A NEW ASTEROID GENUS FROM THE JURASSIC OF ENGLAND AND ITS FUNCTIONAL SIGNIFICANCE

by DANIEL B. BLAKE

ABSTRACT. The new asteroid (Echinodermata) genus *Brachisolaster* is based on *Solaster moretonis* Forbes (Solasteridae), described from Jurassic rocks of Gloucestershire. *Brachisolaster* (Order Velatida) demonstrates that characteristic solasteroid features were defined by the Bathonian (Middle Jurassic); other fossils belonging to different orders further demonstrate the presence of close relatives of the living fauna by this time. Arms are more numerous in *Brachisolaster moretonis* than in living solasteroids; the appearance is suggestive of that of living *Heliaster* (Asteriidae). *Heliaster* feeds largely on molluscs and barnacles, whereas the diet of living solasteroids stresses more active echinoderms. Solasteroids use their fewer but larger arms to subdue and manipulate prey. *Brachisolaster* is suggested to have had feeding habits more like those of *Heliaster* than like those of extant solasterids. The interpretation complements an earlier suggestion that Jurassic asteriid behaviour might have involved more active predation. A solasteroid with fewer arms is known from the Jurassic, therefore to the extent that the suggested functional significance of arm number is accurate, disappearance of species with supernumerary arms reflects a narrowing of the active solasteroid adaptive zone rather than a functional shift. Together, the fossil asteriids and solasterids suggest some narrowing of adaptive zones since the Jurassic.

THE oldest relatively complete asteroids assignable to living families are from the Hettangian (lowest Jurassic) of Switzerland and southern Germany (Blake 1984, 1990); they represent two taxonomically widely separated orders, the Forcipulatida and Notomyotida. Isolated Triassic ossicles described by Zardini (1973) also have been included within living families (Gale 1987), although affinities are difficult to verify from isolated ossicles. Representatives of three additional orders, the Paxillosida, Valvatida and Velatida (including the Solasteridae) have been recognized from somewhat younger strata (e.g. Hess 1972), and some Jurassic species are assignable to extant genera (Blake 1986). Only two surviving orders (*sensu* Blake 1987), the Spinulosida and the deep-water Brisingida, have not been documented from the Jurassic. Jurassic solasteroids have long been recognized, and both Forbes (1856) and Wright (1863) provided good descriptive information on *Brachisolaster moretonis* (under the name *Solaster*); but the holotype is in need of modern illustration and added comparison. In order to further delineate the emergence of the modern asteroid fauna, this paper compares *B. moretonis* with living species.

SYSTEMATIC PALAEONTOLOGY

Class ASTEROIDEA de Blainville, 1830
Order VELATIDA Perrier, 1891
Family SOLASTERIDAE Perrier, 1884
Genus BRACHISOLASTER gen. nov.

Type species. *Solaster moretonis* Forbes, 1856.

Derivation of name. From '*brachium*' (Latin), arm; living members of the Solasteridae have between 5 and 15 arms; the presence of approximately 33 in *Brachisolaster* is noteworthy. Retention of 'solaster' in the name reflects familial affinities and historical usage.

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Diagnosis. Solasteroid with approximately 33 arms and relatively narrow adambulacral ossicles; the dorsal skeleton is reticulated and ossicles are stout; spines are large, forming clusters at arm tips. Spines have bulbous bases and long, tapering shafts.

Remarks. Brachisolaster can be distinguished from other solasteroids based on arm number, presence of relatively narrow adambulacrals, and clusters of spines distally on the arms. Forbes (1856) recognized arm number as the most striking difference between *B. moretonis* and living species, but he judged this difference did not justify recognition of a new genus. The living fauna is much better known now than it was in 1856, and the unique nature of arm number, and its possible functional significance, can be more clearly recognized. Recognition of a new genus therefore is now warranted.

Brachisolaster moretonis (Forbes, 1856)

Plate 1, figs 1–2, 5; Plate 2, figs 1–4

1856	*Solaster moretonis* Forbes, p. 1.
1863	*Solaster moretonis* Forbes; Wright, p. 104.
1966	*Solaster*? *moretonis* Forbes; Spencer and Wright, p. U67.

Material. The holotype, BM(NH) 40421, in The Natural History Museum, London, is from Windrush Quarry situated 400 m SE of Windrush Church, about 8 km east of Northleach, Gloucestershire, UK. Included at this locality are the top of the Taynton Limestone, overlain by the Hampen Marly Formation and the basal Shipton Member of the White Limestone. The rocks belong to the *progracilis* and *subcontractus* Zones of the Middle Bathonian. Geological information was provided by Richardson (1933, section on p. 43) and Cope *et al.* (1980).

The specimen is essentially complete, with the ventral surface exposed. The dorsal surface is covered by a well-sorted pelletoidal calcarenite whereas minor amounts of mudstone remain among the unusually well-preserved ossicles of the ventral surface; some spines are also present on this surface. The individual would appear to have been quickly buried by calcarenite while on a soft, terrigenous mud, which was squeezed in among the ossicles and protected them. Most spines of the ventral surface were lost (during preparation?), although many remain near the tips of the arms and at scattered sites elsewhere, especially near the mouth angle ossicles. In addition, there is some disruption of the arm tips and of some of the main body ossicles. The proximal tips of the mouth angle ossicles have been rotated upward into the disc.

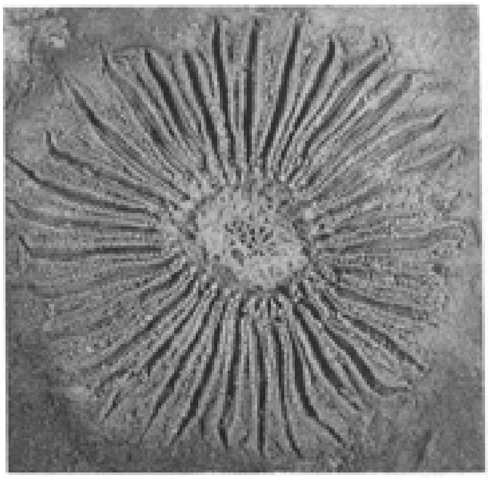
Although ossicles are very well preserved, exposure is incomplete; the lower portions of ambulacrals, adambulacrals, mouth angle ossicles, and actinal interbrachials are visible, but not their upper surfaces. Only the lower portion of some dorsal disc ossicles are exposed through the mouth frame. Few probable marginals are visible, and their orientation is disrupted; actinal interbrachials are also partly disrupted. The madreporite is not exposed, although a gap in ossicular arrangement and shape (curvature) of dorsal ossicles suggests its location. Terminals are not exposed.

Diagnosis. As for the genus.

EXPLANATION OF PLATE 1

Figs 1–2, 5. *Brachisolaster moretonic* (Forbes). BM(NH) 40421; Windrush Quarry, Gloucestershire; Middle Bathonian. 1–2, views of ventral surface of specimen; compare overall proportions with that of modern solasterid (fig. 3); note enlarged mouth opening with dorsal ossicles exposed, robust mouth angle ossicles, and closely-spaced arms with comparatively large ambulacral ossicles; 1, ×0·5; 2, ×1. 5, ventral view of dorsal disc ossicles showing general arrangement, papular pores between ossicles; compare general arrangement with that of *Crossaster papposus*, ×6.

Figs 3–4. *Crossaster papposus* (Linné). USNM Div. Echinoderms 39942; Firth of Lorn, Scotland; Recent. 3, dorsal view showing general proportions of a modern solasterid, ×1. 4, dorsal view showing arrangement of dorsal ossicles, ×6.



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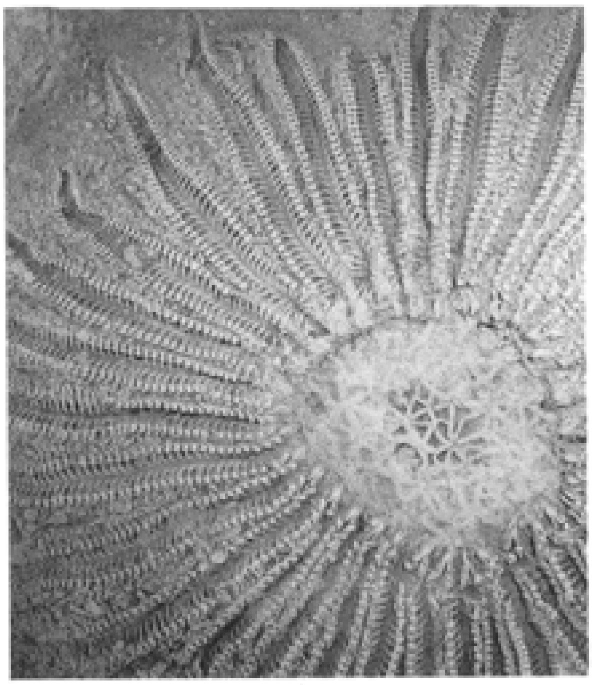

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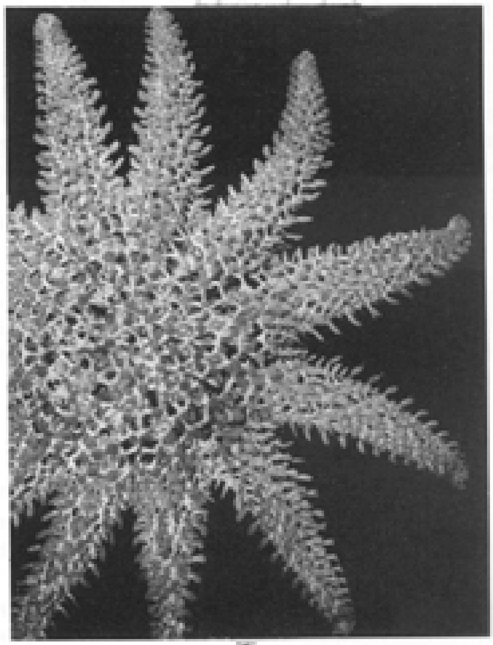

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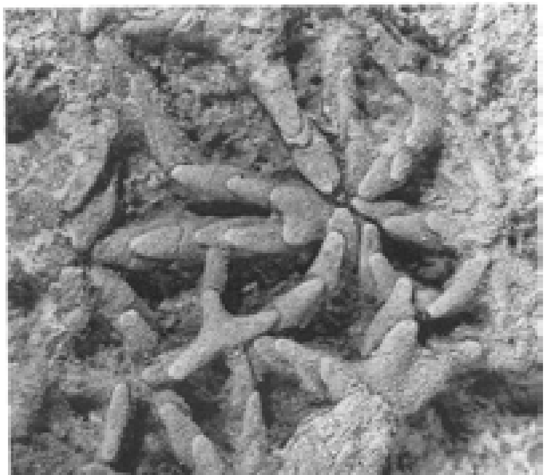

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BLAKE, *Brachisolaster*, *Crossaster*

Description. Primary radius (from disc centre to arm tips) between 65 and 70 mm, interbrachial radius between 45 and 50 mm; the mouth opening is distorted and now roughly elliptical (Pl. 1, figs 1–2) with a greater axis of about 38 mm, the lesser about 28 mm; mouth opening size in life probably was intermediate. The dorsal surface is an open reticulum (Pl. 1, fig. 5), but papularia are not large (largest exposed example approximately 5 mm in length) and each probably could contain few papulae. Larger paxillate? dorsal ossicles bear multiple basal facets which overlap and are overlapped by one or more rod-like and Y-shaped connecting bars, or by other paxillate? ossicles; other than presence of the open reticulate pattern, no general dorsal ossicular arrangement is in evidence, and no dorsal spines are exposed.

Because of the partial collapse near arm tips, marginals are poorly exposed, but probable marginals appear laterally flattened (Pl. 2, fig. 4) and they probably were arranged in an upright orientation in life, with a crown of spine bases, similar to corresponding ossicles in living species; apparent marginals are about 1 mm in both height and width. Actinal interbrachials (Pl. 2, figs 3–4) are somewhat irregular; some are subpetalloidal but most are relatively elongate, tapering ossicles which appear to have formed a double column over much of the disc. Ventral areas near the oral frame are narrow so that proximal adambulacrals of some adjacent series now are abutted, but varied development and exposure from arm to arm show that actinal interbrachial areas reached the oral frame in life; some actinal interbrachials were taphonomically folded upward into the disc interior and are now obscured. Adambulacrals and probably ossicles lateral to the adambulacrals at the free tips of the arms bear distally-directed fans of slender conical spines 2–3 mm in length that apparently formed a closely arranged pavement between the arm tips in life (Pl. 2, fig. 4).

Ambulacrals near the disc are about 3 mm wide; the body of the ossicle is slender, and the proximal adradial tip strongly projects proximally (Pl. 2, fig. 1), overlapping the distal adradial margin of the next proximal ossicle and yielding an almost sinuous appearance; the ventral cross-furrow muscle depression, dentition, and ambulacral–adambulacral muscle articulation surfaces (Pl. 2, figs 1–4) are all well developed. Proximal ambulacrals are foreshortened, thus providing more tube feet per unit arm length near the mouth; midarm intervals have approximately 20 ambulacrals in 20 mm. Adambulacrals are strongly overlapping, and relatively narrow (proximally, 1 mm or slightly more in width) and elongate (nearly 2 mm in length). The distal (or ventral) muscle depression is large and deep. The outer face is relatively large and bears a transverse row of large spine bases; preserved spines are at least 2·5 mm in length. The characteristic (for solasteroids) palmate row of spine bases along the furrow margin does not remain on any ossicle, but spine base development suggests such a row was present; the furrow margin of the outer face is angular, providing a guide and separation between subsequent podia. Mouth angle ossicles (Pl. 2, figs 1–2) form a broad keel-like prominence on the ventral surface and have a row? of spine bases near the dorsal margins at the proximal ends of the ossicles. The few remaining enlarged spines appear typical of solasteroids although most of the lower portion of the ossicle lacked spines. The articular depression for the first adambulacral is deep and prominent.

MORPHOLOGY AND BEHAVIOUR OF *BRACHISOLASTER*

Morphology of surviving representatives of most living asteroid orders converge on a single pattern suggested to reflect closely the ancestral appearance of these taxa (Blake 1987). In the Velatida, this morphology is best represented by the seven-armed genus *Rhipidiaster*, although *Lophaster*, with five arms, is primitive in this character.

Hypothesizing a five-armed *Rhipidiaster*-like ancestry, arm number and disc size of *Brachisolaster* is derived. The dorsal surface of most living solasteroids is constructed of closely arranged, rather

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EXPLANATION OF PLATE 2

Figs 1–4. *Brachisolaster moretonis* (Forbes). BM(NH) 40421; Windrush Quarry, Gloucestershire; Middle Bathonian; ventral views showing general ossicular form, which is essentially similar to that of Recent solasterids; × 6. 1–2, part of the mouth frame and proximal portions of ventral surface of the disc (distal to bottom of page); note well-developed articular structures, keel-like mouth angle ossicles in figure 2, with few spine bases and therefore few spines in life, and the sinuous ambulacrals; arrow in figure 2 shows typical solasterid articular structures linking ambulacrals to adambulacrals. 3, mid region of arms showing ossicular form, left side of ambulacral ossicular column is obscured, distal to top of page. 4, tips of two arms, distal to top of page, with spines extended to form a tight pavement; most of the area between adambulacrals is occupied by interbrachial ossicles but arrow points to probable marginal.

PLATE 2

1

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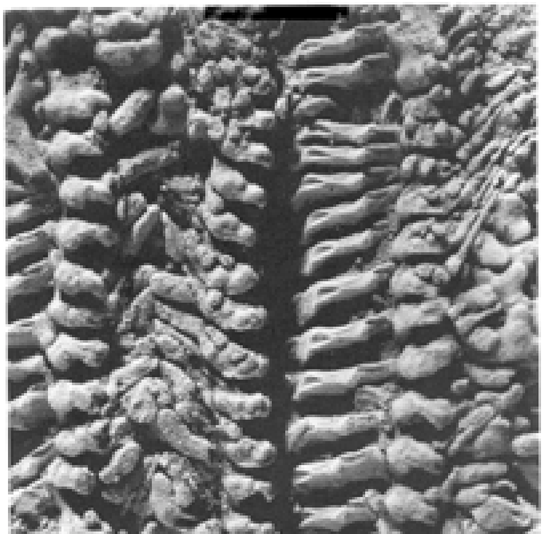

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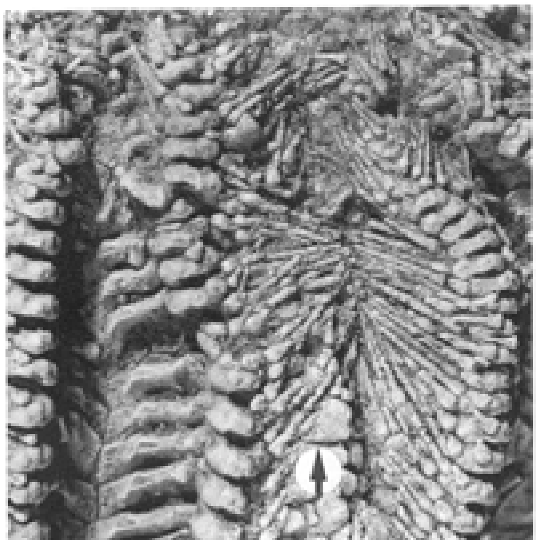

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BLAKE, *Brachisolaster*

low paxilliform ossicles bearing tufts of spinelets. In a few species (e.g. *Crossaster papposus*, Pl. 1, figs 2, 4), the skeleton is in the form of an open reticulum with larger paxillae linked by smaller cross bars. *Brachisolaster* shares this derived pattern (Pl. 1, fig. 5), although its ossicles appear relatively stout and closely spaced. In *Brachisolaster*, marginals are difficult to identify with any certainty (Pl. 2, fig. 4), and they are no longer clearly aligned where exposed; nevertheless, probable marginals have a well-developed spine-bearing ridge, a state apparently derived relative to the condition in *Rhipidiaster* in which the ridge is less prominent. Adjacent marginals are abutted in *Rhipidiaster* but they do not appear abundant enough to have abutted in *Brachisolaster*; if so, this state is also derived. Ambulacral and adambulacral ossicular forms (Pl. 2, figs 1–4) in *Brachisolaster* are essentially similar to those of living solasteroids, although the adambulacrals are proportionately narrow. Development of mouth angle ossicles (Pl. 2, figs 1–2), including the absence of spines from much of the ossicular surface, is typical of that of living solasteroids.

Brachisolaster moretonis clearly is a solasteroid, in which many characters are derived relative to their state in *Rhipidiaster* and *Lophaster*, and suggestive of their state in *Crossaster*. Derived characters include presence of supernumerary arms (although more occur in the fossil than are known among living representatives), disc size, dorsal ossicular form and arrangement, ambulacral column arrangement (but adambulacral proportions are distinctive), and perhaps marginal development. Arm number, adambulacral breadth, and clusters of elongate distal spines are unlike arrangements in living solasteroids. Most living solasteroids have relatively wide adambulacrals whereas those of *Brachisolaster* are narrow; this seemingly primitive condition is a likely result of space constraints, in that the presence of many arms around the disc axis leaves only limited room for adambulacrals. Living solasteroids have between 5 and 15 arms (Clark and Courtman-Stock 1976) whereas the present specimen of *Brachisolaster* has 33; Lawrence and Komatsu (1990) noted that arm number is variable in asteroids with more than 12 arms, and therefore number likely was variable in *Brachisolaster* as well.

The functional significance of supernumerary arms seems important. Inferences for behavioural generalists such as asteroids are difficult, but comparisons of form suggest one explanation. *Brachisolaster* is superficially similar to the eastern tropical Pacific genus *Heliaster* (Forcipulatida: Heliasteridae) in terms of overall size, relative disc size (i.e. ratio of arm to disc radius) and arm number. Living solasteroids commonly feed on relatively large, mobile prey such as other echinoderms; *Solaster dawsoni*, for example, is a predator of other asteroids in the North Pacific. It searches the substrate with forward arms and a portion of the disc raised; when the extended tube feet contact the dorsal surface of a victim, *S. dawsoni* drops down and impedes retreat of the prey individual using rows of large transverse adambulacral spines (Van Veldhuizen and Oakes 1981). Comparison of ambulacra between certain Recent *Crossaster papposus* specimens in the collections of the National Museum of Natural History (Washington) and *Brachisolaster* suggests less robust construction in the fossil. The *Brachisolaster* specimen, with a primary radius of 60–70 mm, has approximately 20 ambulacral ossicles in 20 mm, whereas two *Crossaster* specimens with radii of approximately 80 and 90 mm have 12 or 13 ambulacral ossicles in 20 mm, and one specimen of radius approximately 45–50 mm has about 16–18 in 20 mm. The specimen of radius of about 80 mm has a proximal ambulacral breadth in excess of 9 mm, compared with about 3 mm in *Brachisolaster*. Deep muscle depressions and prominent articular facets suggest very strong articulation capabilities in the living species. All these traits suggest a robust construction well suited to manipulation of comparatively active prey in living solasteroids.

Heliaster is found along rocky shorelines where it commonly withstands high energy wave impact and feeds on molluscs and barnacles (Jangoux 1982). *Brachisolaster*, which lacked the ambulacral construction typical of many solasteroids, would seem to have been relatively inefficient in manipulating larger, more active prey. In addition, the open dorsal reticulum probably would have been less resistant to wave impact than apparently is the tightly interconnected skeleton of *Heliaster*. It is suggested that *Brachisolaster* was a predator on relatively small, passive prey individuals, much as *Heliaster* is today, but in quieter settings.

Arm number among the few known Jurassic solasteroids includes both those with supernumerary arms (Blake 1887) as well as one with an uncertain number, but apparently within the range of that of living solasteroids (Hess 1972). Feeding on more active echinoderm prey perhaps represents a behavioural complexity beyond that involved in feeding on relatively inactive molluscs, but if arm number is taken as indicative of this complexity, then predation on active prey had evolved by the Jurassic. Loss of a viable life mode (i.e. predation on molluscs) might have resulted from competition from asteriids.

As noted above, the pavement-like arrangement of the adambulacral spines toward the arm tips appears natural, but unlike patterns in living solasterids, if only because fewer arms means more widely separate arm tips for any given radius (Pl. 1, figs 1–3). Spines might have provided support on a soft substrate, they could have served to help smother prey, or perhaps other functions are possible.

Asteriids also might have suffered a narrowing of functional range since the Jurassic. It has been suggested (Blake 1990) that the prominent adambulacral spines of Jurassic asteriids, not known among living species, were similar to those of living solasterids, and might similarly have been used to impede prey retreat. Thus, limited evidence suggests a narrowing and specialization of adaptive zones of solasterids and asteriids since the Jurassic. This conjectural interpretation unfortunately can be only partly tested through studies of behaviour of living asteroids.

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