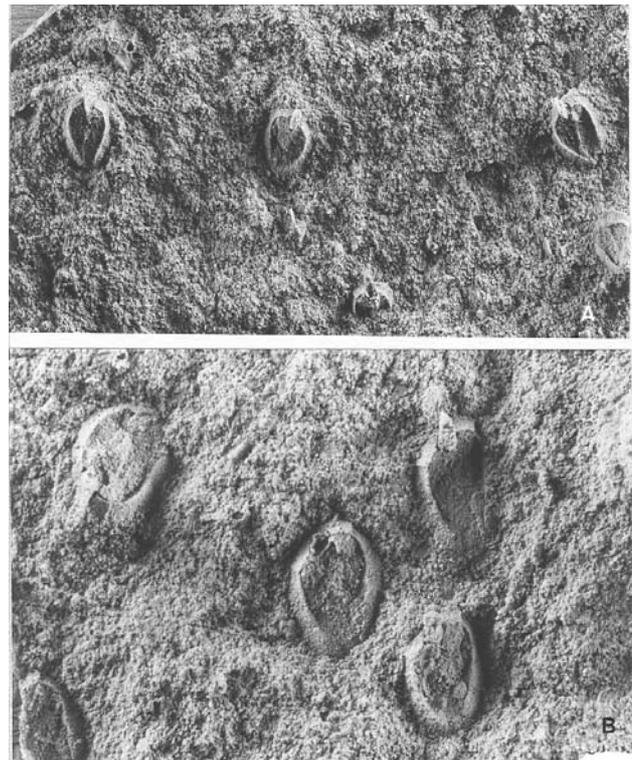


Figure 6. Latex cast of a slab (portions) with aligned *Vizcainocarpus naimae* sp. nov. specimens. Specimen whitened with sublimate of NH₄Cl. A – specimens aligned along sand ripple. B – specimens aligned to paleocurrent but relationship to a particular ripple is indistinct. MGM 2207, magnification $\times 1.4$.

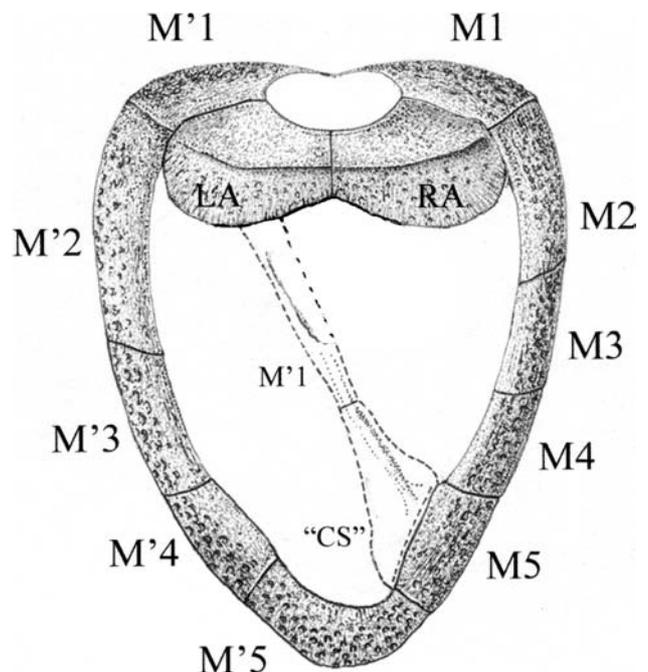


Figure 7. Partial reconstruction, upper surface of *Vizcainocarpus naimae* sp. nov. M = marginal plate on right side, M' = marginal plate on left side, LA = left adoral, MA = medial adoral, RA = right adoral, "CS" = posterior plate of the transverse strut or the central somatic. Reconstruction based on type material.

length of the distal aulacophore, and are important in attaching and orienting these animals into a feeding posture.

Acknowledgements: Marcello Ruta, Field Museum, Chicago skilfully made the line drawing of *Vizcainocarpus*. We are further grateful to him for insightful discussions of the material. We thank the anonymous reviewer and O. Fatka, Charles University, Prague, whose reviews helped greatly in improving the paper.

References

- Allix P. (1978): Coupes lithologiques mesurées dans les terrains paléozoïques de la Meseta côtière, entre Imfout et Oulad Abbou (Maroc). Rapport de mission (juillet–septembre 1978). Trav. Lab. Sci. Terre (St-Jérôme) 10, 28, 1–18.
- Bather F. A. (1913): Caradocian Cystidea from Girvan. Trans. R. Soc. Edinb.-Earth Sci. 49, 2, 6, 359–529.
- Beisswenger M. (1994): A calcichordate interpretation of the new mitrate *Eumitrocystella savilli* from the Ordovician of Morocco. Paläont. Z. 68, 443–462.
- Chauvel J. (1966): Echinodermes de l'Ordovicien du Maroc. Cahiers Paléont. CNRS, Paris, 1–120.
- Chauvel J. (1971): Les échinodermes carpoïdes du Paléozoïque inférieur marocain. Not. Serv. géol. Maroc 31, 237, 49–60.
- Cripps A. P. (1990): A new stem craniate from the Ordovician of Morocco and the search for the sister group of Craniata. Zool. J. Linn. Soc. London 100, 27–71.
- Destombes J. (1971): L'Ordovicien au Maroc. Essai de synthèse stratigraphique. Mém. Bur. Rech. géol. min. 73, 237–263.
- Destombes J., Hollard H., Willefert S. (1985): Lower Palaeozoic rocks of Morocco. In: Holland C. H. (ed.): Lower Palaeozoic rocks of the world, vol. 4. Lower Palaeozoic of north-western and west central Africa. John Wiley and Sons, Chichester, 91–336.
- Fisher D. (1993): Life orientation of mitrate stylophorans and its implications for the calcichordate theory of vertebrate origins. Abstracts with programs 25, 6, A105, Geological Society of America.
- Gigout M. (1942): Note préliminaire sur le Cambro-Ordovicien d'Imfout (cours inférieur de l'Oum-er-Rbia, Maroc). C. R. somm. Séanc. Soc. géol. France 11, 101–103.
- Gigout M. (1951): Etudes géologiques sur la Méséta marocaine occidentale (arrière pays de Casablanca, Mazagan et Safi). Thèse Sciences, Paris, Travaux du Institut scientifique chérifien, Rabat, 3. Not. Mém. Serv. géol. Maroc 86, pp. 507.
- Gigout M. (1954): Sur un hétérostélé de l'Ordovicien marocain. Bull. Soc. Sci. nat. phys. marocaines 34, 3–7.
- Gigout M. (1956a): Précisions nouvelles sur l'Ordovicien inférieur de la Meseta marocaine occidentale. C. R. Séanc. Acad. Sci. Paris 242, 2378–2741.
- Gigout M. (1956b): Levés géologiques sur la feuille Sidi-Bennour (Meseta marocaine occidentale). Not. Mém. Serv. géol. Maroc 14, 133, 33–54.
- Gigout M. (1965): Notice explicative de la carte géologique (1 : 200.000) de la Méséta entre Mechra ben Abbou et Safi (Doukkala et massif des Rehamna), avec contributions de J. Destombes (Minerais et substances utiles) et M. Ferré (Hydrogéologie). Not. Mém. Serv. géol. Maroc 84, 1–48.
- Gill E. D., Caster K. E. (1960): Carpoïd echinoderms from the Silurian and Devonian of Australia. Bull. Amer. Paleont. 41, 1–71.
- Hamoumi N. (1988): La plate forme Ordovicienne du Maroc: dynamique des ensembles sédimentaires. Thèse d'Etat, Université Louis Pasteur, Strasbourg.
- Hamoumi N. (1996): Lower Paleozoic evolution of north-Gondwanan Moroccan margin. Serie Correlación Geológica, Tucumán 12, 275–276.
- Jefferies R. P. S. (1968): Some fossil chordates with echinoderm affinities. In: Millott N. (ed.) Echinoderm Biology. Symp. Zool. Soc. London 20. Academic Press, London, 163–208.
- Jefferies R. P. S. (1973): The Ordovician fossil *Lagynocystis pyramidalis* (Barrande) and the ancestry of amphioxus. Phil. Trans. R. Soc. Lond. 265, 409–469.
- Jefferies R. P. S. (1986): The ancestry of the vertebrates. British Museum (Natural History), London.
- Jefferies R. P. S. (2001): Ichnological evidence on the behaviour of mitrates: comments on the reply. Lethaia 34, 262.
- Kolata D. R., Frest T. J., Mapes R. H. (1991): The youngest carpoïd: occurrence, affinities, and life mode of a Pennsylvanian (Morrowan) mitrate from Oklahoma. J. Paleontol. 65, 5, 844–855.
- Lefebvre B. (2000): A new mitrate (Echinodermata, Stylophora) from the Tremadoc of Shropshire (England) and the origin of the Mitrocystitida. J. Paleontol. 74, 890–906.
- Lefebvre B. (2003): Functional morphology of stylophoran echinoderms. Palaeontology 46, 3, 511–555.
- Lefebvre B., David B. (2001): Ichnological evidence on the behaviour of mitrates: reply. Lethaia 34, 260–261.
- Parsley R. L. (1981): Echinoderms from the Middle and Upper Ordovician rocks of Kentucky. US Geol. Surv. profess. Pap. 1066-K.
- Parsley R. L. (1988): Feeding and respiratory strategies in Stylophora. In: Paul C. R. C., Smith A. B. (eds) Echinoderm phylogeny and evolutionary biology. Oxford Science Publications and Liverpool Geological Society, Oxford and Liverpool, 347–361.
- Parsley R. L. (1991): Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata). Bull. Amer. Paleont. 100, 1–57.
- Parsley R. L. (1998): Taxonomic revision of the Stylophora. In: Mooi R., Telford M. (eds) Echinoderms: San Francisco. A. A. Balkema, Rotterdam, 111–117.
- Piqué A., Bossière G., Bouillin J.-P., Chalouan A., Hoepffner C. (1993): Southern margin of the Variscan belt: the north-western Gondwana mobile zone (eastern Morocco and northern Algeria). Geol. Rundsch. 82, 432–439.
- Piqué A., Cornée J.-J., Müller J., Roussel J. (1991): The Moroccan Hercynides. In: Dallmeyer R. D., Lécorché J. P. (eds) The West African Orogens and Circum-Atlantic Correlatives. Springer-Verlag, Heidelberg, 229–263.
- Rais-Assa R. (1984): Etude géologique de la partie occidentale du massif hercynien des Rehamna septentrionales (Meseta marocaine). Lithostratigraphie, plissement et métamorphisme, chevauchement et nappes. Thèse 3^{ème} cycle, Université de Aix-Marseille III.
- Ruta M. (1997): A new mitrate from the Lower Ordovician of southern France. Palaeontology 40, 2, 363–383.
- Ruta M. (1999): Brief review of the stylophorans debate. Evol. Dev. 1, 2, 123–135.
- Ruta M. (2000): A new stylophoran echinoderm, *Juliaecarpus milneorum*, from the late Ordovician Upper Ktaoua Formation of Morocco. Bull. Nat. Hist. Mus. London (Geology) 55, 47–79.
- Sutcliffe O. E., Südkamp W. H., Jefferies R. P. S. (2000): Ichnological evidence on the behaviour of mitrates: two trails associated with the Devonian mitrate *Rhenocystis*. Lethaia 33, 1–12.
- Ubahgs G. (1961): Sur la nature de l'organe appelé tige ou pédoncule chez les carpoïdes Cornuta et Mitrata. C. R. Séanc. Acad. Sci. Paris 253, 2738–2740.
- Ubahgs G. (1967): Stylophora. In: Moore R. C. (ed.) Treatise on invertebrate paleontology, Echinodermata 1 (2). Geological Society of America and University of Kansas Press, Boulder and Lawrence, 495–565.
- Ubahgs G. (1969): Les échinodermes "carpoïdes" de l'Ordovicien inférieur de la Montagne Noire (France). Cahiers Paléont. CNRS, Paris, pp. 112.
- Ubahgs G. (1979): Trois Mitrata (Echinodermata: Stylophora) nouveaux de l'Ordovicien de Tchécoslovaquie. Paläont. Z. 53, 98–119.
- Yovanovitch B. (1933): Les boutonnières de Paléozoïque entre Casablanca et Azemmour. C. R. somm. Séanc. Soc. géol. France, 31–33.