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OMANASTER IMBRICATUS (ECHINODERMATA, ASTEROIDEA), A NEW GENUS AND SPECIES FROM THE SAKMARIAN (LOWER PERMIAN) SAIWAN FORMATION OF OMAN, ARABIAN PENINSULA

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Abstract. *Omanaster imbricatus* is a new genus and species of Sakmarian (Early Permian) asteroids collected from the basal *Pachycyrtella* Bed of the Saiwan Formation of Oman, Arabian Peninsula; the family Omanasteridae is recognized. Late Paleozoic and especially Permian asteroids are rare and *O. imbricatus* differs significantly from those previously described, thereby providing an important addition to known late Paleozoic diversity. Unfortunately the single available specimen is incomplete with remaining ossicles both leached and partially fused, and available data are limited. Adambulacral form and arrangement of *O. imbricatus* are both suggestive of corresponding expressions of certain earlier Paleozoic species and unlike those of the crown-group, suggesting an enduring Paleozoic lineage but one not phylogenetically a part of the Mesozoic diversification. The *Pachycyrtella* Bed has been interpreted as recording a succession of pioneer palaeocommunities colonizing a turbulent, shallow-water setting affected by oscillatory flows. The apparently flattened appearance of *O. imbricatus* is suggestive of appearances of certain Cretaceous and extant species recovered from similar environments thus suggesting both homoplasy and the versatility of asteroid evolution across extended spans of geologic time.

Introduction

Asteroid fossils are rare almost wherever they occur, and Permian examples are all but unknown (but see Kesling 1969). The discovery of an Early Permian representative of unusual configuration in a preservational setting atypical of occurrences of the relatively weakly constructed Asteroidea is noteworthy, and it is described here.

The geologic setting of the new fossil, from Oman, Arabian Peninsula, was comprehensively treated in Angiolini et al. (2003), Angiolini (2007), and Webster et al. (2009); only limited pertinent data are summarized here.

Two asteroid fossils were collected from the base of the Lower Permian Saiwan Formation of Interior Oman, Arabian Peninsula, and specifically from the *Pachycyrtella* Bed, which was described by Angiolini et al. (2003) and Angiolini (2007). The Saiwan Formation is late Sakmarian in age as based on ammonoids and brachiopods, and on correlation with the Haushi limestone which contains fusulinids and palynomorphs (Angiolini et al. 2003; Angiolini et al. 2006).

The *Pachycrytella* bed, which characterizes its base in the Haushi-Huqf area (Interior Oman), is a coarse bioclastic calcareous sandstone which transgresses the glacial deposits of the Al Khlata Formation. This bed is dominated by the mostly articulated shells of *Pachycyrtella omanensis* Angiolini, 2001, a spiriferinide brachiopod free-living on a sandy bottom characterized by high energy flow condition in a shoreface setting, above the fair-weather wave base (Angolini 2001; Shiino & Angiolini 2014). Sedimentary structures and flow experiments on *P. omanensis* indicates bottom oscillatory flow velocities between 0.15 and 0.5 m/s (Shiino & Angiolini 2014).

Studies of population dynamics and community structure of the *Pachycyrtella* Bed (Angiolini 2007) suggest a physically stressed environment dominated by opportunist brachiopod and bivalve species adapted to

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high substrate mobility and also able to benefit from the high nutrient influx brought about by the raised temperatures, increased humidity, and increased fluvial run-off that accompanied the end of Gondwanan deglaciation.

Brachiopods and bivalves are numerically dominated by two opportunist species (*P. omanensis* and *Dickinsartella pistacina* Larghi, 2005) characterized by r-strategy, rapid growth rates and high infant mortality rates (e.g. Larghi 2005; Angiolini 2007). Large size, thick shells and fast growth of the dominant species have been related both to increased biocalcification in a high O_2/CO_2 atmosphere (Angiolini 2007) and to the need of avoiding burial and dislodgement, in a high energy nearshore environment (Shiino & Angiolini 2014).

Due to its opportunist strategy and successful colonization, *P. omanensis* changed the physical properties of the substrate (producing a taphonomic feedback) and influenced the structure of the benthic paleocommunities. It made the substrate more stable and topographically more complex, assuring the formation of sheltered environments for the smaller biota (i.e. the molluscs) and providing, through its large thick shell, hard substrates for such epizoons as barnacles (Angiolini et al. 2003) and cemented brachiopods (*Strophalosia ericinia* Angiolini, 2007). This associated fauna took advantage of the stable, more complex and sheltered settings provided by *P. omanensis* and was in turn encrusted by bryozoans.

The *Pachycyrtella* paleocommunity was held at some intermediate point in the ecological succession between the early and mature stages by continuous physical perturbation, which prevented it from reaching a climax stage. Its end above the basal bed of the Saiwan Formation is related to a drastic change caused by the interplay of the final steps of the Gondwanan deglaciation and initial opening of the Neotethys Ocean (Angiolini et al. 2003).

Two asteroid specimens are available, but the smaller (MPUM 8432) is obscured by a firmly cemented sandstone matrix. Overall shape of the smaller specimen, partial exposure of some ossicles at the tips of three truncated arms, and exposure of ossicles of the dorsal surface serve to identify asteroid affinities, but it cannot be taxonomically aligned with the larger specimen and it is not a part of the hypodigm of *Omanaster imbricatus*.

Terminology

More extended treatments of asteroid terminology are provided in Spencer and Wright (1966) and Blake et al. (2000). Primary ossicles form the foundation framework of asteroids; accessory granules, spines, and spinelets rest on and attach to primaries. Paired ambulacral ossicles form the vaulted ambulacral furrow, and they abut the ventrally placed adambulacrals. Marginal ossicles, occurring in one or two series ("supramarginals" and "inferomarginals"), form the ambital edge of asteroids. Abactinal ossicles are dorsal to the marginals and actinal ossicles are ventral to marginals, occurring between the marginals and adambulacral series. Mouth frame ossicles are not preserved in available *O. imbricatus*.

Orientation terminology for individual ossicles parallels that for complete specimens. Proximal is toward the vertical (dorsal-ventral) axis centered on the mouth, and distal is away from this axis. Adradial is toward and approximately perpendicular to the arm midline whereas abradial is away from and perpendicular to the midline. Length is parallel to the arm midline and width is perpendicular to the midline; as a result, many ossicles are "wider" than "long". Height is the third dimension, perpendicular to length and width.

Material and methods

The larger specimen (Pl. 1), now separated on two blocks, consists of portions of three arms and an interbrachial arc; proximal intervals of arms and disk are unknown. It is the ventral surface of the specimen that is exposed, as is demonstrated most clearly by the ventral aspect of the ambulacral ossicles. Although the dorsal surface is now largely obscured, loss of the ventral ossicles adradial to the ambital marginal series did expose some interior surfaces of the unusual, imbricate abactinal ossicles.

Partial exposure of the proximal-most remaining ossicles suggests much of the skeleton was lost prior to final entombment. This need not imply prolonged exposure; the somewhat delicate, articulated construction of asteroids is subject to comparatively rapid decomposition, perhaps especially so under the unstable conditions suggested by the interpretations of Angolini et al. (2003). Specimens at similar stages of decay can be found from time to time washed up along modern beaches. No accessory ossicles were recognized, further suggesting decay. Although remaining ossicles are fused and leached, they do not appear to have been significantly abraded prior to final burial. A few dorsal body ossicles were exposed during preparation with dental tools but otherwise ossicles are largely leached and fused, and the characteristic sponge-like echinodermal skeletal meshwork was obliterated.

Systematic paleontology

Class **Asteroidea** de Blainville, 1830

Order unknown

Discussion. Difficulties of classification were surveyed by Mah & Blake (2012): a generally agreed upon classification of Paleozoic asteroids at the ordinal level has not emerged and therefore the new taxon is left in open taxonomy above the family level.

Family Omanasteridae n. fam.

Remarks. Although known from a single specimen, the combination of overall form and ossicular shape and arrangement as described below justifies recognition at the familial level.

Diagnosis: As for the only-known species.

Omanaster gen. n.

Type species: *Omanaster imbricatus* n. sp.

Etymology: Named for the national origin of the only-known specimen.

Diagnosis: As for the only-known species.

Omanaster imbricatus n. sp.

Pl. 1; Fig. 1

Etymology: Named for the imbricate nature of the marginals and adjacent abactinals.

Holotype: Museo di Paleontologia, Università degli Studi di Milano, Dipartimento di Scienze della Terra "A. Desio", MPUM 8433, only specimen known.

Type locality: site I4 (20°52'15"N-57°36'24"E).

Type horizon: *Pachycyrtella* Bed, base of Saiwan Formation, Late Sakmarian (Permian).

Geographical Distribution: Haushi-Huqf, Interior Oman, Arabian Peninsula.

Diagnosis: Robust, stellate, five-armed asteroid. Arms foliate, lower surfaces flattened, dorsal surfaces low arched, interbrachial angles acute. Abactinal, marginal, adambulacral, and ambulacral ossicles aligned, transversely elongate. Abactinals and marginals gutter-shaped, marginal edges ridged. Ambulacrals and adambulacrals paired, ambulacrals abutting near dorsal adradial edge of adambulacrals.

Description. Arms broad, foliate (Pl. 1, fig. 1), lower surfaces flat, interbrachial arcs angular (Pl. 1, fig. 1, 2); dorsal surface low, broadly rounded (Fig. 1). Lateral abactinal ossicles (Pl. 1, figs 2, 5, 7) in at least three series, these aligned with each other and the marginal series (Pl. 1, figs 1-8). Lateral abactinals concave or gutter-like, transversely elongate, and shingled (Pl. 1, fig. 7). Medial abactinal ossicles (Pl. 1, figs 3-5) not recognized with certainty, possible medial abactinals quite small and robust but not paxilliform. Madreporite unknown. Marginals clearly differentiated, ambital in position, only a single series recognized. Marginals low, triangular in transverse section, scoop-shaped, the concave surface directed ventrally and abradially; proximal and distal edges rimmed, central depression bearing transverse, low ridges (Pl. 1, figs 7, 8). Lateral (abradial) marginal ossicular edge straight, the marginal series forming a more or less linear ambital body margin. Abradial edges of marginals not clearly preserved, spine remnants not recognized; spine presence or absence in life unknown. Adradial ossicular surface forming an articular surface, a medial vertical groove separating two bulbous lateral surfaces (Pl. 1, figs 4, 7). Actinal ossicles not recognized; space available for any such ossicles limited (Pl. 1, figs 1, 2).

Ambulacral ossicles (Pl. 1, figs 3, 6) robust, proportionately short and wide. Radial water channel large, interior surface as preserved irregular (Pl. 1, figs 3, 6). Ventral ambulacral outline hourglass or figure-8 shaped, the lateral ossicular surfaces smooth, suggesting presence of lateral podial pores (Pl. 1, fig. 6). Abradial ends of ossicles bearing flattened medial ventral surface and small muscle flanges for linkage to adambulacrals (Pl. 1, figs 3, 6).

Adambulacrals (Pl. 1, figs 5, 8) transversely elongate, upright, successive adambulacrals closely abutted, with small medial adradial articular surfaces, the dorsal adradial edges of successive adambulacrals overlapping proximally. Ventral adambulacral exterior surface flattened.

Mouth frame not preserved. No accessory ossicles definitely recognized.

Reconstruction of *Omanaster imbricatus* gen. n. n. sp.

The arms as preserved are broadly triangular and leaf-like (Pl. 1, fig. 1) and the interbrachial arc is angular (Pl. 1, fig. 2). Ambulacral series were pulled apart along the arm midlines (Pl. 1, figs 3, 4), and ossicular orientation also suggests specimen flattening, presumably under the weight of sediment. Abactinal series (Pl. 1, figs 4, 5) are aligned with each other and the ambulacral series (Pl. 1, fig. 6), together forming a low, vaulted dorsal surface. Midarm marginal (Pl. 1, fig. 7) and adambulacral ossicles (Pl. 1, fig. 8) together are about 15 mm in breadth, and their lower surfaces appear to have been aligned in the ventral plane of the living animal (Fig. 1). Together with the ambulacral pair but not including any possible marginal lateral spines, arms would have been in excess of 30 mm in breadth in a specimen of arm length between 75 and 80 mm. The disk appears flattened, its radius in life probably significantly less than the preserved approximately 35 mm. Overall form together with ossicular shapes suggest a fairly low, triangular arm cross-section and a flat lower surface. The single preserved interbrachial arc does not appear to have been much distorted and therefore interbrachial arcs of *O. imbricatus* were angular.

Discussion. Identification of the inferred marginal series is based on their shape and lateral positioning, an interpretation aided by similar expressions in Ordovician *Platanaster* Spencer, 1919. Three or four partially exposed adjacent abactinal series ossicles are similar to each other and broadly similar to the marginals, but distinctive enough to allow the fairly confident recognition of only a single marginal series in *Omanaster*. The disarticulated central portion of distal arm intervals are locally preserved (Pl. 1, figs 1, 3-5); remaining ossicles appear to be abactinals, although displaced ossicles of other series, e.g. ambulacrals, might also be represented.

No ambulacral nor adambulacral ossicle is well-preserved, and inferences must be based on the best available examples. The stout nature of the ambulacral ossicles (Pl. 1, figs 3, 6) is consistent with the remainder of the skeletal system. The enlarged radial water-vascular channel of the ambulacrals (Pl. 1, fig. 6) is reminiscent of expressions in the early Ordovician somasteroids, but it is unknown whether similarities reflect phylogenetic linkage, functional homoplasy, or some other factors. Ossicular preservation is generally poor but the irregularity of the interior surfaces of the radial water channel in successive ossicles (Pl. 1, fig. 6) are uniform enough to suggest an irregular surface in life, perhaps reflecting soft tissue differentiation, but a differentiation for unknown purpose(s). The smooth and regular curvature of the vertical surfaces of the medial portions of the ossicles (Pl. 1, fig. 6) is strongly indicative of the presence of podial pores to the arm interior. The ventral abradial edge of the ambulacrals is flat (Pl. 1, fig. 6), and this, combined with alignment with adambulacrals, indicates that ambulacrals and adambulacrals were paired in life. The broad apparent marginals and adambulacrals document the flattened body ventral surface; the dorsal body outline is based on inferred projection of the lateral arm ossicles (Pl. 1, fig. 1; Fig. 1). One interbrachial arc is available (Pl. 1, fig. 2).

Phylogenetic and paleoecological implications of *Omanaster imbricatus*

Few late Paleozoic asteroids are known, and discovery of *O. imbricatus* provides a small but important bit of documentation of this fauna. Although the holotype of *O. imbricatus* is incomplete, its skeletal structure is unlike that of any previously described late Paleozoic asteroid (Kesling 1969; Kesling & Strimple 1966; Blake & Hagdorn 2003). In contrast, the broad, upright, flattened form of the adambulacrals (Pl. 1 figs 5, 8) with limited lateral articular faceting is reminiscent of shapes seen in Ordovician *Platanaster* and *Jugiaster* Blake, 2007, and even in the aberrant very early *Eukrinaster* Blake et al. (2007). The shield-like marginal ossicles of *O. imbricatus* are also suggestive of equivalent ossicles found in *Platanaster* and *Jugiaster.*

Encompassing the crown group, Blake and Hagdorn (2003) recognized the subclass Ambuloasteroidea, its diagnosis based on two inferred apomorphies, presence of mid-ambulacral ossicle podial pores to the arm interior, and offset of the ambulacral and adambulacral ossicles. Podial pores are absent from the earliest asteroids but begin to appear during the mid-Paleozoic. In contrast, ambulacral-adambulacral ossicular offset, which is typical of the crown group, was clearly recognized by these authors in only one species, *Calliasterella americana* Kesling and Strimple, 1966. Based on adambulacral and marginal form and positioning of ambulacrals and adambulacrals, *Omanaster* is not a member of the Ambuloasteroidea. Available data support *O. imbricatus* as a survivor of an early Paleozoic lineage, and importantly, although occurring late in the Paleozoic, not phylogenetically close to the source of the crown group.

As described in the introductory paragraph, the *Pachycyrtella* Bed, source of the two asteroid fossils, is a coarse bioclastic interval at the base of the Saiwan Formation. The interval was interpreted as having been

PLATE 1

Omanaster imbricatus gen. n. n. sp., MPUM 8437; scale bars equal 10 mm (fig. 1) and 5 mm (figs 2-8).

Fig. 1 - Dorsal view of entire specimen showing overall configuration.

Fig. 2 - Interbrachial arc, the left arm directed down in fig. 1; interbrachial ventral field (arrow) is small, allowing little if any space for actinal ossicles.

Fig. 3 - Left arm of fig. 1, remnant of adambulacral or marginal series ossicles are aligned with the ambulacral series (far left inclined arrow); left vertical arrow at point of contact of two successive ambulacrals, the articular surfaces above and to the left, the podial pore above and to the right. The two inclined upper arrows mark the adradial and abradial edges of the radial water channel; ossicular debris, perhaps including medial abactinal ossicles, is above the arrows. Lower right arrow shows articular facet on a marginal, the lateral edges of subsequent marginals are variously exposed.

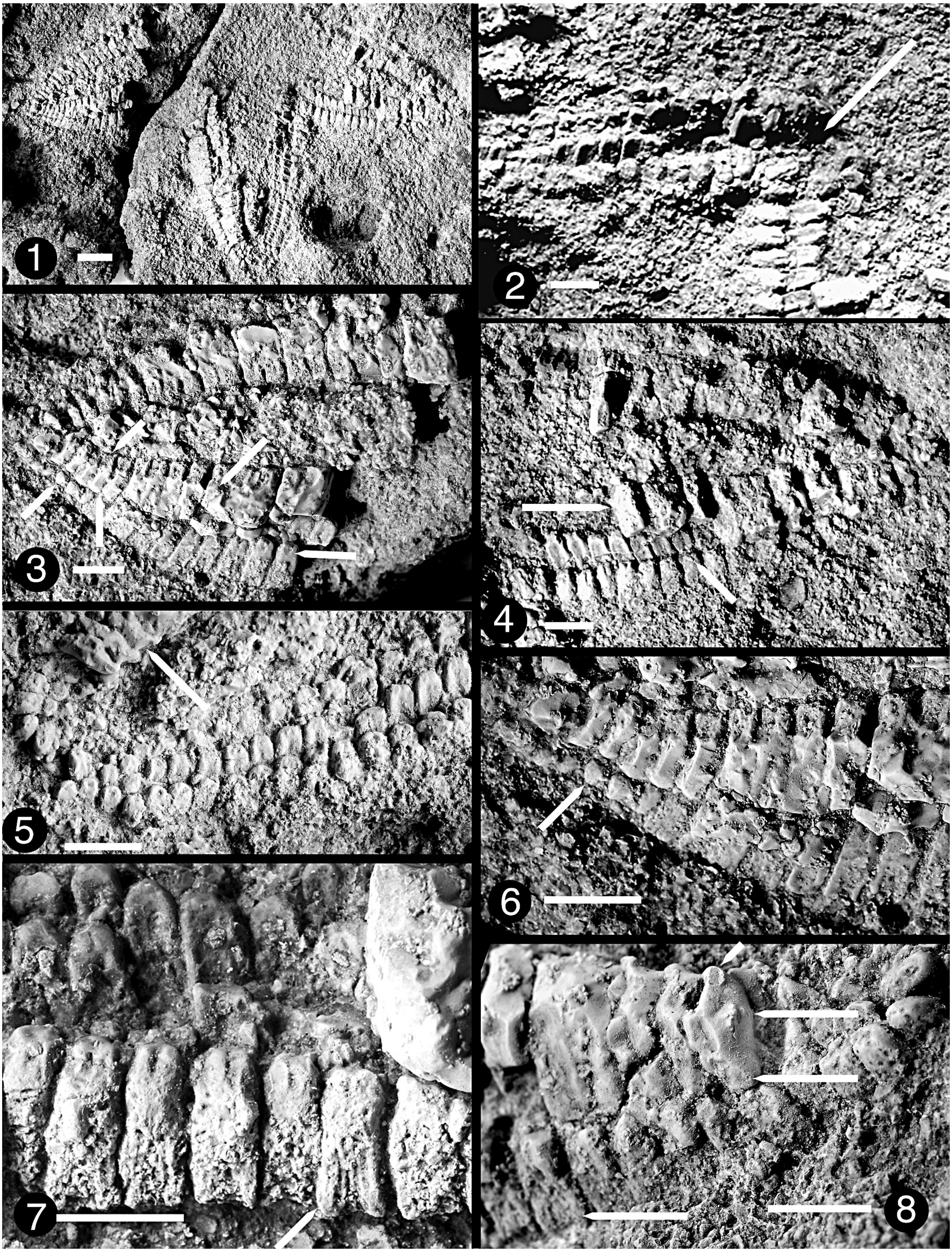
Fig. 4 - Right arm of fig. 1, probable adambulacral series (left arrow) and marginal articular facet (right arrow), compare fig. 7.

Fig. 5 - Inclined view of lower arm of fig. 1, showing marginal and imbricated abactinal series at the arm tip, the terminal and immediately adjacent ossicles missing. Overlapping adambulacrals of fig. 8 at arrow.

Fig. 6 - Detail of fig. 3, arrow in position of lower left arrow of that figure.

Fig. 7 - Marginal series below abactinal series, lower left interval of lower arm of fig. 4. Arrow at edge of ridged, gutter-like abradial depression of marginal, the articular facet above. Ossicle to upper right probably is a badly altered adambulacral.

Fig. 8 - Adambulacral series extending toward left; approximate point of ambulacral contact (upper right arrow); dorsal margin of ossicle aligned with articular facet and ventral adradial ossicular corner (middle right arrow); ventral abradial corner of ossicle (lower right arrow); grooved gutter of marginal ossicle (lower left arrow).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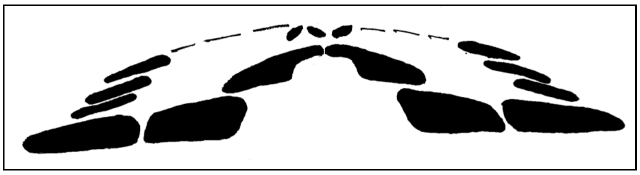

Fig. 1 - *Omanaster imbricatus* gen. n. n. sp., mid-arm cross section reconstructing the broad, flattened ventral surfaces of the adambulacral and marginal ossicles together with the inferred low profile of the arm, the shingled positioning of the abactinals, and the proportionately large radial channel of the water vascular system. Specifics of ossicular outlines, sizes, and proportions are uncertain.

deposited in a shoreface setting, likely under a storm-related, rapid sedimentation event or events. The overall fauna was diverse, including brachiopods, bivalves, gastropods, conularids, bryozoans, barnacles, crinoids (Webster et al. 2009), and fish, along with the asteroids. *Omanaster imbricatus* contributes little in the way of new insights to the understanding of the depositional setting, although its morphology is consistent with the earlier environmental interpretations.

The asteroid body wall is formed by relatively small, unfused skeletal elements held in a dermal tissue layer, the two together enclosing a more or less enlarged coelom. The typically fleshy asteroid body is attractive to scavengers, and it is relatively readily destroyed in most depositional settings, although the dermal layer appears to have some ability to keep specimens intact. The holotype of *O. imbricatus* appears to have been partially disarticulated prior to final burial, and no accessory ossicles are preserved, but its presence is consistent with rapid burial and the high energy conditions postulated above. A few remaining mid-arm abactinal ossicles appear displaced but other elements seem to be in approximate life positions.

Although the holotype of *O. imbricatus* is quite incomplete, two aspects are noteworthy from a paleoenvironmental perspective: the robust nature of the ossicles and the apparently relatively flat form, the latter most clearly suggested by the broad, ventrally flattened expression of the arm marginals and the adjacent adambulacrals. The paleoenvironmental setting of *O. imbricatus* together with its unfortunately incompletely understood morphology documents an important evolutionary versatility not previously recognized among Paleozoic asteroids. Certain extant species, including most strikingly *Luidia* (*Platasterias*) *latiradiata* Caso, 1945, and *Astropecten regalis* Gray, 1840, are noteworthy because of a flattened form that is very atypical among species within their respective genera; this striking form in part led to the interpretation of Fell (1963) that *L. latiradiata* is a surviving member of an otherwise extinct Somasteridea Spencer, 1951. Both *P. latiradiata* and *A. regalis* live in turbulent, shallow-water environments apparently similar to that suggested for the *Pachycyrtella* Bed, and the broad, flat ventral form of the apparent marginal and adambulacral ossicles of *O. imbricatus*, together with the imbricated adjacent lateral abactinals, suggest a relatively flattened form comparable to those found in the living species. Also within the crown group, Blake & Kues (2002) described *Codellaster keepersae,* a Cretaceous member of the family Goniasteridae, and an only distant relative of *Astropecten* and *Luidia*. *Codellaster keepersae* is of a flattened configuration similar to those of the living species, and it was derived from an inferred similar setting, as summarized in Blake & Kues (2002). Discovery of a similar configuration in the extinct and very distant lineage of *O. imbricatus* from an apparently similar setting documents an aspect of the versatility and enduring evolutionary potential of the Asteroidea.

Angiolini (2007, p. 238) suggested that the thickened shell of the *Pachycyrtella* Bed brachiopods is consistent with an opportunistic life mode; individual ossicles of *O. imbricatus* are robust, an expression that might be correlated with the active environment posited by this author, as well as with an opportunistic life mode. Angiolini (2007) noted that no sign of predation has been detected in *Pachycyrtella* Bed fossils, the paleocommunity being dominated by suspension feeders, with rarer grazers (gastropods), deposit feeders (a bivalve species) and commensalism (barnacles). Some modern asteroids are specialized, but many asteroids are of a generalized, varied feeding habit (Jangoux 1982). Modern asteroids include both sediment swallowers and more selective substrate feeders, and such feeding behavior seems suitable for *O. imbricatus*.

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