ECHINOIDS FROM THE JURASSIC OXFORD CLAY OF ENGLAND

by ANDREW B. SMITH

ABSTRACT. The echinoids of the Oxford Clay (Callovian–Oxfordian) of southern England have, until now, remained very poorly known. Three species are described: *Eosalenia jessoni* is shown to be a member of the Aspidodiadematidae, a rare deep-water family of Diadematoida, and *Trochotiara superbum* and *Disaster moeschi* are both reported from Britain for the first time.

THE Oxford Clay Formation, which extends from the Lower Callovian Calloviense Zone to the Lower Oxfordian Cordatum Zone, is widely developed in southern England. It has been divided traditionally into Lower, Middle and Upper Oxford Clay, but these have now been defined formally as the Peterborough, Stewartby and Weymouth members respectively (Cox *et al.* 1992). The formation is well-known for its beautifully preserved molluscs, especially ammonites, which are both abundant and diverse, and have been studied extensively (Martill and Hudson 1991). In contrast, echinoids from the Oxford Clay have remained almost unknown. In Wright's comprehensive monograph on British Jurassic echinoids, the Oxford Clay and underlying Kellaways Beds are the only formations listed as yielding no echinoids (Wright 1861, p. 434). The first published record of echinoids from the Oxford Clay appears in Penning and Jukes-Browne (1881, p. 7), where *Acrosalenia spinosa*? Agassiz is listed as coming from the Oxfordian St Ives Clays [= Weymouth Member]. Roberts (1892, p. 18) also recorded an *Acrosalenia* from the Oxford Clay of St Ives. However, the first description of an Oxford Clay echinoid did not appear until 25 years later when Gregory (1896) provided a brief description of his new species *Pseudodiadema jessoni*. The only other published record, until recently, was a report of 'crushed Collyritidae' from the Lower Spinosum Clays [= Stewartby Member] of Woodham Brickpit, Buckinghamshire, by Arkell (1939).

The echinoid fauna from the equivalent lithofacies and age in Europe are no better known. Thierry and Néraudeau (1994) point out that the lowest standing diversity of echinoids in the French Jurassic is reached towards the end of the Late Callovian and at the beginning of the Early Oxfordian, coinciding with a sea-level high-stand. Callovian and Oxfordian echinoids do occur more abundantly in facies other than clays, but these have a very different taxonomic composition from the fauna described here.

In 1989, Neville Hollingworth (then at Oxford Polytechnic) started making faunal collections from the Oxford Clay exposed in the ARC quarry at Stanton Harcourt, Oxfordshire. He collected a large number of echinoids, and additional specimens have been collected by Jon Todd (University of Wales, Aberystwyth) and myself subsequently. By far the most common echinoid present at this locality is the irregular species *Disaster moeschi* Desor. This belongs to the family Disasteridae which previously was unrecorded from Britain. In addition, a few specimens of a small regular echinoid, belonging to the rare diadematoid family Aspidodiadematidae, were also collected. These two species were listed in Hollingworth and Wignall (1992, p. 20), and illustrated by Martill (1991) as *Disaster granulosus* (Goldfuss) and *Eosalenia* sp. nov, respectively.

Although larger specimens are inevitably crushed and pyritization often obscures surface detail, preservation of Oxford Clay echinoids can be exquisite. Prompted by the importance of the new finds at Stanton Harcourt and their excellent preservation, additional specimens were sought

[Palaeontology, Vol. 38, Part 4, 1995, pp. 743–755, 3 pls]

amongst museum collections and a third species, this time a true *Pseudodiadema*, was found, along with a number of indeterminate fragmentary spines of cidaroids.

This paper describes the Oxford Clay echinoids and their autecology. The environmental setting and palaeoecology of the fauna from Stanton Harcourt quarry have been discussed in Hollingworth and Wignall (1992), and for the Oxford Clay in general by Martill and Hudson (1991).

LOCALITIES AND STRATIGRAPHY

Oxford Clay echinoids are known from the following localities and horizons (stratigraphical nomenclature follows Cox *et al.* 1992):

(a) Woodham Brick Pit, Akeham Street Station, Buckinghamshire [National Grid Reference SP 694183]. Stewartby Member; Upper Callovian, Athleta Zone. Details of the section are given by Arkell (1939) and Callomon (1968).

(b) ARC Quarry, 1 km west of Stanton Harcourt, Oxfordshire [National Grid Reference SP 410048]. The great majority of echinoids comes from the Lamberti Limestone at the top of the Stewartby Member; latest Callovian. However, uncommon specimens of *Disaster* come from immediately beneath, from the Athleta Zone Spinosum Subzone. Full details of this section are given in Hollingworth and Wignall (1992).

(c) Pit just west of the railway station at Warboys, Cambridgeshire [National Grid Reference TL 310818]. Weymouth Member; Lower Oxfordian, Mariae Zone. One specimen is recorded as coming from '4 feet [1·2 m] below the topmost cementstone, i.e. 8 feet [2·4 m] below the Corallian Limestone'. Others are stated to be from 'near [the] bottom' of the pit. Spath (1939) and Callomon (1968) give details of this section.

(d) St Ives Brick Pit [Howe Brick Pit], St Ives, Cambridgeshire [National Grid Reference TL 304718]. Weymouth Member; Lower Oxfordian, Mariae Zone. This section is described in Roberts (1892).

(e) Somersham Brick Pit, 8 km north-east of St Ives, [National Grid Reference TL 373791]. Weymouth Member; Lower Oxfordian. Section details unknown.

SYSTEMATIC PALAEONTOLOGY

Museum repositories are indicated as follows: BMNH = The Natural History Museum, London; OUM = Oxford University Museum, Oxford; SM = Sedgwick Museum, Cambridge.

Subclass EUECHINOIDEA Bronn, 1860
Order DIADEMATOIDA Duncan, 1889
Family ASPIDODIADEMATIDAE Duncan, 1889

Mortensen (1940) included two extant genera, *Aspidodiadema* Agassiz and *Plesiodiadema* Pomel, and two fossil genera, *Eosalenia* Lambert and *Tiaridia* Pomel, in this family, which clearly belongs to the Diadematoida, as argued by Smith and Wright (1990, p. 110). Members possess an aulodont lantern and have just ten local buccal plates like all acroechinoids. Apical disc plating is monocyclic, and plates are not sutured to the corona but are imbricate. Primary tubercles are large, perforate and strongly crenulate, whereas miliary tuberculation is sparse, being restricted to the margins of

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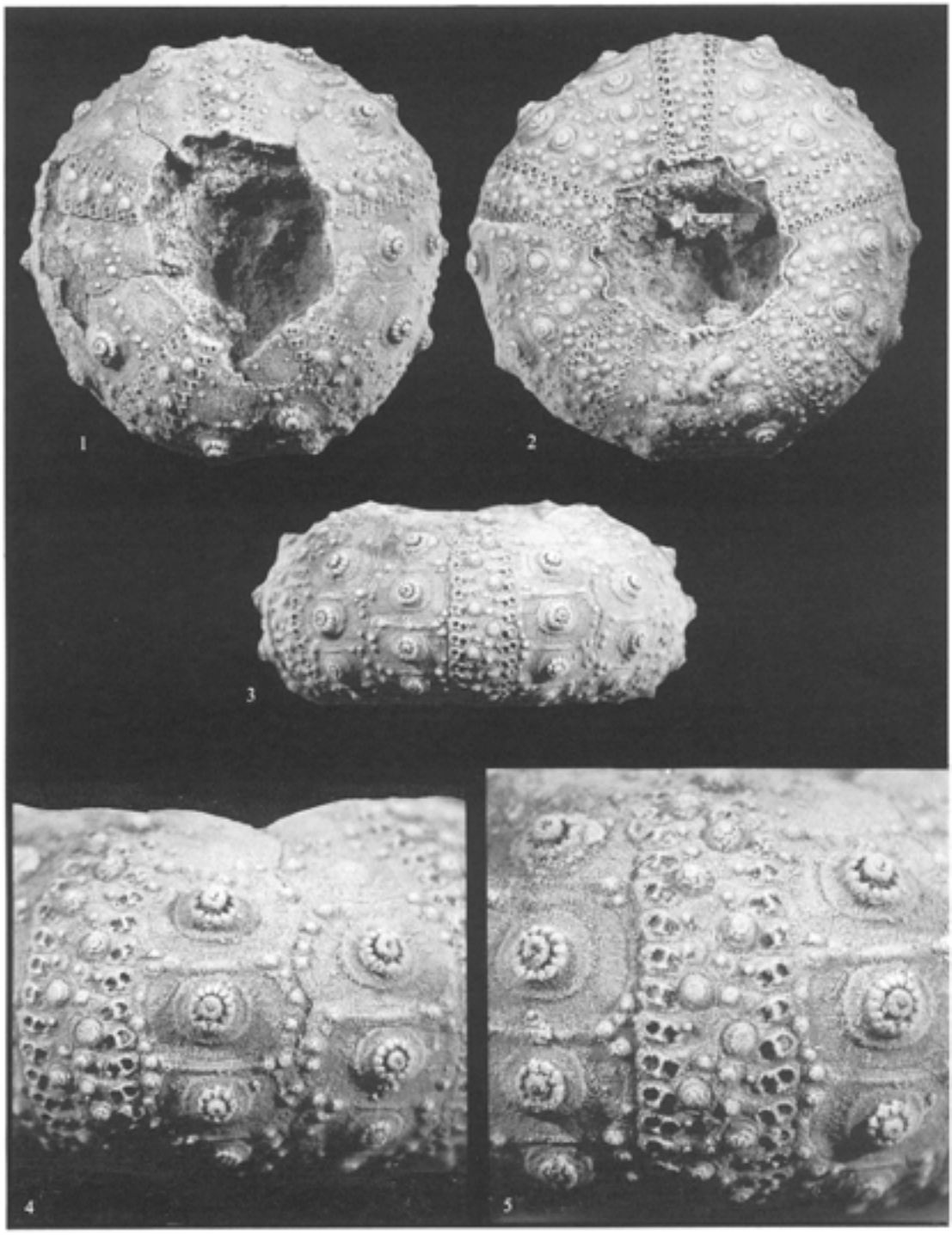
EXPLANATION OF PLATE 1

Figs 1–5. *Eosalenia jessoni* (Gregory); BMNH EE1294; Upper Callovian Lamberti Zone, Stanton Harcourt, Oxfordshire. 1, apical view; 2, oral view; 3, lateral view; 4, detail of interambulacrum in lateral view; 5, detail of ambulacrum in lateral view. 1–3, ×6; 4–5, ×12.



SMITH, *Eosalenia jessoni*

plates. The most diagnostic features of aspidodiadematids are their spine structure and sphaeridial arrangement. Their spines are solid, and the shaft deeply ridged and verticillate. In cross section, they are constructed of an outer ring of stout calcite wedges and a central meshwork that forms horizontal dissepiments (Mortensen 1940, text-figs 6–7). Spines are always very much longer than the test diameter. Sphaeridia are developed uniformly on every plate from peristome to apex, and are placed in small depressions on the lowest of the three elements in each compound plate. They are attached to a small tubercle and hang downwards in life.

The two extant genera differ in their relative development of primary ambulacral tubercles; in *Aspidodiadema*, primary ambulacral tubercles are very large at the ambitus and adorally, occupying virtually the entire compound plate. In *Plesiodiadema*, by contrast, primary tubercles remain small and are restricted to the central of the three elements forming each compound plate.

Smith and Wright (1990, p. 113) were uncertain as to the placement of the genus *Eosalenia* since spines, apical disc, lantern and sphaeridia were all unknown. Specimens of *Eosalenia* from the Oxford Clay, described here, show the highly characteristic development of sphaeridial pits, and associated spines are now also known. On the basis of this new information, there seems little doubt that Mortensen (1940) was correct to place this genus in the Aspidodiadematidae. Indeed, the species described below, *E. jessoni* (Gregory), is strikingly similar to *Plesiodiadema* in almost all test details, differing only in having rudimentary interambulacral tuberculation adapically. Lambert (*in* Lambert and Savin 1905) described the ambulacra of *Eosalenia* as being composed of simple plates becoming bigeminate adapically. However, specimens in the Lambert Collection housed in the Department of Geology, Université de Paris VI, have simple ambulacral plating throughout, although occasional elements are expanded and bear larger tubercles (Text-fig. 1B). Exactly the same is true for the *Eosalenia* described here from the Oxford Clay. Thus there is no difference in ambulacral structure that merits separation of *Eosalenia* from *Plesiodiadema*, and the two genera are differentiated solely on the relative development of periapical interambulacral tubercles.

Genus EOSALENIA Lambert *in* Lambert and Savin, 1905

Type species. Eosalenia miranda Lambert *in* Lambert and Savin, 1905, by monotypy, from the Oxfordian of Joyeuse, Ardèche, and Courry, Département de Gard, France and Late Callovian–Early Oxfordian of England. Treated here as a subjective junior synonym of *Pseudodiadema jessoni* Gregory.

Other species. Pseudodiadema varusense Cotteau from the Pliensbachian of Plan d'Aup, Var, France, and *Pseudodiadema dumortieri* Cotteau from the Bajocian of Saint-Rambert, Ain, France.

Range and distribution. Pliensbachian to Oxfordian of France and England. This lineage presumably gave rise to the extant *Plesiodiadema*.

Diagnosis. Aspidodiadematid resembling *Plesiodiadema* in ambulacral structure and tuberculation, but with periapical interambulacral plates having rudimentary tubercles only.

Eosalenia jessoni (Gregory, 1896)

Plate 1, figures 1–5; Text-figure 1

1892 *Acrosalenia*, sp. Roberts, p. 18 [listing only].
1896 *Pseudodiadema jessoni* Gregory, p. 465, text-fig. a–b.
1905 *Eosalenia miranda* Lambert *in* Lambert and Savin, 1905, p. 311, pl. 2, figs 10–14.
1911 *Eosalenia miranda* Lambert; Lambert and Thiéry, p. 166.
1935 *Eosalenia miranda* Lambert; Mortensen, p. 318, text-fig. 173.
1966 *Eosalenia miranda* Lambert; Fell, p. U352, text-fig. 261.4.
1991 *Eosalenia* sp. nov. Martill, p. 187, text-figs 7–8.
1992 *Eosalenia jessoni* (Gregory); Hollingworth and Wignall, p. 20.

Types. The holotype of *P. jessoni* is BMNH E3936, and there are two paratypes, BMNH E3937 and E3938. The holotype of *Eosalenia miranda*, by monotypy, is the specimen in the Gevrey Collection figured by Lambert and Savin (1905). Its whereabouts is unknown. A second specimen, L6.22 in the Lambert Collection at the Université de Paris VI, and identified by Lambert as *E. miranda*, has been examined.

Material. In addition to the types, this species is represented by the following specimens: SM J27143a,b, J27149–64, J27165–6, J35958, J46219–21, J48143, J69401; BMNH EE1294 and ? E41896.

Range and distribution. In England, the species is known from the Late Callovian, Lamberti Zone, of Stanton Harcourt and the Early Oxfordian, Mariae Zone, of Warboys Pit, Somersham Pit and St Ives (localities b–e above). Poorly preserved regular echinoids from the Late Callovian, Athleta Zone, of Woodham Pit (locality a above) may also belong to this species, although all are too badly affected by pyrite decay to be identified with confidence. The species is also known from the Oxfordian of France.

Description. Tests range from about 10 to 14 mm in diameter and 5 to 6·5 mm in test height (height is approximately 50 per cent. of the diameter). The test is circular in outline and wheel-shaped in profile, with the ambitus at about mid-height (Pl. 1, figs 1–3). The diameter of the apical disc is 41–49 per cent. of that of the test, and is circular in outline with small notches both radially and interradially. No plates of the apical disc remain in any specimen.

Ambulacra are narrow and straight-sided, hardly tapering either adapically or adorally. Plating is simple throughout with a primary tubercle developed on approximately every third plate (Pl. 1, fig. 5; Text-fig. 1A–B), although this is not strictly regular and there may be larger tubercles on every second plate adapically. Pore-pairs are small P2-type isopores (as defined in Smith 1978) and show no crowding towards the peristome. There is generally a small secondary tubercle on the plate immediately above that carrying the primary tubercle. The plate beneath each primary tubercle has a shallow sphaeridial pit associated with a minute granule immediately perradial of the pore-pair (Pl. 1, fig. 5). These sphaeridial pits are developed regularly on every third plate thoughout most of the length of the ambulacrum, being absent only adapically in the largest specimen, where tuberculation also becomes less regular.

Interambulacra are broad, with eight or nine plates in a column. All but the periapical plates carry a large primary perforate, crenulate tubercle. This tubercle is surrounded by a large areole which occupies virtually the entire plate (Pl. 1, fig. 3). A few miliaries lie scattered around the adradial and interradial edges of the plate. Areoles are confluent.

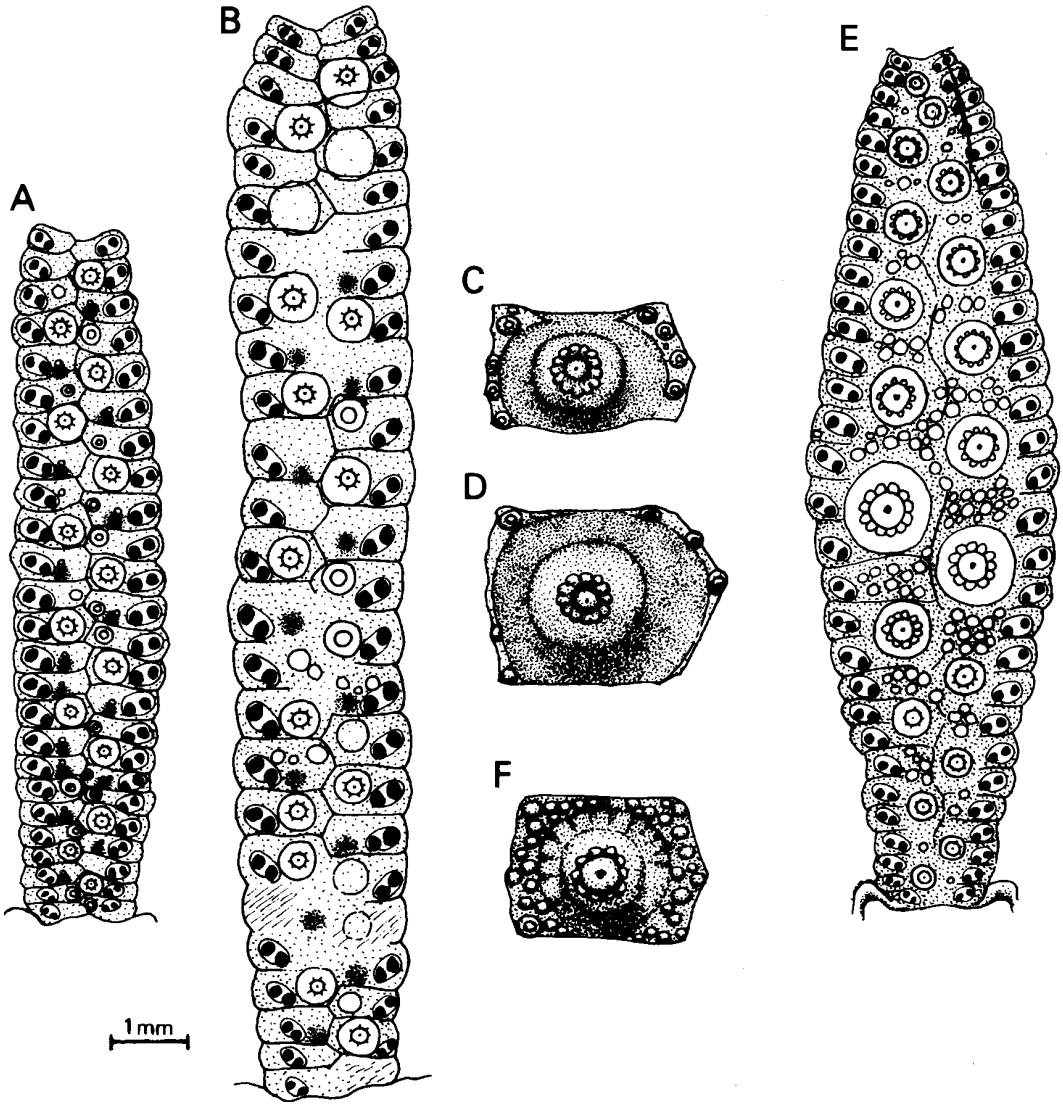
The peristome is slightly smaller than the apical disc, its diameter being about 35–40 per cent. that of the test. Buccal notches are broad and shallow, and give the peristomial edge a very undulose appearance (Pl. 1, fig. 2). Lantern elements and perignathic girdle remain unknown.

Spines are found in association with the test in SM J27143 and J48145. Unfortunately all are broken so that their length in life is unknown. They appear slender and lightly constructed and have no cortex. The shaft is deeply grooved and verticillate, though the thorns are not arranged into well defined whorls. In cross-section, the spine has a relatively large labyrinthine core and an outer ring of wedge-shaped rods. The longitudinal cross section is unknown.

Remarks. The species was first recorded from the Oxford Clay of England as *Acrosalenia* in the faunal list given by Roberts (1892). It was recognized as a new species by Gregory (1896), who gave only a brief description and sketch. He failed to realize its true relationships, however, and ascribed it to the genus *Pseudodiadema*. The species was later described under the name *miranda* by Lambert (*in* Lambert and Savin 1905) from the Oxfordian of Joyeuse, Ardèche, France. Lambert realized that the species was closely related to *Plesiodiadema* and created the new genus *Eosalenia* for it. In addition, a specimen, also Oxfordian in age, in the Lambert collection comes from Courry, Gard, France.

As noted by Lambert and Savin (1905), this species is remarkably similar to extant species of *Plesiodiadema*, differing primarily in lacking primary tubercles on periapical plates. The distinction between *E. jessoni* and earlier *Eosalenia* species is slight, but those from the Pliensbachian and Bajocian have better developed miliary rings around primary interambulacral tubercles.

There is very little difficulty in distinguishing this species from the other Oxford Clay regular echinoid, *Trochotiara superbum* (Agassiz), described below, which differs markedly in its tuberculation and ambulacral structure.



TEXT-FIG. 1. Camera lucida drawings of plating. A–D, *Eosalenia jessoni* (Gregory). A, C, BMNH EE1294; Upper Callovian, Lamberti Zone, Stanton Harcourt, Oxfordshire; A, ambulacrum, from apex to peristome; C, ambital interambulacral plate. B, D, L.6.22 (Lambert Collection, Université de Paris VI); Oxfordian, Courry, Gard, France (specimen identified by Lambert as *Eosalenia miranda* Lambert); B, ambulacrum from apex to peristome; D, ambital interambulacral plate. E–F, *Trochotiara superbum* (Agassiz), SM J27148; Lower Oxfordian, Mariae Zone, St Ives, Cambridgeshire; E, ambulacrum from apex to peristome; F, ambital interambulacral plate.

Plesiodiadema is restricted to deep water at the present day and is found between 300 and 3000 m depth (Mortensen 1935). Neither this form nor *Trochotiara superbum* show development of adoral pore-pair crowding, and are thus probably entirely soft-bottom dwellers.

Order PHYMOSOMATOIDA Mortensen, 1904
Plesion (Genus) TROCHOTIARA Lambert, 1901

A discussion of this genus is given in Smith and Wright (1993), and need not be repeated here.

Trochotiara superbum (Agassiz, 1840)

Plate 2, figures 1–5; Text-figure 1E–F

1840 *Diadema superbum* Agassiz, p. 23, pl. 17, figs 6–10.
1882 *Pseudodiadema superbum* (Agassiz); Cotteau, p. 273, pl. 334, figs 1–9.

Types. The holotype is M92 in the Agassiz Collection, Museum de Histoire Naturelle de Neuchâtel. It comes from the Oxfordian Marls of Mont Vohayes, Switzerland.

Material. The best preserved specimen, on which the following description is based, is SM J27148. Other, less well preserved material includes SM J35954–5, SM J35958, BMNH E4242, and possibly OUM J42906–7.

Range and distribution. In England, the species comes from the Early Oxfordian Mariae Zone, of Warboys (locality c above) and St Ives (locality d above). Two poorly preserved regular echinoids from an unspecified level in the Oxford Clay have been found at St Clements and Cowley Field, Oxford, and may also belong to this species. It has not been found at other horizons. In France, it is widely distributed in the Oxfordian, and it also occurs in Switzerland at the same level.

Diagnosis. A *Trochotiara* with fine tuberculation and small mamelons. Peristome smaller than apex, its diameter only about 30–33 per cent. of that of the test. Broad naked interradial zone developed adapically.

Description. The only well preserved test is 12 mm in diameter and 5·5 mm in height (64 per cent. of the diameter). It is subpentagonal in outline and rather tumid in profile (Pl. 2, fig. 3), with the ambitus a little below mid-height. The circular apical disc opening is rather small for a trochotiarid, with a diameter only 40 per cent. of that of the test. All plates of the apical disc have been lost.

Ambulacra are two-thirds the width of interambulacra at the ambitus and taper both adapically and adorally (Pl. 2, figs 1–2). Pore-pairs are uniserial throughout and there is no pore crowding adorally (Pl. 2, fig. 2; Text-fig. 1E). Plates are trigeminate throughout with a large primary tubercle occupying almost the entire compound plate adorally and ambitally. Adapically, the primary tubercles reduce in size gradually and a 2+1 style of compounding is found. Primary ambulacral tubercles are as large as the interambulacral tubercles at the ambitus and have circular, non-confluent areoles (Pl. 2, fig. 4). Miliary granules surround the primary tubercle areoles so as to form a single zig-zag series perradially. There are 30 ambulacral pores and nine primary tubercles in a column.

Interambulacra have 12 plates in a column, which are generally slightly broader than tall. Primary tubercles with circular non-confluent areoles are present on all plates. These are moderately large at the ambitus but become gradually smaller both apically and adorally. Adapically, the primary tubercles are displaced towards the adradial suture. Areoles are typically striated radially (Pl. 2, figs 3–4). Miliaries are well-developed at the ambitus forming a broad interradial zone. Adapically, they become sparse, leaving a broad and well defined naked zone interradially.

The peristome is remarkably small, much smaller than the apical disc, with a diameter only 32 per cent. of that of the test. It is circular and notched by relatively deep and prominent buccal notches (Pl. 2, fig. 2). It is hardly invaginated.

Remarks. The species was referred to the genus *Pseudodiadema* by Cotteau (1882). However, the type species of *Pseudodiadema*, *P. pseudodiadema* Agassiz, has a compact dicyclic apical disc which is rather firmly bound to coronal plates, whereas *Diadema superbum* Agassiz has a large pentagonal apical disc scar, and presumably a monocyclic apical disc. It is therefore transferred to the genus *Trochotiara* Lambert, 1901.

The most characteristic feature of this species is the relatively small size of its peristome. In almost all other trochotiarids, the peristome and apical disc are both large, and approximately equal in size. A second distinctive feature of *T. superbum* is the small size of the mamelons on its primary tubercles, although this is less pronounced in the English specimens than in the French. The small peristome, broad flat oral surface, small numerous interambulacral tubercles that decrease gradually adapically, and the well developed interradial naked zone give this species a very distinctive appearance.

Series ATELOSTOMATA Zittel, 1879
Plesion (Family) DISASTERIDAE Gras, 1848
Genus DISASTER Agassiz, 1836

Type species. Nucleolites granulosus Goldfuss, 1826, by subsequent designation of Desor, 1858, p. 201.

Other species. There are two other well-defined species, *D. moeschi* Desor, 1858, and *D. subelongatus* (Orbigny), as well as a number of other nominal species.

Range and distribution. Known from the Callovian (Middle Jurassic) through to the Barremian (Lower Cretaceous) of Europe and North Africa. The species has not previously been reported from Britain.

Remarks. Disasterids belong to the stem group of the Atelostomata and are characterized by their disjunct apical disc plating which, unlike that of collyritids, has only the posterior oculars well separated and posterior to the remainder of the apical disc. In *Disaster*, these posterior oculars border the periproct, which is situated on the posterior surface. Thus, the posterior ambulacra are initiated from the periproct margin and lie at the posterior extremity of the test.

The presence of differentiated peristomial pore-pairs and the arrangement of tubercles suggests very strongly that *Disaster* was a deposit feeder using phyllode tube-feet to collect sediment (Smith 1984). The presence of just a few large pore-pairs rather than a larger number of small pore-pairs is a clear indication that the tube-feet have a broad terminal disc and are utilizing mucus secretion to pick up fine-grained sediment, like most extant holasterids and spatangoids.

The fact that plastronal spines (which provide the forward thrust in modern irregular infaunal echinoids) and lateral oral spines (which provide the digging capability) are so poorly developed argues against *Disaster* having led an infaunal mode of life. So too does the low density of aboral tubercles; it is hard to envisage how such an open canopy of spines could have maintained a water-filled cavity around the test when buried within a mud substratum. However, the subanal tufts of spines are associated with the construction of a subanal drainage channel in living infaunal or semi-infaunal spatangoids (Smith 1984), and *Disaster* clearly had well developed subanal cones of spines. The cones occur very low down, more or less at the base of the test, and once again their function in *Disaster* is problematical. The simplest explanation for them is that they are retained from an ancestral disasterid that inhabited coarser-grained sediments and constructed subanal drainage channels. *Disaster* is thus interpreted as being a secondarily epifaunal detritivore.

Disaster moeschi Desor, 1858

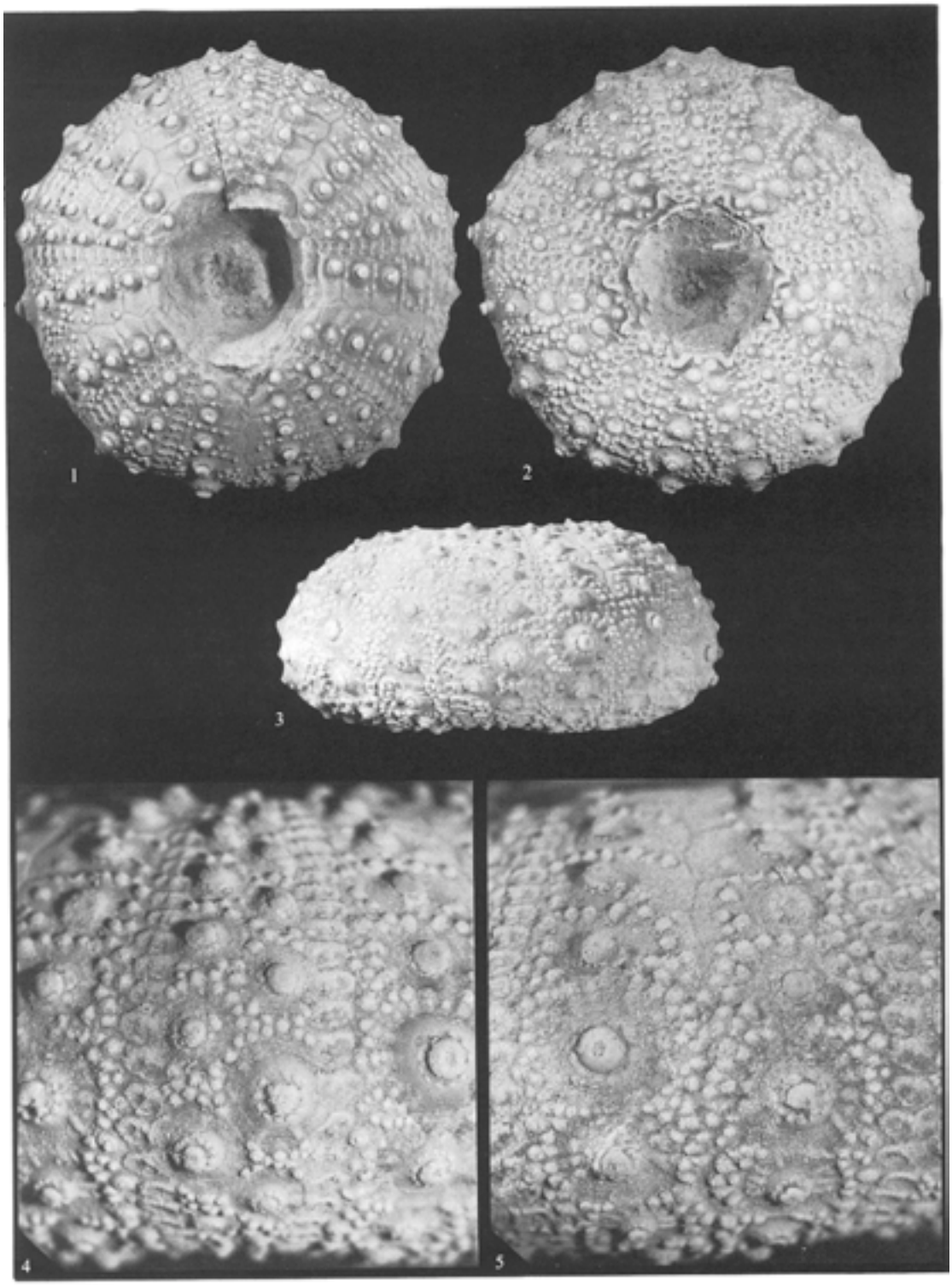
Plate 3, figures 1–6

1858 *Dysaster moeschi* Desor, p. 202.

EXPLANATION OF PLATE 2

Figs 1–5. *Trochotiara superbum* (Agassiz); SM J27148; Lower Oxfordian Mariae Zone, St Ives, Cambridgeshire. 1, apical view; 2, oral view; 3, lateral view; 4, detail of ambulacrum in lateral view; 5, detail of interambulacrum in lateral view. 1–3, ×6; 4–5, ×12.

PLATE 2



SMITH, *Trochotiara superbum*

1867 *Dysaster moeschi* Desor; Cotteau, p. 107, pl. 24, figs 1–7.
1934 *Disaster moeschi* Desor; Beurlen, p. 120, fig. 24a.
1963 *Disaster moeschi* Desor; Jesionek-Szymanska, p. 382, pl. 7, fig. 1 [see also for extended synonymy].
1991 *Disaster granulosus* (Goldfuss); Martill, p. 187, pl. 35, figs 1–3.

Type. The holotype, by original designation, is V63 in the collections of the Museum de Histoire Naturelle de Neuchâtel.

Material. A large number of specimens of this species was collected. The description given below is based on BMNH E83558–65 and EE1046–68.

Range and distribution. In England, this species is known only from the top of the Late Callovian, Athleta Zone (Spinosum Subzone) and Lamberti Zone of Stanton Harcourt (locality b above; Hollingworth and Wignall 1991), and the Athleta Zone of Woodham Brickpit (locality a above). Elsewhere, it is known from the Early Callovian through to the Early Oxfordian of France, Switzerland and Poland (Jesionek-Szymanska 1963; Thierry and Néraudeau, 1994).

Diagnosis. Differs from *D. granulosa* (Goldfuss) in being squatter and broader, in having the apical disc more central, and in having a more squarely truncated posterior with the posterior ambulacra largely restricted to this face.

Description. This species is relatively well known and, because the English material is mostly crushed, there is no point in presenting biometric data. However, the English material does preserve excellent surface detail, and this allows tuberculation and pore-pair arrangement to be described in full for the first time.

The apical disc is as in *D. granulosa*, with genital plates 1 to 4 forming a compact ethmophract-style disc. The madrepores are well developed and genital plate 2 is somewhat larger than other genital plates. Gonopores are rimmed (Pl. 3, fig. 5). The posterior oculars are generally lost, but their position is indicated clearly by a pair of notches in the upper corners of the periproct (Pl. 3, fig. 6).

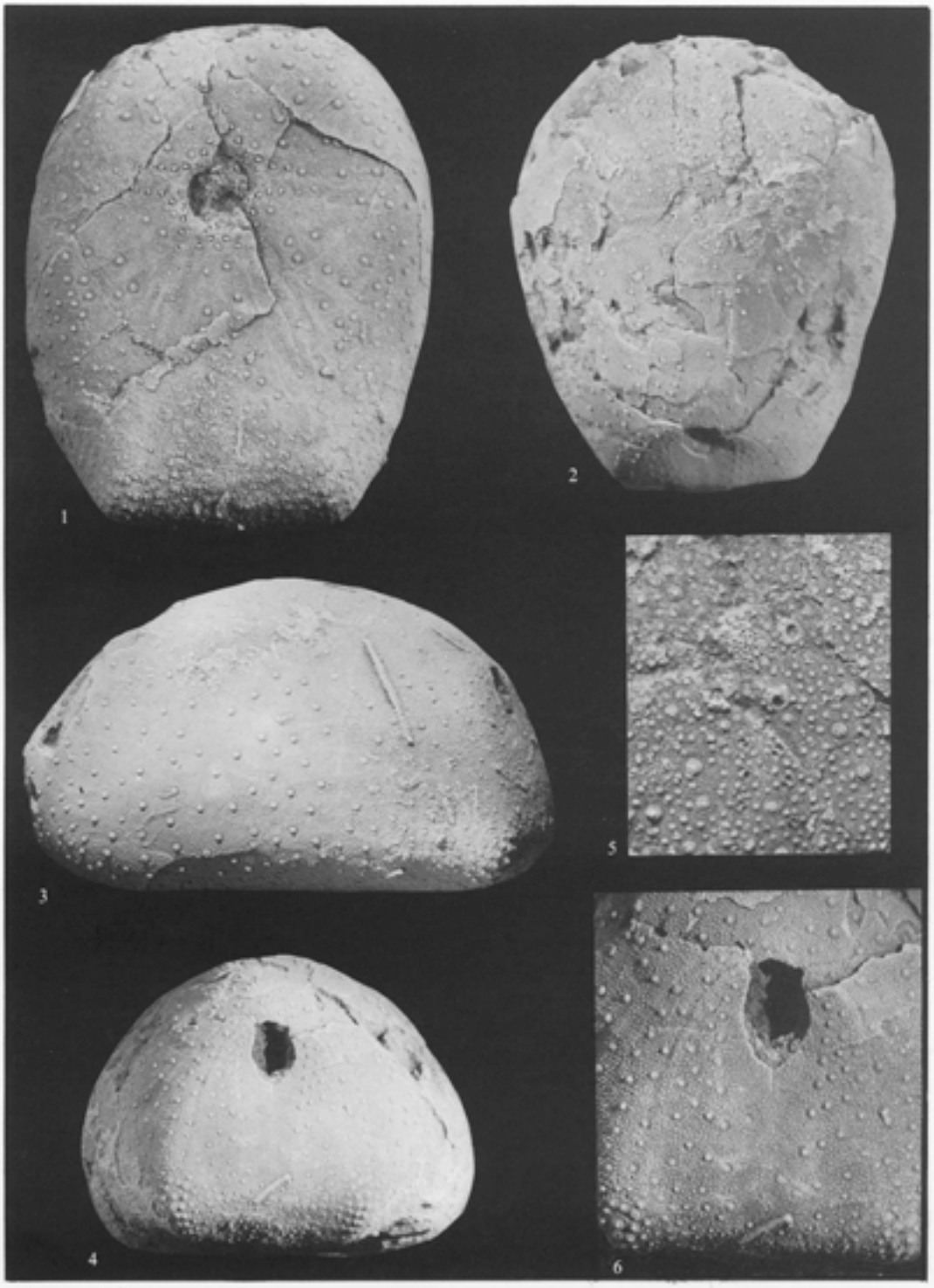
Ambulacral pores are for the most part reduced to rudimentary P1-type isopores (*sensu* Smith 1978) (e.g. Pl. 3, fig. 5). There is no differentiation of aboral petals, and pores in the posterior ambulacra may be simple unipores. Pores remain rudimentary over most of the oral surface also, except adjacent to the mouth where enlarged phyllodal pore-pairs are found. There are approximately three such pore-pairs in each anterior ambulacral column, five in each lateral ambulacral column, and three or four in the posterior ambulacral columns. These pores are considerably enlarged (Pl. 3, fig. 1), and have a very large and swollen interporal partition.

Aboral tuberculation comprises a relatively dense and uniform array of miliaries with a rather sparse scattering of small crenulate and perforate tubercles amongst them (Pl. 3, figs 3, 5–6). Primary tubercle density is about one per mm^2 or less. Areoles are circular in all aboral tubercles. The only place where tubercles become concentrated is on either side of the periproct (Pl. 3, fig. 6) where a vertical band of tubercles with circular areoles is found.

Tubercles are equally sparse over the oral surface, but here there are very few miliaries. Tubercle density increases slightly towards the ambitus, and there is also a ring of tubercles adjacent to the peristome, presumably to help in feeding. The plastron has the highest density of tubercles towards the rear (Pl. 3, fig. 1). Over the plastron and the postero-lateral interambulacra, primary tubercles have asymmetrical areoles that are enlarged towards the latero-posterior, indicating that the spines' power stroke was in that direction. The greatest development of tubercles, however, occurs on the two subanal nodes (Pl. 3, figs 3–4, 6). Here, primary tubercles are larger than elsewhere and so densely packed as to be contiguous. What is more, the tubercles show a distinctly concentric pattern of areole enlargement, areoles being consistently enlarged away from each

EXPLANATION OF PLATE 3

Figs 1–6. *Disaster moeschi* Desor; Upper Callovian Lamberti Zone, Stanton Harcourt, Oxfordshire. 1, 3, BMNH E83558; 1, oral view; 3, lateral view, anterior to the left. 2, 4–6, BMNH E83563; 2, apical view; 4, posterior view; 5, detail of apical disc; 6, posterior view, detail of periproct. 1–4, ×4; 5, ×10; 6, ×8.



SMITH, *Disaster moeschi*

centre. Clearly, *D. moeschi* possessed a well developed pair of sub-anal tufts of spines, and these spines had their power stroke arranged radially outwards.

Remarks. D. moeschi is very similar to *D. granulosa* (Goldfuss) but is consistently squatter and taller and more truncated posteriorly. Stratigraphically, *D. moeschi* predates *D. granulosa*, and there can be little doubt that the two form a single evolving lineage.

Acknowledgements. I thank Neville Hollingworth for first bringing my attention to the occurrence of echinoids in the Oxford Clay and for providing a substantial number of speimens upon which to work, and Beris Cox for drawing my attention to pertinent literature.

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ANDREW B. SMITH

Department of Palaeontology
The Natural History Museum
Cromwell Road
London SW7 5BD, UK

Typescript received 27 December 1993
Revised typescript received 15 March 1995