REDESCRIPTION AND INTERPRETATION OF THE ASTEROID SPECIES *TROPIDASTER PECTINATUS* FROM THE JURASSIC OF ENGLAND

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ABSTRACT. *Tropidaster pectinatus* is redescribed based on the original collection from Lower Jurassic (Pliensbachian) strata of England. It is the only recognized member of the Tropidasteridae, which is assigned to the Order Velatida in an intermediate phylogenetic position between the extant families Solasteridae, the earliest known representative of which is from Middle Jurassic (Bathonian) strata and considered primitive in the order, and the Korethrasteridae, known only from Holocene species. Surviving asteroids have been separated into three superorders; all are recognized from strata of Early Jurassic age, and *Tropidaster* provides additional evidence for the early diversification of extant asteroids. Based on arm curling and robust disc construction, *Tropidaster* might have been a selective predator.

TROPIDASTER PECTINATUS Forbes, 1850 is the only known member of the Tropidasteridae. It is significant because it represents an important surviving echinoderm order only rarely encountered in the fossil record. Unlike many fossil asteroids, *Tropidaster* is represented by a large suite (42) of well-preserved, more or less complete specimens (Pl. 1, fig. 1) and therefore relatively detailed treatment is possible.

The stratigraphical occurrence of *Tropidaster pectinatus* was indicated by Simms (1986, 1989) in his studies of Lower Jurassic crinoids. The type suite was collected from the Lower Lias at Mickleton Tunnel (town of Mickleton, SP 1.45 W, 52.06 N), near Chipping Campden (SP 1.45 W, 52.06 N), Gloucestershire. Strata are Pliensbachian (Carixian) in age, from the *Aegoceras capricornis* Subzone of the *Prodactylioceras davoei* Zone. The locality unfortunately no longer is exposed (D. Lewis, pers. comm.).

Included among the echinoderms from this locality are the asteroids '*Asterias*' *gaveyi*, an undescribed member of the Astropectinidae, the ophiuroid *Palaescoma milleri*, the crinoid *Chladocrinus robustus* and the echinoid *Procidaris edwardsi*. Echinoderms were found at many horizons at interfaces between different lithologies; Simms (1986) interpreted these occurrences as obrution deposits, and he suggested periodic smothering resulting from the influx of sand and finer sediments.

The fossil record of asteroid echinoderms is unfortunately sketchy, and timing of events must be pieced together from incomplete evidence. The Velatida represents one of three post-Palaeozoic asteroid superorders (*sensu* D. B. Blake 1987); representatives of the other two have been recognized from the Hettangian (D. B. Blake 1984, 1990), and therefore diversification of all major groups of modern asteroids was under way during the Early Jurassic. The Superorder Spinulosacea includes the Spinulosida as well as the Velatida. The superorder is based largely on developmental characters, whereas the two orders are separated on a number of characters of the adult skeleton. In D. B. Blake (1987), the Solasteridae was considered to be the primitive velatidan family, and the oldest known velatidans are the Pliensbachian *Tropidaster* and *Solaster murchisoni* (Wright 1863; J. F. Blake 1887; D. B. Blake 1993). In addition to the Solasteridae and Tropidasteridae, several families are known only from living representatives. The Tropidasteridae shares a number of features with both the Solasteridae and the Korethrasteridae (Pl. 1, fig. 3; Pl. 2, fig. 1) and it is here

[Palaeontology, Vol. 39, Part 1, 1996, pp. 179–188, 2 pls]

assigned an intermediate position between the two (Text-fig. 1). Fossils therefore are known only from relatively primitive families; differentiation of the Velatidae was under way by the Pliensbachian, but it cannot be demonstrated to have proceeded to more advanced families at that time.

Tropidaster morphology and preservational nature suggest aspects of life mode. In 18 (mostly smaller) of the 42 available specimens, arms are more or less strongly arched downward, enveloping a space below the mouth (Pl. 1, fig. 1). Ambulacrals are strongly imbricated (Pl. 2, fig. 8), demonstrating a capacity for considerable arm motion in the vertical plane, although exaggerated flexure might have been a near-death protective response. The rounded petaloid outline of the arm suggests limited lateral motion or twisting about the longitudinal axis of the arm (a fragmentary larger specimen noted in the description section might have had different proportions and different abilities). Podial basins are large, suggesting well developed tube feet. Although arms might have been lifted for suspension-feeding, both preservation and ambulacral overlap suggest downward motion was more natural.

Disc construction of *Tropidaster* is robust. The mouth frame is particularly sturdy and provided strong support to the disc. Modern Asteriidae and the Ordovician *Promopalaeaster* share a so-called 'adoral carina' formed by adambulacral ossicles abutted across the interbrachial area immediately distal to the oral frame; the arrangement provides disc support during feeding. In a similar if less strongly differentiated manner, the abradial ends of the adambulacrals abut across the actinal interbrachial areas in *Tropidaster* (Pl. 2, figs 3–4) suggesting a comparable bracing function. Naturally truncated dorsal paxillae (Pl. 1, figs 5–6) apparently abutted across the interbrachial plane, further bracing *Tropidaster* in certain orientations.

Stegnaster inflatus, a flattened member of the Asterinidae, uses its flexible body to trap small amphipods beneath its disc (Grace 1974). *Tropidaster* also would seem to have been capable of enclosing small food particles, and the sturdy mouth frame and large tube feet (suggested by large podial basins) might have helped subdue even active prey. Although no shells have been recognized within discs of available specimens, small arthropods, annelids and other soft organisms might have provided appropriate food.

Phylogenetically, *Tropidaster* is derived relative to the Solasteridae, members of which are aggressive predators. It is primitive to the Pterasteridae, which have been observed feeding on smaller invertebrates (Mauzey *et al.* 1968), and which have been collected with echinoderms, molluscs and crustaceans in the gut (Carey 1972). Clark and Downey (1992) reported that nothing is known about feeding in the rare Korethrasteridae except that at least one species has an eversible stomach.

SYSTEMATIC PALAEONTOLOGY

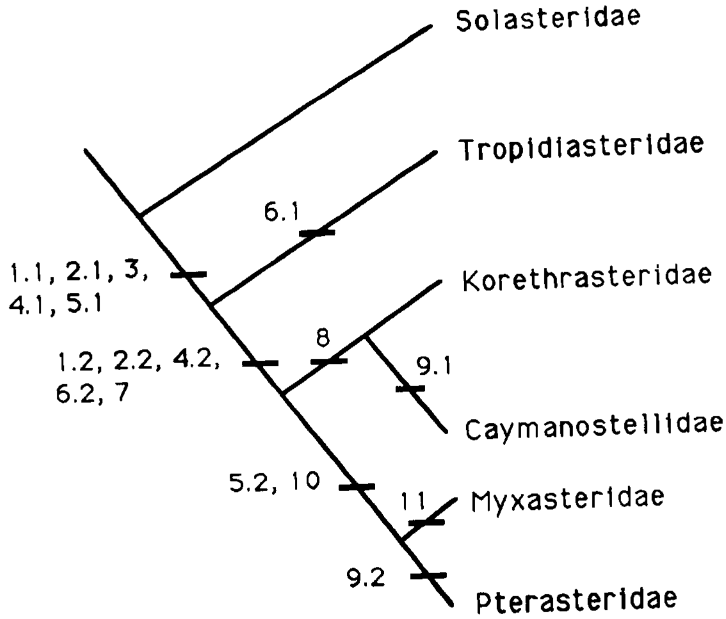
Class ASTEROIDEA de Blainville, 1830

Order VELATIDA Perrier, 1891

Family TROPIDASTERIDAE Wright, 1880

Diagnosis. A velatidan family in which the ossicles are stout in comparison with most members of the order. A distinct groove on the dorsal interbrachial axis is plated, lined by partially differentiated paxillae. The ossicles about the anus are enlarged and block-like. On the ambulacral ossicles, the adradial ambulacral body is prolonged and strongly overlapping and a ventral medial articular flange linking subsequent ambulacrals is developed. Adambulacral ossicles are large, occupying the entire ventral surface of the arms beyond the ambulacra; they are like those of the Solasteridae except that the ambulacral articular structures are restricted to the adradial end of the adambulacral; actinal ossicles are lacking, and the adambulacrals abut across the ventral interbrachial surface.

Remarks. D. B. Blake (1987) assigned the Tropidasteridae to a derived position relative to the Korethrasteridae; the opportunity for more extended study suggests an intermediate position between the Solasteridae and Korethrasteridae (Text-fig. 1). D. B. Blake (1987) did not recognize



TEXT-FIG. 1. Revised phylogeny of the basal families of the Velatida modified from Blake (1987); the diagram clarifies the position of the Tropidasteridae but does not treat comprehensively the Myxasteridae and Pterasteridae, which are unchanged from D. B. Blake (1993). Key: 1p, ambulacrals robust with ambulacral bodies overlapping but not prolonged; ambulacral–adambulacral articular structures are sturdy and a ventral medial articular flange is lacking. $1d_1$, as 1p except that the ambulacral body is prolonged and strongly overlapping and a ventral medial articular flange is developed. $1d_2$, like $1d_1$ except that the ossicles, including the ambulacral–adambulacral articular structures, are delicate in comparison with equivalent structures in $1d_1$. 2p, adambulacrals robust, transversely elongate; ambulacral articular structures extend across the dorsal surface of the ossicle. $2d_1$, like 2p except that ambulacral articular structures are restricted to the adradial end of the ossicle. $2d_2$, adambulacrals reduced to an elongate, transverse bar with the ambulacral articular structures restricted to the adradial end of the ossicle. 3p, in some species, the dorsal interbrachial axis appears as a leathery line of tissue. 3d, the dorsal interbrachial line is a distinct plated groove lined by partially differentiated paxillae. 4p, actinals present. $4d_1$, actinals absent; adambulacrals abut across the interbrachial surface. $4d_2$, actinals absent; actinal interbrachial surface covered only by soft tissue. 5p, marginals paxilliform, inferomarginals large; in addition, superomarginals are reduced in size in most taxa. $5d_1$, marginals paxilliform, only one series differentiated, and that only marginally, so that recognition requires careful inspection. $5d_2$, differentiated marginals not developed. 6p, ossicles around anus not differentiated. $6d_1$, ossicles around anus enlarged, block-like. $6d_2$, ossicles around anus paxilliform but enlarged in comparison with closest neighbours. 7p, mouth angle ossicles keel-like, relatively large, prominent. 7d, mouth angle ossicles not significantly enlarged nor prominent. 8p, terminal of typical asteroid U-shaped. 8d, terminal either circular or nearly circular but not fully closed, rather than U-shaped. 9p, abactinals paxilliform, pedicels not highly elongate. $9d_1$, abactinals flattened, tessellated. $9d_2$, abactinals paxilliform, pedicels highly elongate. 10p, osculum absent. 10d, an enlarged, webbed osculum surrounds the anal area. 11p, spines are not webbed with flesh. 11d, various spines are webbed with flesh.

differentiated marginals in *Tropidaster*; these ossicles are weakly enlarged in at least one member of the Korethrasteridae (*Remaster palmatus*) as well as in *Tropidaster*.

Plumaster ophiuroides Wright was tentatively included in the family by Spencer and Wright (1966). Available material is poorly preserved. The broad adambulacrals and prominent spines in *Plumaster* are suggestive of those of *Tropidaster*. However, the large, triangular ambulacrals are unlike those of the Velatida, but are like those of the Astropectinidae; adambulacrals and spines are unusual but not sufficiently so as to preclude reassignment. Although poorly known, *Plumaster* is reassigned tentatively here to the Astropectinidae.

Genus TROPIDASTER Forbes, 1850

Type species. Tropidaster pectinatus Forbes, 1850.

Diagnosis. As for the family

Tropidaster pectinatus Forbes

Plate 1, figures 1–2, 4–7; Plate 2, figures 2–8

1850 *Tropidaster pectinatus* Forbes, p. 1.
1853 *Tropidaster pectinatus* Forbes; Gavey, p. 33.
1863 *Tropidaster pectinatus* Forbes; Wright, p. 102.
1966 *Tropidaster pectinatus* Forbes; Spencer and Wright, p. U67.
1993 *Tropidaster pectinatus* Forbes; Lewis, p. 66.
1993 *Tropidaster tropidatus* Forbes; Lewis, p. 67.

Material. The type suite consists of approximately 42 specimens, including some that are incomplete, partially enclosed in sediment, or fragmentary. Although preservation on portions of specimens is strikingly good, details differ among specimens and careful comparisons are needed (e.g. see comments on the squamose plates of Forbes under Remarks). There was some disruption; most spines are lost and a few isolated ossicles are present. In spite of the size of the sample, certain features, such as the proximal side of the ambulacrals and the nature of the odontophore, are unavailable. Specimens available to the writer included Department of Palaeontology, Natural History Museum (NHM) syntypes, 75690, 75691, E2693 and E3760; E1871; E2693; E3335; E3336; and E52345.

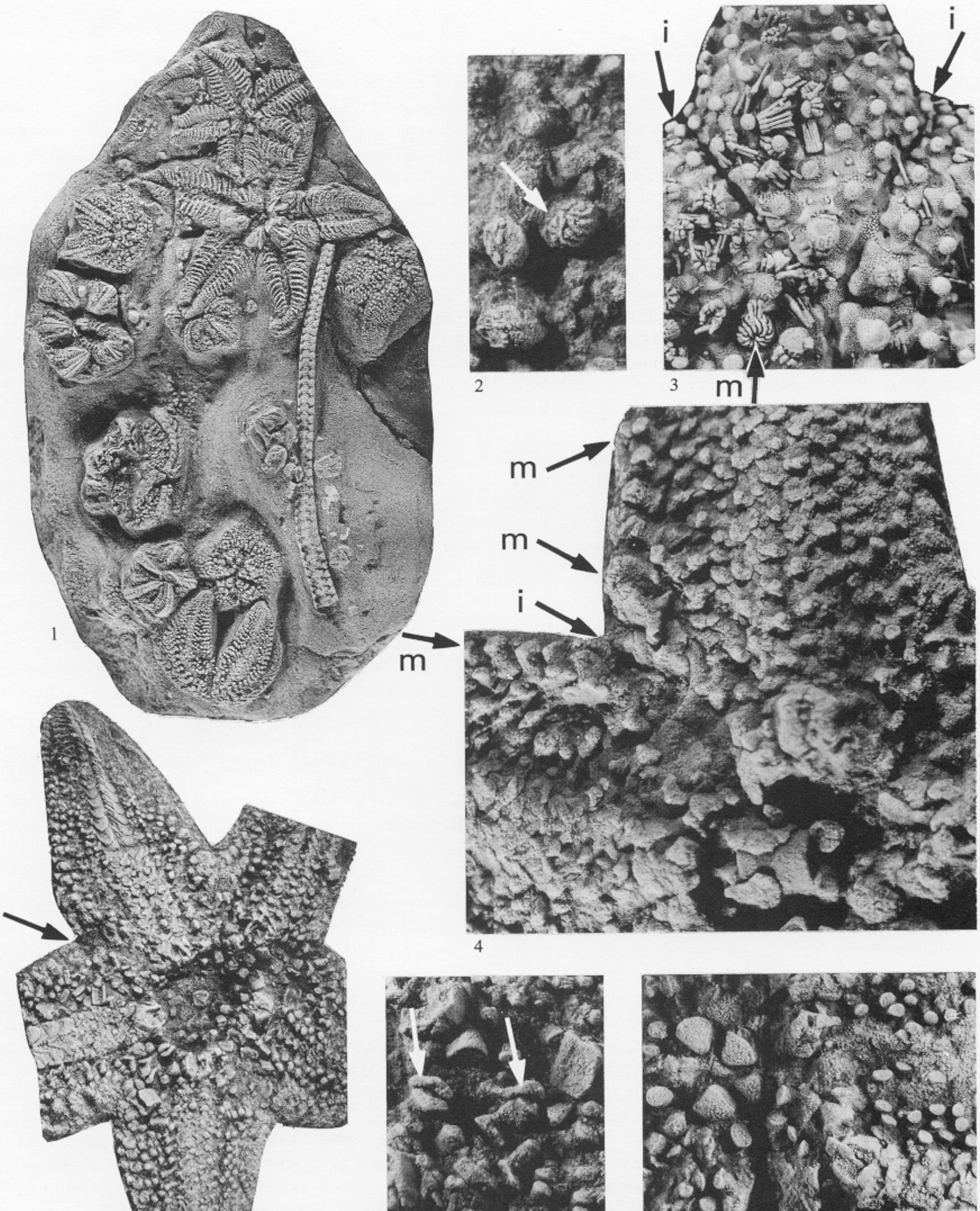
Diagnosis. As for the family.

Description. Five-armed species; disc large, arms sub-petaloid, the ratio of arm length to interbrachial radius is approximately 2:1 in the relatively small specimens dominating the type suite. The primary radius of most specimens is 33 mm or less but the species apparently reached a significantly larger size because a single fragmented and crushed, but partially reconstructed (by Forbes?), individual consists of a proximal fragment (including part of the disc) 30 mm long aligned with an arm fragment 20 mm long; the 50 mm interval does not represent a complete arm. Arm cross-sections have been somewhat distorted by compaction but in life the ventral surfaces probably were arched, following the curvature of the adambulacrals; dorsally, the steep orientation of the ambulacrals suggests the mid-arm was relatively high and perhaps angular, if the dorsal surface closely followed the arch.

EXPLANATION OF PLATE 1

Figs 1–2, 4–7. *Tropidaster pectinatus* Forbes; dorsal aspects; Mickleton Tunnel, near Chipping Campden, Gloucestershire; Lower Lias, Pliensbachian. 1, NHM E3335; overall view of a single block with numerous specimens in various orientations; note curling of arms in a ball-like pattern; a large ophiuroid arm fragment is to the right; ×1. 2, NHM E3335 (specimen is at the middle right of fig. 1); hemispherical madreporite (arrow) and adjacent paxillae (compare with figure 3); ×10. 4, NHM E1871; disc and portions of arms showing interbrachial groove (i), marginal rows (m) and form of the paxillae; paxillae from the midarm position have been truncated taphonomically; ×10. 5–6, syntype, NHM 75691; 5, overall dorsal aspect showing form, paxillary arrangement, central area collapsed into disc; double row of ambulacrals breaches dorsal surface of midarm; ×3; 6, detail of abutted paxillae (arrows) at mid-interbracial position; ×10. 7, NHM E52345; detail showing central ring of stout plates to left, and paxillary form; ×6.

Fig. 3. *Remaster palmaster* (Perrier), NHM E20985; Florida Straits between 304 and 320 m; Recent; dorsal aspect, madreporite (m), paxillae, paxillary spines and mid-interbrachial furrow (arrows) are similar to corresponding features in *Tropidaster*; ×6.



BLAKE, *Tropidaster*, *Remaster*

Ossicular series beyond the ambulacral column are paxilliform. Dorsal ossicles are arranged in well defined transverse and longitudinal rows on the disc and arms, and they gradually diminish in size distally (Pl. 1, fig. 5). Marginal differentiation is limited (Pl. 1, fig. 4), and there are no actinal ossicles (Pl. 2, figs 2–4). Paxillary row numbers on the arms are uncertain but numerous, with six longitudinal rows exposed on one side of the arm of one small (R approximately 12 mm) individual. Paxillae are stout with a weakly enlarged, domal crown tapering into a short pedicel; bases apparently are scalar with digitate margins; ossicular bases on the disc and laterally on arms appear weakly scalar, perhaps digitate. The apparently reduced pedicel of certain specimens (Pl. 1, fig. 4) is a taphonomic feature. Crown diameter is 0·5 mm to 1 mm on the disc in a specimen of R about 12 mm. A closely plated skeletal groove lies between the columns of the interbrachial paxillae (Pl. 1, fig. 4); some paxillae are abutted, truncated and apparently slightly enlarged along this plane (Pl. 1, figs 4, 6). Paxillary crowns are covered by many closely arranged glassy (?) or openly spicular spinelets of a length apparently somewhat greater than crown diameter. Close spacing of paxillae suggests any papulae were single, small and located between overlapping basal facets.

The central portion of the disc is not well preserved on available specimens. A ring of five stout triangular ossicles which probably enclosed the periproct is present in the central area (Pl. 1, fig. 7); the ossicles are about 1 mm in breadth in a recurved specimen of diameter in life probably of 20–25 mm; the dorsal surfaces of the ossicles are weakly arched and bear small spinelet bases. The madreporite is small, polygonal and somewhat domed (Pl. 1, fig. 2). It abuts the juncture of two of the ring ossicles; gyri apparently do not form continuous grooves.

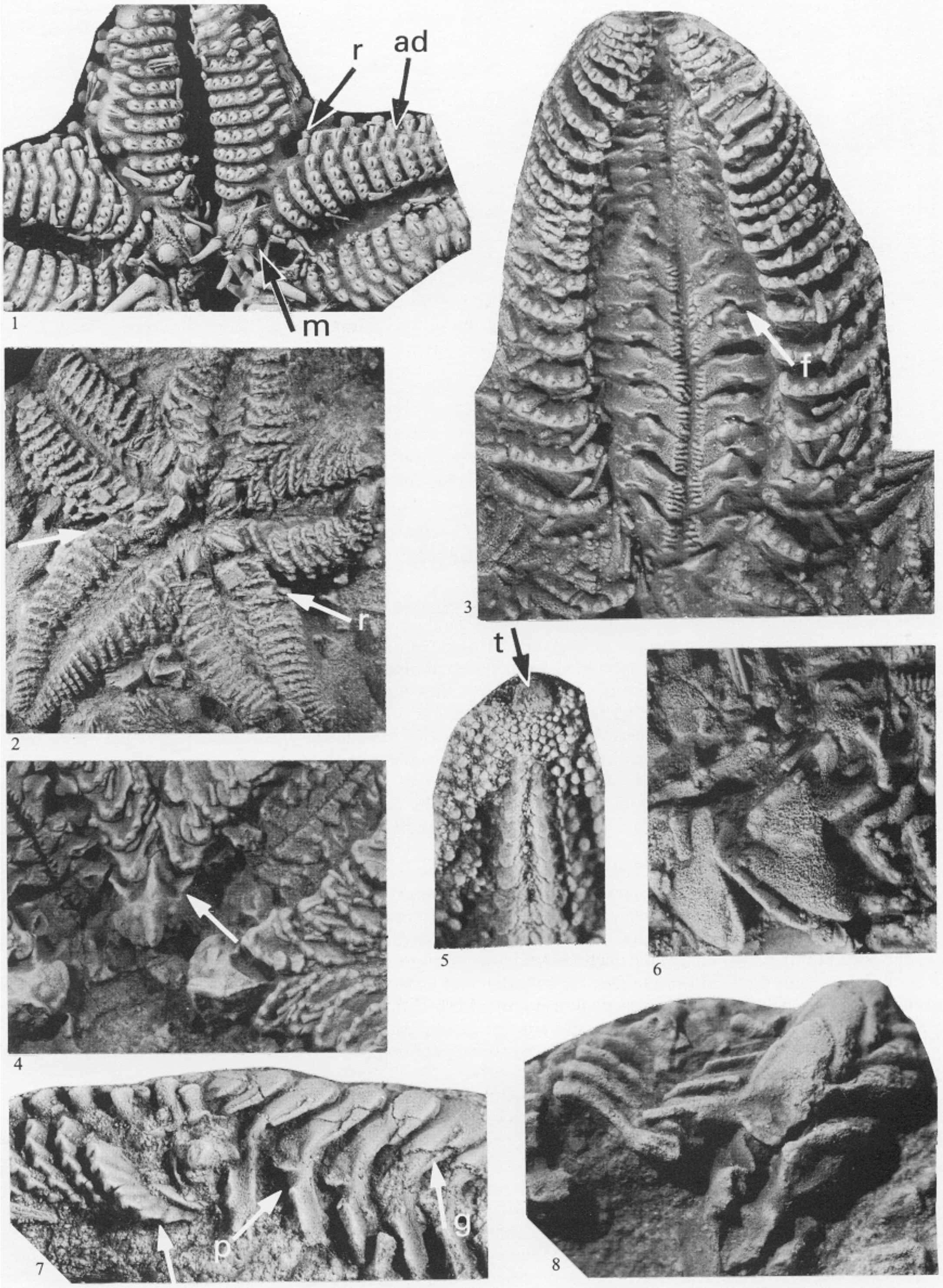
A single row of marginals is present (Pl. 1, fig. 4); morphology is similar to that of the paxillae. Interbrachial marginals are clearly enlarged and differentiated relative to adjacent paxillae; crowns are elongated transversely and bases stout, probably scalar. Marginals rapidly become more equidimensional away from the interbrachial angle; the fourth marginal is rounded in outline rather than elongate transversely, and distal marginals are enlarged and differentiated rather weakly. Actinal ossicles are lacking; proximal adambulacral ossicles curve across the actinal interbrachial areas with the adradial extremities from neighbouring arms closely adjacent (Pl. 2, fig. 4).

Ossicles of the ambulacral column are robust (Pl. 2, figs 2–8; Text-fig. 2A) with approximately seven in 7 mm on the arm of syntype, 75690. In dorsal view, ambulacrals are dominated by a prolonged, strongly overlapping, flange-like ambulacral body (Pl. 2, figs 7–8). On the dorsal (or distal) side of the flange, the adradial part of the ossicle is broad and smooth, apparently a sliding surface for arm flexure; the surface extends ventrally and abradially to a depressed apparent tissue basin; a narrow articular groove is along the proximal edge. A deep, subcircular groove is present on the distal side of the ossicle for the podium (Pl. 2, fig. 7). Although exposed incompletely in available specimens, the podial pore seems less well defined on the proximal side of

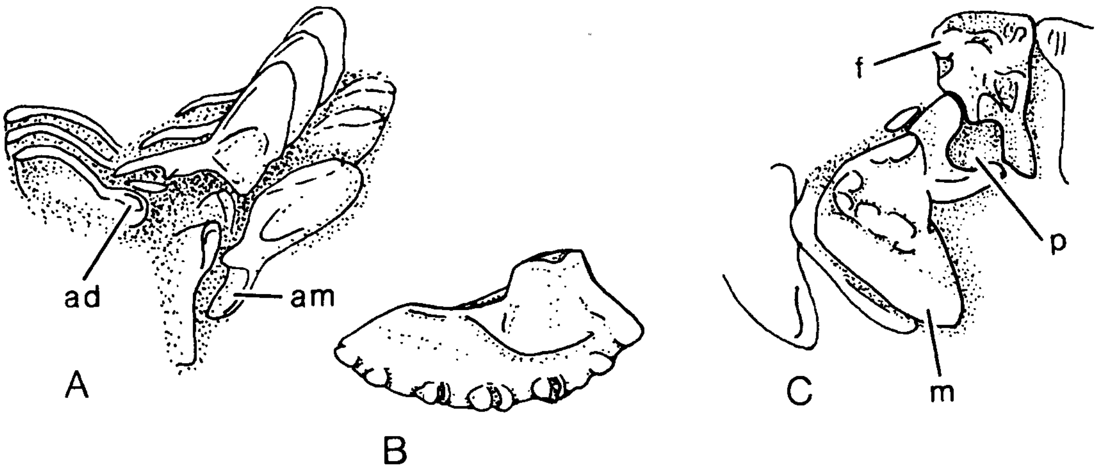
EXPLANATION OF PLATE 2

Fig 1. *Remaster palmatus* (Perrier), NHM E20985; Florida Straits between 304 and 320 m; Recent; ventral aspect; adambulacrals occupy entire vental surface beyond furrow; flange (right arrow) is a part of the adambulacral; ventral interbrachial area lacks actinal ossicles, although the adambulacrals do not abut across surface, as in *Tropidaster*; re-entrant (left arrow) at interbrachial edge of disc is suggested in some specimens of *Tropidaster*; mouth angle ossicles (m) are less prominent than in *Tropidaster*; ×6.

Figs 2–8. *Tropidaster pectinatus* Forbes; ambulacra and ventral aspects of morphology; Mickleton Tunnel, near Chipping Campden, Gloucestershire; Lower Lias, Pliensbachian. 2, NHM E3335 (specimen is at the top of Pl. 1, fig. 1); overall ventral aspect showing form, prominent adambulacral and mouth angle ossicles; interbrachial re-entrants (r) are similar to those in *Remaster*; ×3. 3, syntype, NHM 75690; subpetaloid arm showing ambulacrals with mid-ossicular articular facets (f), broad adambulacrals; ×6. 4, syntype, NHM E2693; adambulacrals abut across interbrachial areas; prominent muscle scars for first adambulacral (arrow); ×6. 5, NHM E3336; arm tip with terminal (arrow), arrangement of distal paxillae and dorsal aspect of strongly imbricate ambulacrals; ×10. 6, NHM E2693; mouth angle ossicles and first ambulacral are somewhat flattened but near to life orientation; the area is illustrated in Text-fig. 2C; ×10. 7, syntype, NHM E3760; ambulacral row in distal-dorsal aspect with podial pore (p) and articular groove (g) along proximal edge of adradial body; adambulacral (ad) row with spine bases strengthened by radial ridges; paxillae are above adambulacrals; ×10. 8, NHM E3335 (specimen is the disrupted, isolated individual at the middle left of Pl. 1, fig. 1); inclined view of ambulacral-adambulacral series; the area is illustrated in Text-fig. 2A; ×10.



BLAKE, *Remaster*, *Tropidaster*



TEXT-FIG. 2. Ossicular arrangement and detail of *Tropidaster pectinatus*. A, ambulacral (am) and adambulacral (ad) rows from Pl. 2, fig. 8; lines point to articular surfaces. B, distal adambulacral, furrow to right; ambulacral contact is the process at the right side of the ossicle. C, oral frame ossicles from Pl. 2, fig. 6; mouth angle ossicle (m), first ambulacral (f) and podial pore (p).

the ossicle. The podial pore lies immediately adradial to the flattened dorsal surface of the adambulacral articular flanges. There is no well-defined dorsal ossicular ridge, although the medial dorsal part of the ossicle is angular.

In ventral view (Pl. 2, fig. 3), the ambulacrals are somewhat sinuous in appearance with approximately half of the adradial part of the ossicle deflected toward the disc. The cross-furrow articular facets-and-grooves are well defined and oriented largely in the vertical plane. Inferior transverse muscle scars are not clearly defined, although they might have extended from the medial articular surface on the proximal side of the ambulacral. A prominent inter-ambulacral articular flange-and-facet structure is developed medially; as preserved in different specimens, either the proximal or distal side of the flange can project more prominently producing very different appearances. Adradial to the medial flange, the distal ossicular edge is somewhat raised; the corresponding proximal edge of the next distal ossicle is bevelled, the two together forming a subtle articular contact. Abradially, the ventral ossicular surface in the furrow is quite broad, and is deflected ventrally to the ambulacral-adambulacral articular area. The terminal (Pl. 2, fig. 5) is small, approximately trapezoidal in dorsal outline, 0·55 mm wide and 0·5 mm long in a specimen of R between 15 and 20 mm; the dorsal ossicular surface is flat.

Adambulacral width in the syntype, 75690, reaches about 3·0 mm at the widest portion of the arm; adambulacrals are proportionately large and apparently formed all of the ventral portion of the arm beyond the furrows. The adambulacrals are prolonged laterally beyond the abradial edge of the ambulacrals (i.e. ambulacrals articulate at the adradial ends of the adambulacrals; Pl. 2, fig. 8; Text-fig. 2A–B), and they are strongly overlapping with large inter-ossicular furrows; outer faces are short and crescentic with the convex edge of the crescent directed proximally; the adradial end is angled distally to form a subtle adradial furrow prominence. Dorsally, the ossicle is prolonged into a broad, semicircular flange with proximal ossicles apparently larger (taller) than those from more distal arms positions. About seven prominent spine bases are spaced evenly across the outer face; adambulacral spines are conical, the most complete spine remaining on the syntype, 75690, is about 2 mm in length.

The oral frame is robust (Pl. 2, fig. 6; Text-fig. 2C). The mouth angle ossicular pair is keel-like and about 3 mm long in the syntype, 75690; ossicular faces directed toward the furrow are convex so that the ossicular pair is broadly rounded. The first ambulacral articular flange is near the oral end of the ossicle; it is large and flares over the furrow. This area is raised above the surface of the remainder of the ossicle, forming the proximal side of a large, first podial pore. Three or four spine bases are aligned along the ventral and proximal edges of the articular flange but away from the ventral edge of the ossicle; spines are about 0·75 mm in length in a specimen with a radius of approximately 12 mm; there are no spine bases on the remainder of the outer face. Most of the distal portions of the mouth angle ossicles abut the first adambulacral. The articular surface is large and deep. An odontophore is not exposed in available material.

The ambulacral body of the first ambulacral is robust and square in outline (Pl. 2, fig. 6; Text-fig. 2C). The proximal articular flange is relatively small, and the distal articular flange is similar to the abradial part of the ambulacrals. The ventral cross furrow muscle depression is clearly defined; its position and shape suggest that the proximal interambulacral articular flange of the ambulacrals also served as a transverse muscle support.

Remarks. Forbes (1850, p. 1) suggested the presence of a 'kind of keel' along the centre of each arm (Pl. 1, fig. 5; Pl. 2, fig. 5); the keel as interpreted by Forbes is formed by a double row of squamose ossicles. Certain eroded paxillae have low pedicels and broad, overlapping bases and therefore a squamose appearance, but the keel-like appearance noted by Forbes was probably produced by the underlying ambulacral ossicles. In certain specimens, these ossicles breached the dorsal surface producing a double row.

Asteroids are complex organisms; nevertheless some belonging to separate orders are remarkably similar. *Tropidaster* is an exception; a number of complex features (Text-fig. 1) establish its position relative to closely related families. It is assigned to the Velatida based in part on overall appearance (a relatively large disc and thickened, rounded arms), its exclusively paxilliform ossicles beyond the ambulacra with only weakly differentiated marginals and its prominent, keel-like mouth angle ossicles.

Adambulacrals are similar to those of the Solasteridae but are relatively broad, with small ambulacral articular surfaces; ambulacrals are also similar to those of the solasterids in overall form whereas both adambulacrals and ambulacrals of korethrasterids and pterasterids are more delicate and almost rod-like. The inter-ambulacral articular flanges of *Tropidaster* are similar to those found in korethrasterids and pterasterids. *Tropidaster* is like members of the Korethrasteridae and Pterasteridae in overall body shape, the shape of the mouth angle ossicles and the presence of strongly interlocking ambulacrals. It is also like members of the Korethrasteridae in the presence of relatively short paxillae. The interbrachial row of abutted paxillae is a feature shared with the Korethrasteridae and suggested in certain Solasteridae (e.g. *Lophaster gaini* (Koehler)) by the presence of a leathery membrane along the interbrachial axis. (The development sequence of marginal and paxillary ossicles is unclear from adult morphology; it is possible that the abutted ossicles (Pl. 1, fig. 6) are marginal in origin.) Inferomarginals are rather weakly differentiated in *Tropidaster*, yet very similar to those in certain korethrasterids, e.g. *Remaster palmatus*.

Tropidaster differs from *Peribolaster* in the presence of only two rows of tube feet (*Peribolaster* has four) and it differs from *Korethraster* in the presence of paxilliform abactinal ossicles rather than rounded, somewhat flattened, imbricate ossicles. The stout, articulated ambulacrals and very broad adambulacrals serve to separate *Tropidaster* from all three korethrasterids, whereas in korethrasterids and pterasterids, the adambulacral is a reduced ossicle in which the abradial end forms a distinct process. The Pterasteridae is distinct in the presence of highly elongate paxilliform abactinals which serve to support the unique supradorsal membrane.

Adambulacral form is distinct in *Tropidaster* and the robust form of the ambulacrals, with medial-lateral articular flanges, is also distinctive. The stout periproctal ossicles of *Tropidaster* are unique, although somewhat enlarged ossicles about the periproct occur in korethrasterids, e.g. in *Remaster palmatus*. Given the unifying characteristics of velatidan families, these differences warrant continued recognition of the Tropidasteridae.

Tropidaster tropidatus is a slip of the pen (D. N. Lewis, pers. comm.).

Acknowledgements. I am indebted to David N. Lewis, Andrew B. Smith and Paul Taylor for information on the collection and stratigraphy; and to these individuals and the authorities of the Natural History Museum for their kind hospitality where I was at the Museum and for permission to borrow many specimens.

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Typescript received 17 December 1993
Revised typescript received 7 December 1994