

Gymnodiadema and the Jurassic roots of the Arbacioida (stirodont echinoids)

Andrew B. Smith

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Abstract The morphology of *Gymnodiadema*, until now incompletely documented from a single poorly preserved individual from the Callovian of Portugal, is clarified based on a new species from the Bajocian of Morocco. The new species has a plating and tuberculation pattern that is identical to that of the Cretaceous arbacioid *Codiopsis*, but has perforate tubercles. *Gymnodiadema* is accompanied in Morocco by the oldest species of *Magnosia* whose morphology is also described. Both *Gymnodiadema* and *Magnosia* are shown to retain their basicoronal interambulacral plates as adults, suggesting arbacioid affinities. The composition of arbacioids is reviewed and a phylogenetic analysis carried out of the better-known relevant taxa. Crown group arbacioids are shown to include the fossil taxa *Noetlingaster* and *Arbia*, and thus originated in the late Cretaceous. Like other echinoid groups, therefore, the expansion of arbacioids into deep-water settings occurred from the late Cretaceous onwards. *Codiopsis*, *Gymnodiadema* and *Magnosia* are identified as stem group members. The presence of two morphologically distinct clades of arbacioid in the Bajocian suggests that arbacioids must have split from their nearest living sister group much earlier, probably in the early Jurassic.

Keywords Echinoids · Systematics · Cladistic analysis · Morocco · New taxa

Introduction

The arbacioids are a small clade of short-spined regular sea urchins with imperforate, non-crenulate tubercles that today are widely distributed in tropical to temperate latitudes (Mortensen 1935). There are just nine extant genera, the majority of which live in deep shelf to continental slope habitats and thus are not often encountered: only *Arbacia*, *Arbaciella* and *Tetrapyrgus* are commonly found within scuba-diving depths (Baumeister and Koch 1998; Schultz 2005). These extant arbacioids are distinguished from other short- to medium-spined regular echinoids with imperforate, non-crenulate tubercles by five key features; the style of their ambulacral plate compounding, the nature of their aboral tube feet and pore-pairs, the structure of their lantern, the retention of a single basicoronal interambulacral plate bounding the peristome, and the positioning of sphaeridia. All these features point to living arbacioids being a monophyletic clade. However, the early history and sister group relationships of this clade are far from clear. Molecular data suggests that arbacioids are sister group to another group of stirodons, the stomopneustids (Smith et al. 2006), whereas morphology weakly supports sister group pairing with camarodonts (Kroh and Smith 2010).

Over the years, a large number of fossil taxa have been assigned to the arbacioids, extending their history back to the Jurassic. Indeed, this group was at its most diverse taxonomically in the Mesozoic. The earliest representatives can first be distinguished confidently from the Middle Jurassic, which is thus the key period for tracing the roots of arbacioids. However, many of these Middle Jurassic taxa remain incompletely documented and there are additional arbacioid-like taxa that need considering. One of the most important of these is *Gymnodiadema*, a taxon erected by de Loriol (1890) for the species *Gymnodiadema choffati*. This

A. B. Smith (✉)
Department of Palaeontology, The Natural History Museum,
Cromwell Road, London SW7 5BD, UK
e-mail: a.smith@nhm.ac.uk

was based on a single badly preserved specimen from the Callovian of Portugal. de Loriol noted that, while this taxon bears some resemblance to the Cretaceous arbacioid *Codiopsis*, it differs strikingly in having perforate tubercles and simple ambulacral plating. This genus has now been found in the Bajocian of Morocco where it is represented by a new species in a good state of preservation. This allows the detailed morphology of *Gymnodiadema* to be described for the first time, and its taxonomic placement clarified. In doing, this I take the opportunity to review a few other Middle Jurassic genera that are relevant for understanding the early history of arbacioids.

History of classification of the Arbacioida

Although the family Arbaciidae has been accepted as a valid taxon since Gray (1855: 36) first proposed the name, its taxonomic composition and its position within echinoid classification have changed significantly over time. Gregory (1900: 307) included just four genera (*Arbacia*, *Echinocidaris* [now considered a synonym of *Arbacia*], *Coelopleurus* and *Podocidaris*) in his Arbaciidae and united it with the Hemiciidaridae under the name Arbaciina on the basis that all shared a similar style of ambulacral plate compounding. The number of genera assigned to the Arbaciidae was subsequently greatly expanded by Lambert and Thiéry (1914: 261 *et seq.*) by the addition of numerous fossil taxa. They were also the first to attempt to subdivide this group, partitioning genera into three tribes as follows:

1. Glypticinae (including the genera *Glypticus*, *Panglyptus*, *Codiopsis*, *Coelopleurus*, *Baueria*, *Arbaciella*, *Pygmaeocidaris*, *Habrocidaris* and *Podocidaris*) for forms whose tubercles were reduced or absent on the upper surface;
2. Acropeltinae (*Acropeltis*, *Goniopygus*, *Parasalenia*) for those with a single primary tubercle on all interambulacral plates;
3. Eucosmechinae (*Magnosia*, *Eucosmechinus*, *Arbacia*, *Agarites*, *Tetrapygus*) for those with numerous subequal tubercles developed on interambulacral plates.

In his comprehensive monograph Mortensen (1935: 544) discussed the composition of the group, accepted eight extant and nine fossil genera as valid and grouping them all within a single family, Arbaciidae. However, he was unconvinced that these really formed a natural assemblage. Although he was dismissive of Lambert and Thiéry's threefold subdivision, Mortensen recognized the heterogeneity of the family and informally partitioned his Arbaciidae into six groups as follows:

1. *Cottaldia*, *Magnosia* and *Eucosmechinus*: test with numerous small tubercles arranged in horizontal lines on the aboral surface.
2. *Codiopsis*: globular test with tubercles wholly confined to the oral surface.
3. *Acropeltis* and *Goniopygus*: test with a single large primary tubercle on interambulacral and ambulacral plates.
4. *Arbacia* and *Tetrapygus*: uniform tuberculation around the test.
5. *Coelopleurus*, *Pygmaeocidaris*, *Dialithocidaris*, *Arbaciella*, *Habrocidaris* and *Podocidaris*: with prominent glassy papillae developed over aboral plates.
6. *Glypticus*, *Pleocyphus* and *Acrosaster*: with tubercles reduced on the aboral surface and replaced by a coarse epistromal ornament.

Durham and Melville (1957), in their revision of echinoid classification, recognized the distinctiveness of the arbaciids by placing them in their own order, Arbacioida. In the *Treatise on Invertebrate Paleontology* Fell and Pawson (1966) followed Mortensen and Durham and Melville in keeping all these taxa within a single family, and expanded its composition to include the additional fossil genera *Arbia*, *Atopechinus*, *Baueria* and *Heteropodia*. Smith (2005), however, reverted to a modified version of Lambert and Thiéry's threefold division of the Arbacioida based largely on the ambulacral plate compounding pattern and tuberculation style. Arbaciidae were identified by their distinctive style of plate compounding and comprised all the modern arbacioids plus *Codiopsis*, *Baueria*, *Noetlingaster* and *Arbia*. Glypticidae were grouped on their well developed, coarse epistromal ornament and included *Glypticus*, *Pleurodiadema*, *Brochechinus* and *Atopechinus*, while Acropeltidae all had perianal spines and included *Acropeltis*, *Goniopygus*, *Mimiosalenia* and *Glyphopneustes*. *Heteropodia* was identified as a poorly preserved species of *Goniopygus* while the genera *Magnosia*, *Cottaldia* and *Eucosmechinus* were removed from the Arbacioida and placed in the Stomechinidae. Subsequently, in a comprehensive cladistic analysis of echinoid families by Kroh and Smith (2010), Arbaciidae, Glypticidae and Acropeltidae were recovered as a monophyletic clade. However, this analysis simply took the type genus from each family as a representative and did not probe the validity or composition of these families.

A large number of fossil genera have, therefore, at one time or another been associated with the Arbacioida. However, these groups differ in the extent to which they display arbacioid traits and it is not at all clear how these various groups are related. Furthermore, many of the early members remain incompletely documented. I now, therefore, turn to three of the most poorly understood Jurassic

taxa and, based on the new collections from Morocco, provide new, detailed morphological descriptions.

Geological setting of Moroccan Jurassic taxa

The echinoids described in this paper come from three localities in the Central Atlas Mountains, Morocco, two in the vicinity of Enjil and one in the vicinity of Amellago (Fig. 1). A general description of the sedimentary evolution and facies of these Jurassic carbonate sequences can be found in Stanley (1981).

At Amellago, horizons yielding echinoids are dated as late Pliensbachian on the basis of their ammonite fauna (*Tauromenia* sp., *Dactylioceras cf. mirabile* Fucini, *Grammoceras naxense* (Gemmellaro): Termier, in Lambert 1937). Here *Dubarechinus despujolsi* Lambert is found in association with cidarids, *Firmacidaris precincta* (Lambert), *Orthopsis? amellagense* (Lambert) *Stomechinus tinginatus* Vadet and Nicolleau and *Diplechinus hebbriensis* Lambert. The echinoids are confined to a small number of bioclastic-rich levels within a deep-water succession of

well-bedded calcareous sands and silts. These fossiliferous levels represent thin debris flows derived from shallow water and the fauna comprises a diverse, but mostly very small sized shallow water fauna including peri-reefal debris of coral and calcareous algae. R. V. Melville collected specimens from 3 to 4 km North of Amellago in one such level in 1954 and these specimens are now held in the Natural History Museum. Additional material was collected from this locality (at 32°01'04 N 004°57'41 W) in recent fieldwork. The echinoid fauna from these levels has been described by Lambert (1937) and Vadet and Nicolleau (2005).

The second locality lies a few kilometer to the North East of Enjil. Here, a small patch reef crops out on the northern slopes of a prominent scarp face (ca. 33°15'31.4 N 004°31.10.8 W) and yields a diverse fauna of echinoids, molluscs and brachiopods. These beds are dated as late Bajocian on the basis of ammonites (*Parkinsonia* sp.: M. Howarth, personal communication February 2010). Echinoids are both abundant and diverse in the marly peri-reefal sediments and a rich fauna was collected include *Sphaerotiaria koechlini* Cotteau, *Psephechinus quoniamii* Gauthier, *Magnosia forbesii* Wright, *Plegiocidaris* sp., *Acrosalenia incerta* Peron and Gauthier, *Pseudodiadema* sp., *Pseudopedina* sp. *Gymnodiadema hessi* sp. nov. and *Holactypus depressus* Leske. The fauna, which will be described in a future paper, is clearly shallow marine and dominated by the reef crevice-nestling *Sphaerotiaria*.

Specimens of *Magnosia termeiri* Lambert were obtained from a local collector at Enjil and come from a different locality close to Enjil that has not been examined personally. This locality yields a closely similar echinoid fauna. However, while the genera are mostly identical, the species are often subtly different from locality two. It includes rare *Gymnodiadema hessi*, *Diplocidaris mauritanicus*, *Magnosia termeiri*, *Psephechinus globosus* Lambert and *Sphaerotiaria koechlini*. Lambert (1931, 1933) and Petitot (1967) both dated a fauna with *Magnosia termeiri*, collected from the vicinity of Enjil as Bajocian based on the associated ammonites. The environment of deposition is unknown.

Morphology of key Jurassic taxa

Gymnodiadema (Figs. 2, 3, 4)

From the single damaged specimen of *Gymnodiadema choffati* de Loriol (1884, 1890) was able to ascertain key features of its unusual morphology: the simple ambulacral plating, the absence of tubercles over its aboral surface, the perforate non-crenulate tubercles and the presence of glassy papillae. A cast of this specimen (catalogue number 26022

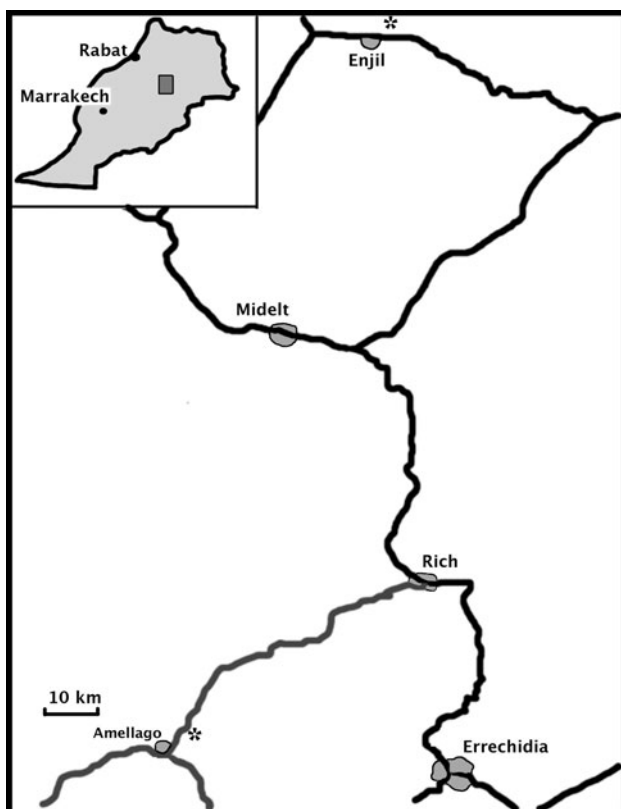


Fig. 1 Map showing the location of the two areas in Morocco from which echinoids in this paper are described. The inset shows Morocco with the dark grey rectangle the position of the larger map. Asterisks mark the two fossil localities from which Jurassic echinoid faunas have been collected

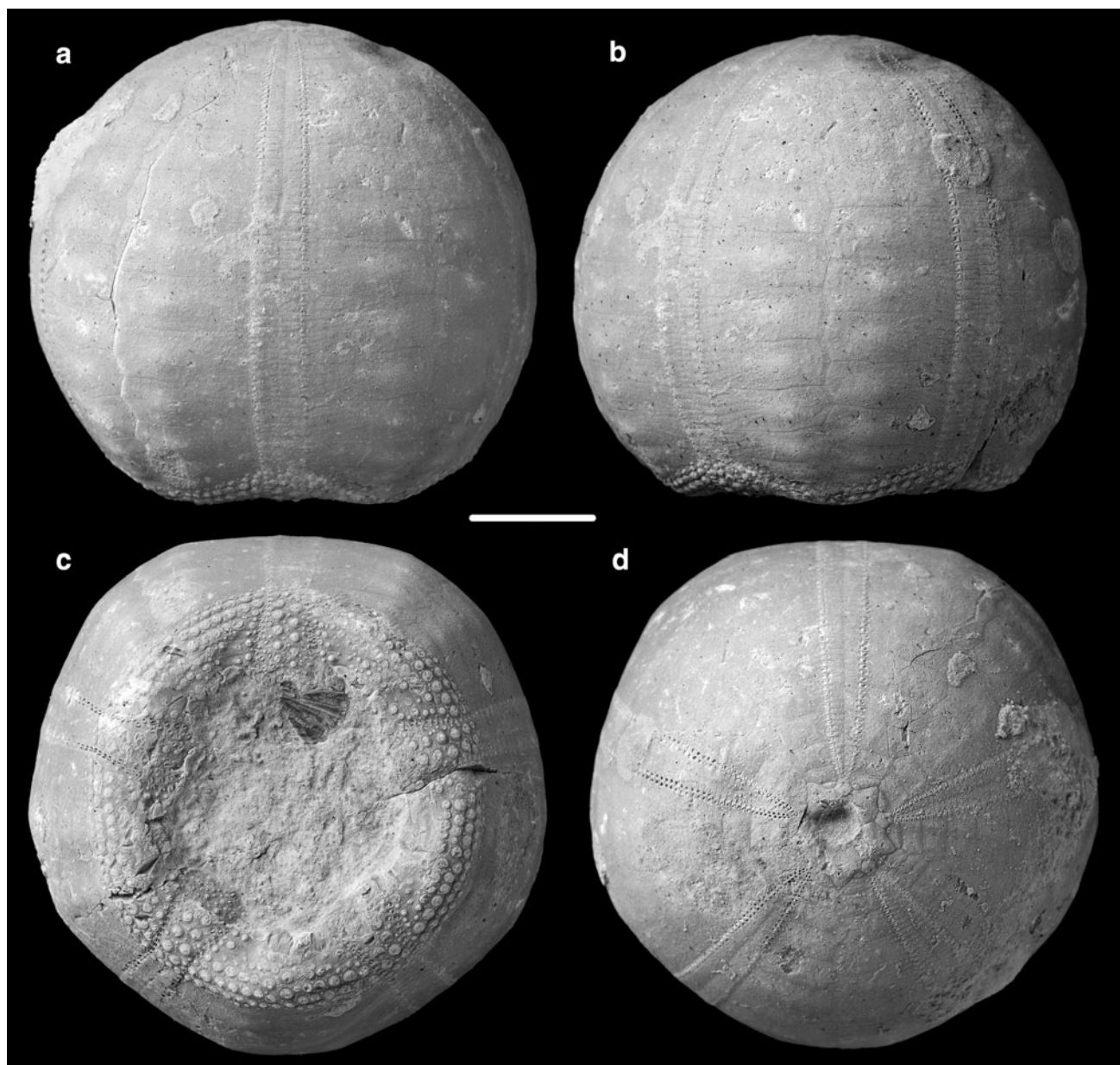


Fig. 2 *Gymnodiadema hessi* sp. nov. NHM EE13923 (holotype), Bajocian, Enjil, Morocco. **a** Lateral view (ambulacral), **b** lateral view (interambulacral), **c** oral view, **d** apical view. Scale bar 10 mm

in the de Loriol collection housed in the Museum de Histoire Naturelle, Geneva; see <http://www.nhm.ac.uk/research-curation/research/projects/echinoid-directory/taxa/taxon.jsp?id=1486>) has been studied and confirms de Loriol's observations. However, the discovery of well-preserved material of a new species of *Gymnodiadema* from the Bajocian of Morocco, *G. hessi*, provides a much fuller understanding of the morphology of this enigmatic taxon.

As de Loriol (1884, 1890) correctly noted the test of *Gymnodiadema* is almost spherical, with a height that is almost as great as its diameter (Fig. 2). The ambitus lies around mid-height and the oral surface is slightly flattened.

The apical disc is small and dicyclic with large, rather pointed genital plates and small, pentagonal and projecting ocular plates (Fig. 3a–c). Apical disc plates lie flush with the corona and are firmly bound to it. The genital and ocular plates are smooth and devoid of tubercles. Unusually, the hydropores are not confined to genital plate 2, but are scattered across adjacent genital and ocular plates (Fig. 3a–c).

The ambulacra are very narrow and parallel-sided over most of the test from the apex to below the ambitus (Fig. 2), but on the oral surface they rapidly expand to form short, broad phyllodes (Fig. 3d). Plating above the

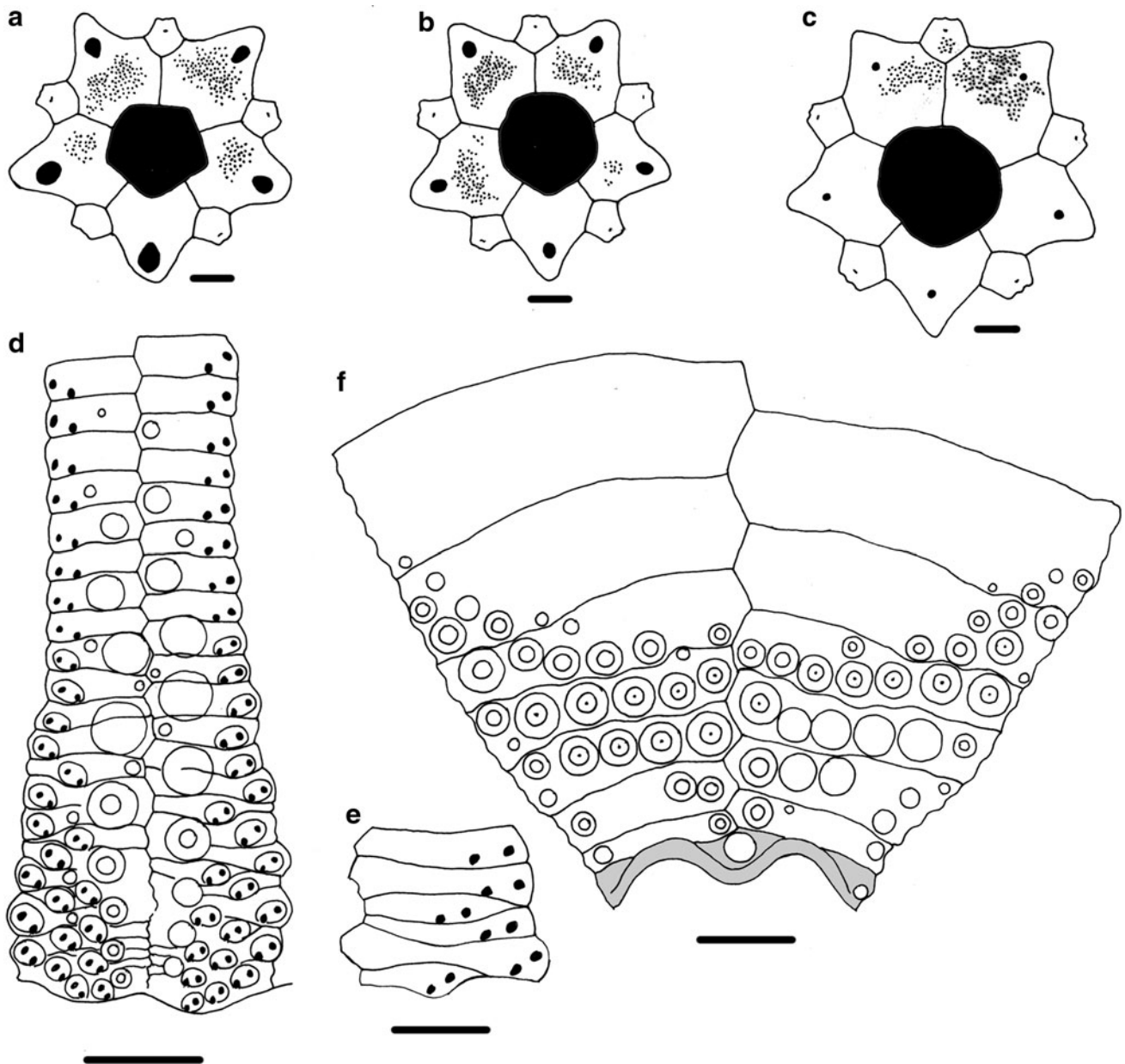


Fig. 3 *Gymnodiadema hessi* sp. nov.; Bajocian, Enfil, Morocco. Camera lucida drawings of plating. Apical disc plating: **a** NHM EE13924 (paratype) **b** NHM EE13925 (paratype), **c** NHM EE13923 (holotype). Ambulacral plating: **d** NHM EE13924 (paratype) from subambital region to peristome, **e** NHM EE13925 (paratype) detail of

two compound plates in phyllode region. **f** Adoral interambulacral plating, NHM EE13924 (paratype), with basicoronal plate shaded grey (basicoronal tubercle in white). Scale bars **a–c** 1 mm, **e** 2 mm, **d**, **f** 5 mm

phyllodes is simple, being composed of a succession of identical elements that meet along a zig-zagged median suture line (Fig. 3d). The pore-pairs in this zone are moderately large, set slightly oblique and have no peripodial zone. However, as the test curves onto the oral surface the ambulacra broaden and plate compounding develops (Fig. 3d). Here plating is trigeminate with a single large, perforate, non-crenulate tubercle overlying two of the three elements. Plate compounding is in the diadematid style,

with a larger median element flanked by smaller upper and lower elements (Fig. 3e). As the phyllode develops adorally these upper and lower elements become progressively occluded from the perradial suture. The pore-pairs in the phyllodes are strongly differentiated from those above in that they are set at a highly oblique angle, are comparatively much smaller pores and are surrounded by large, well-developed muscle attachment rims. Ambulacral tubercles are confined to the adoral region. Tubercles are

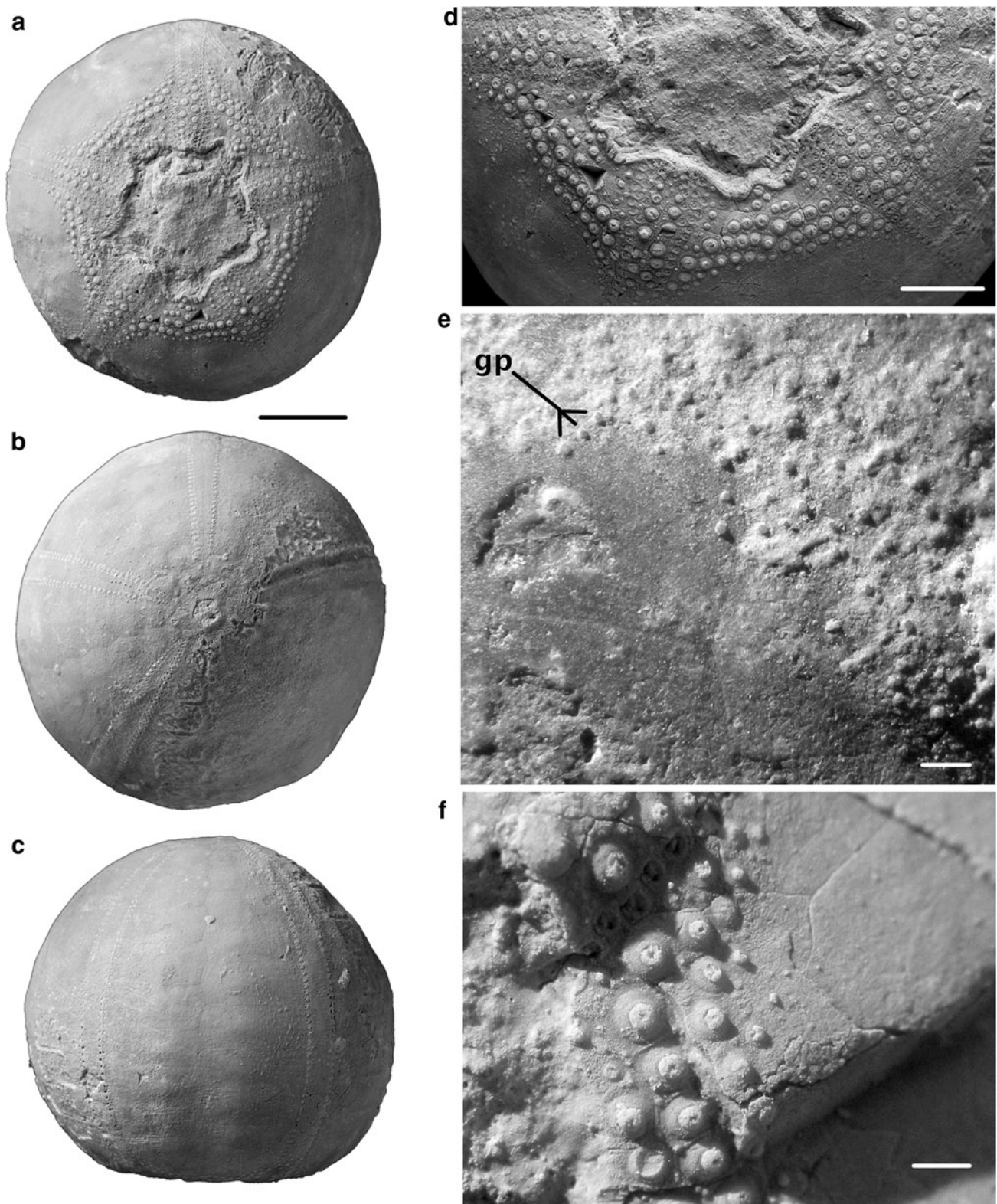


Fig. 4 *Gymnodiadema hessi* sp. nov.; Bajocian, Enjil, Morocco. NHM EE13924 (paratype): **a** oral view, **b** apical view, **c** lateral view, **d** detail of peristomial region. **e** NHM EE13923 (holotype); detail of supra-ambital interambulacral plates in unworn region showing

numerous glassy papillae (*gp*). **f** NHM EE13925 detail showing adoral tubercles (peristome to left). Scale bars **a–c** 10 mm, **d** 5 mm, **e**, **f** 1 mm

well developed around the outer zone of the oral surface, but rapidly diminish in size above the phyllode zone and disappear well before the ambitus is reached. Tubercles also diminish in size towards the peristome creating a notable perradial naked zone (Fig. 3d). No deep sphaeridial pits are present, but in this perradial zone there is a distinctive column of tiny tubercles, one on the adoral perradial corner of each compound plate, forming a slightly offset median row. These are likely to be the sphaeridial attachment points.

Interambulacra are very broad by comparison and entirely devoid of tubercles outside the oral area (Fig. 2). Individual plates are wider than tall and covered in a fine epistroma from which numerous minute glassy papillae project (Fig. 4e). These papillae are never strictly aligned, but occur irregularly scattered across the plate surface about 5 deep so that the entire test above the oral surface would have been densely covered in these structures. At the outer edge of the oral surface primary tubercles appear, first along the adradial margin, but quickly expanding across the entire plate forming single well-defined rows (Figs. 2c, 3f, 4a, d). There is a single basicoronal plate that forms the adoral edge and which bears a single centrally placed tubercle (Fig. 3f). As correctly described by de Loriol, all tubercles are perforate and non-crenulate (Fig. 4f). Buccal notches are well developed and are rather open and U-shaped in outline. The interambulacral zones immediately behind these are tubercle free, but there is no thickened tag developed (Fig. 4d). Spines, lantern and perignathic girdle all remain unknown.

Magnosia (Figs. 5, 6)

Contemporary with *Gymnodiadema* in both Portugal and Morocco are species of another putative arbacioid, *Magnosia*. The oldest known representative of this genus is *Magnosia termieri*, first described by Lambert (1931) from the Bajocian of Algeria. New material recently collected from the Bajocian of Morocco provides additional information about the morphology of this poorly understood taxon.

The test of *Magnosia termieri* is tall hemispherical in shape with a flattened oral surface and the ambitus situated below mid-height (Fig. 5a–c). Like *Gymnodiadema*, it has a small dicyclic apical disc with similar shaped genital and ocular plates (Fig. 6a). The disc plates are without tubercles and hydropores are entirely confined to genital plate 2 in all specimens available. Genital plate 2 is slightly larger than the other genital plates. The periproct is subcircular in outline and proportionally relatively large. Ambulacra are narrow and straight, and expand strongly into broad phyllodes on the oral surface (Figs. 5d, 6c), as in *Gymnodiadema*. *M. termieri* is immediately distinguishable from

the near contemporary species *M. forbesi* (Wright 1851) by its much more extensively developed phyllodes (compare Figs. 6c, d). Trigeminate compound plating is developed throughout, and follows a goniopygid-style pattern (Fig. 6b). There are three elements to each compound plate, with the lowest reduced to a small demiplate, the upper narrowing towards the perradius which it may or may not reach, and the middle element the largest. Compound plates at the ambitus and above bear alternately one or two small subequal tubercles offset on successive plates in a column (Fig. 5c). On the oral surface ambulacral tubercles are larger and only a single row is developed in each half-ambulacrum. Oral tubercles decrease in size towards the peristome. There is a distinct change in the size and shape of the pore-pairs between the oral and adapical surfaces with the adapical pore-pairs wider and with a larger interporal partition, and the oral pore-pairs small, circular and with a very large surrounding muscle platform.

Interambulacral zones are much wider and composed of a large number of relatively low and wide elements. Above the ambitus each plate has two or three moderately well-defined rows of small, subequal tubercles, no larger than 0.25 mm in diameter. These have a prominent glassy mamelon sitting atop of a low boss and are almost certainly spine bearing. A few granules are scattered in amongst these. There is a sharp and distinct change in the size and density of tubercles at the ambitus as well as the height of the plates (Fig. 5c). Tubercles around the outer edge of the oral surface are significantly larger than those above and a single row of tubercles occupies each plate. Tubercles are imperforate and non-crenulate wherever they are unworn.

The peristome is hardly sunken and its rim indented by relatively wide U-shaped buccal notches without an associated tag (Fig. 5d). The test behind the buccal notches has only sparse secondary granules. A single basicoronal plate with a median tubercle forms the adoral border of each interambulacral zone (Fig. 6e). This appears to occupy only the central tongue-like zone between the two buccal slits. Spines, lantern and perignathic girdle remain unknown.

Dubarechinus (Figs. 7, 8)

The genus *Dubarechinus* is recorded only from the Lower Jurassic (late Pliensbachian) of Morocco (Lambert 1937; Vadet and Nicolleau 2005). Lambert initially included two species, *D. despujolsi* and *D. termieri*, but, as these differ in size only, Vadet and Nicolleau (2005) later synonymized these. *Dubarechinus* has a spherical test that is almost as tall as wide and, like *Gymnodiadema*, its ambitus lies at about mid-height (Fig. 7c). The apical disc is firmly attached to the corona and is dicyclic in form, with a relatively small, subpentagonal periproct (Fig. 8a). Genital plates are large and do not project; each is pierced by a

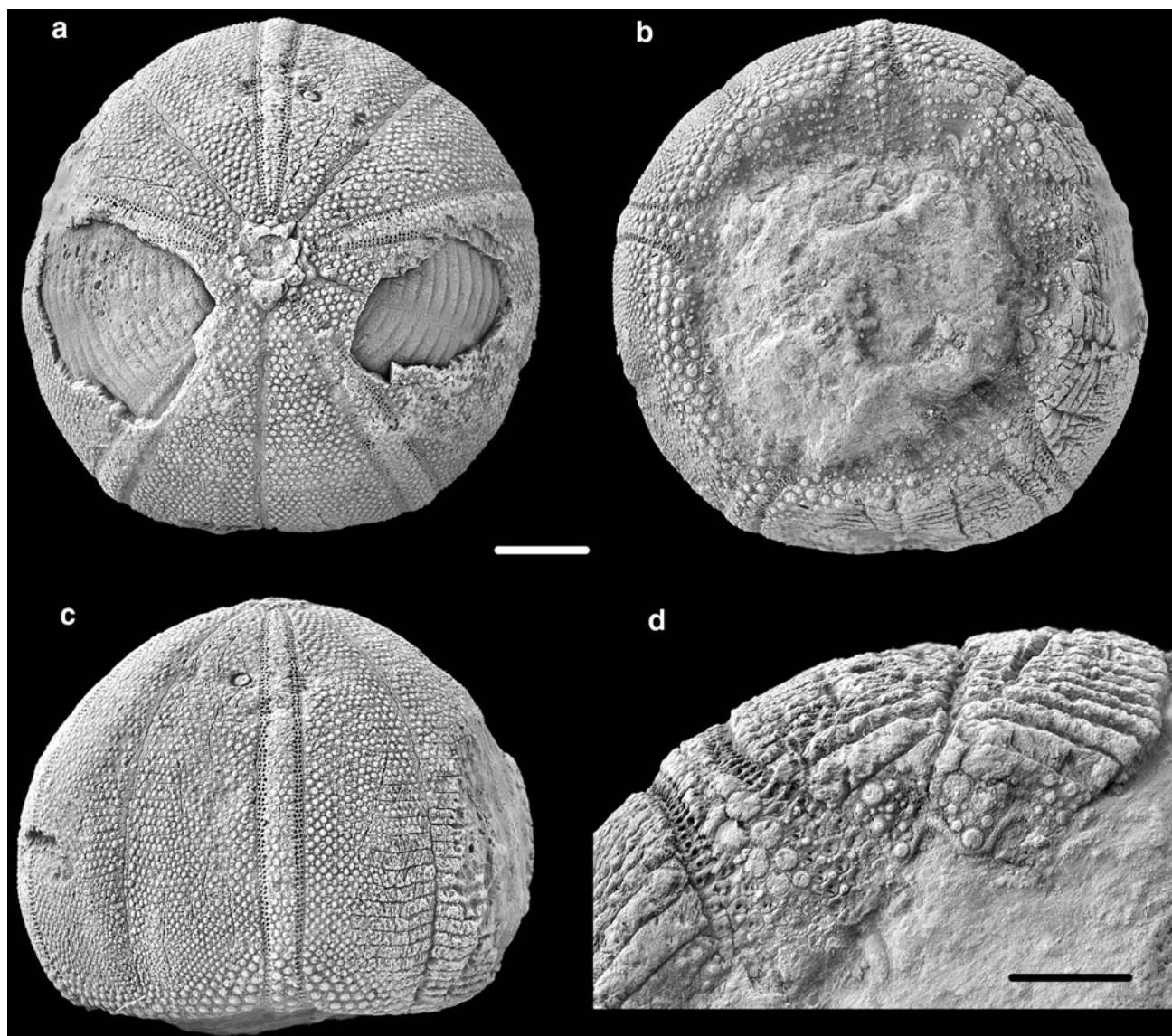


Fig. 5 *Magnosia termieri* Lambert, 1931; Bajocian, near Enjil, Morocco. NHM EE13928: **a** apical view, **b** oral view, **c** lateral view (ambulacral). **d** NHM EE13929 detail of peristomial region showing

prominent basicoronal interambulacral tubercle between buccal notches. Scale bars **a–c** 5 mm, **d** 2 mm

small subcentral gonopore. Ocular plates are small, pentagonal and project. All disc plates appear to be smooth and tubercle free, although all material is abraded to a lesser or greater extent. Ambulacra are narrow and constructed of simple plates, except close to the peristome where plating becomes trigeminate in an acrosaleniid style (Fig. 8b): all elements reach the perradius. Primary tubercles are developed only below the ambitus, are perforate and strongly crenulate, and are accompanied by rather dense granulation (Fig. 7a). In these oral compound plates, a primary tubercle covers just two of the three elements. Pore-pairs are slightly larger above the ambitus and the

most adoral six or nine pore-pairs are offset to form weak phyllodes (Fig. 8b). No sphaeridial pits are present.

Interambulacral zones are wide and plates are relatively tall and show no crowding and narrowing at the ambitus (Fig. 7c). A narrow basicoronal plate is just visible externally, forming a thin, but continuous edge to the peristome (Fig. 8b). This plate comprises only the thickened rim of the buccal notches and there is no median tubercle developed on this element. Other adoral plates bear a single subcentral primary tubercle that is perforate and crenulated (Fig. 7a). These tubercles are widely spaced and occupy only a small part of the plate height; tubercles are absent

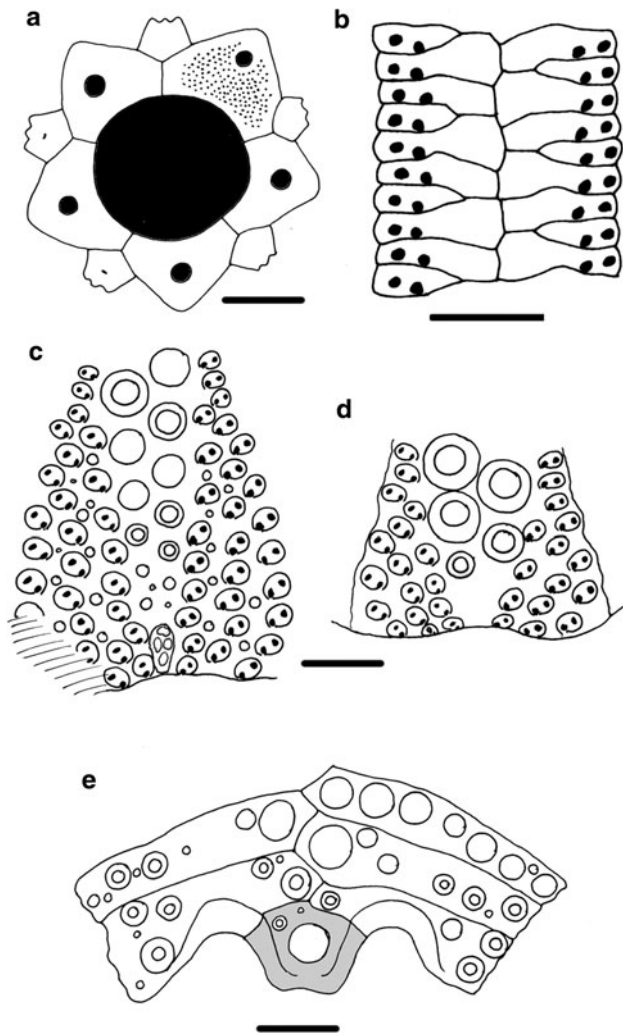


Fig. 6 Camera lucida drawings of plating in *Magnosia*. *Magnosia termieri* Lambert, 1931; Bajocian, Enjil, Morocco: NHM EE13928: **a** apical disc, **b** ambital ambulacral plate compounding, **c** adoral phyllode arrangement, **e** NHM EE13929; adoral interambulacral plating with basicoronal plate shaded (except for basicoronal tubercle). **d** *Magnosia forbesi* (Wright, 1851), NHM 40004, *Garrantiana garantiana* Zone, late Bajocian of Dundry, Somerset, UK; detail of phyllode for comparison

from ambital and adapical plates. The remainder of oral plates is covered in small uniform granules. The peristome is small, circular and not in the slightest depressed. It is indented by double buccal notches that are shallow, but clearly defined. Spine and lantern morphology remains unknown.

Apomorphies of crown group Arbacioida

A number of characters help distinguish the extant Arbacioida from their closest living relatives. Each is discussed

in turn with comments on the character's wider distribution amongst fossil forms.

1. Presence of a basicoronal plate

In the development of euechinoids plating in the interambulacral zones begins with a single element, the basicoronal plate (e.g. Gordon 1926). While this plate is retained in the tests of all irregular echinoids, it is generally resorbed, or at least reduced and internalized, in most regular echinoids. Only in Arbacioida, amongst regular echinoids, does the basicoronal plate remain external and visible, being especially prominent in the smaller, deep-water forms (e.g. Döderlein 1906; Agassiz and Clark 1908; Mortensen 1935). In most arbaciids, this basicoronal plate carries a single, prominent tubercle positioned centrally. In *Arbacia* and *Tetrapyrgus*, however, while the basicoronal plate is retained into adulthood, it is less evident, as there is no obvious median tubercle and suture lines can be difficult to trace.

Amongst fossil genera a basicoronal plate is clearly evident in *Noetlingaster* (Smith 1995), *Codiopsis* (Smith and Rader 2009), *Gymnodiadema* (this paper), *Magnosia* (this paper) and *Eucosmechinus*. It is present but much reduced and without a primary tubercle in *Dubarechinus* (this paper) and in *Glypticus*, where a tiny wedge-shaped element can sometimes be made out bordering the peristome in the interradius. No trace of the basicoronal plate remains in the adult tests of *Goniopyrgus*, *Cottaldia*, *Glyphopneustes*, *Mimiosalenia* and non-arbacioids such as *Psephechinus* and *Hemipedinia*.

2. Sphaeridia positioned in pits at the perradius

Sphaeridia are small, club-like appendages that function as balance receptors and are developed only in euechinoids. They can be positioned either along the mid-line of the ambulacra, between the two columns of primary tubercles, as in all extant Arbaciidae or sandwiched between the pore zone and the perradial band of tubercles, as in most other regular euechinoids (see Kroh and Smith 2010). Furthermore, sphaeridia are situated in obvious pits in the extant Arbaciidae, cassiduloids, clypeasteroids (where they are often fully enclosed within the plates), and in some extinct Salenioida and Aspidodiadematoida, whereas they attach to superficial granules, sometimes with just the slightest trace of a dimple, in all other taxa. In all extant Arbaciidae, with the exception of *Coelopleurus*, there is but a single sphaeridial pit in each ambulacrum, which is found centrally near the peristome edge. *Coelopleurus* differs in having a short, slightly offset row of 4–6 pits lying along its perradial suture close to the peristome.

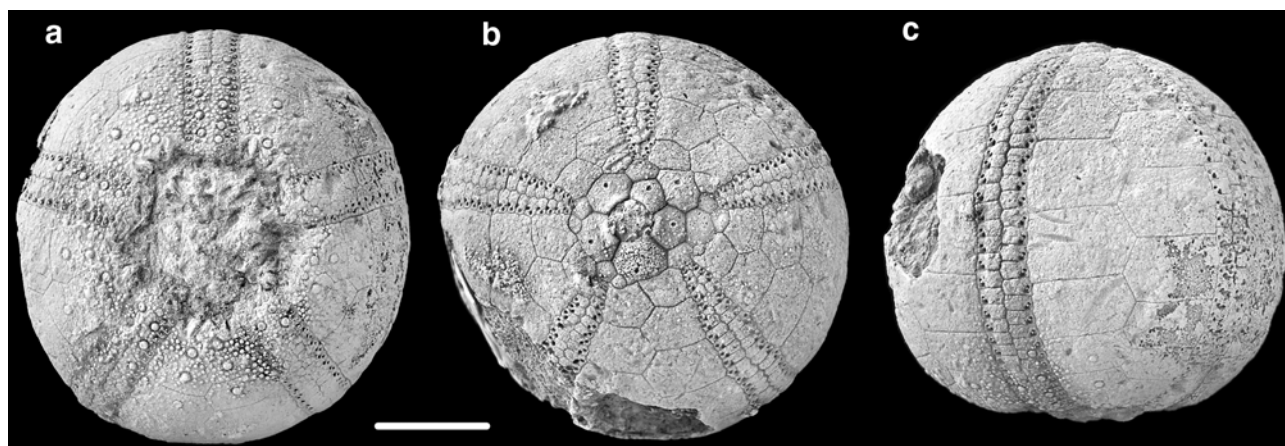


Fig. 7 *Dubarechinus despujolsi* Lambert, 1937, NHM E76732f; Upper Pliensbachian, 4 km NE of Amellago, Morocco; **a** oral view, **b** apical view, **c** lateral view. Scale bar 5 mm

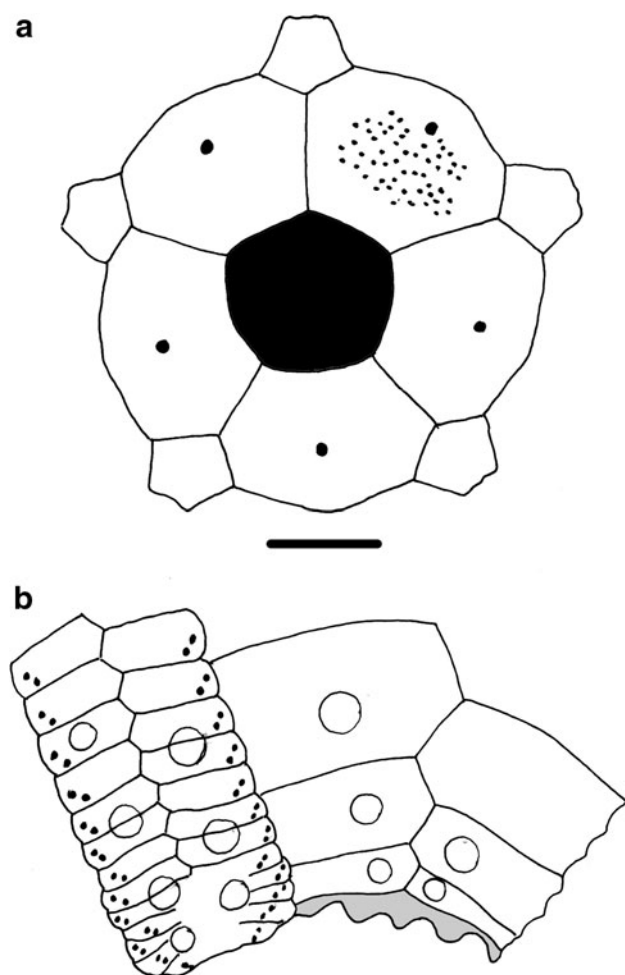


Fig. 8 Camera lucida drawings of plating in *Dubarechinus despujolsi* Lambert, 1937, NHM E76732a, from the Upper Pliensbachian, 4 km NE of Amellago, Morocco. **a** Apical disc, **b** adoral plating showing phyllode and basicoronal plate (shaded in grey). Scale bar 1 mm

In fossil material, the presence of sphaeridia is usually only demonstrable when they are housed in pits. Sphaeridial pits are present in *Noetlingaster*, where a short adoral row of pits is found along the perradius (Smith 1995). A similar pattern is evident in many fossil species of *Coelopleurus*. *Codiopsis* has a single median tubercle in each ambulacrum positioned close to the peristome edge and accompanied by a slight depression on its adapical side. This is likely to be the sphaeridial attachment site. *Gymnodiadema* has no sphaeridial pits, but it does have a series of small distinct granules that is developed down the perradius in the obvious naked zone: these might be sphaeridial tubercles. *Glyphopneustes* has a double series of shallow sphaeridial pits, but these form two adradial columns lying between the two bands of pore-pairs and the median zone of perradial tubercles. This is the position sphaeridia occupy in non-arbacioid taxa. No trace of sphaeridial pits can be found in *Magnosia*, *Eucosmechinus*, *Glypicus*, *Goniopygus*, *Acropeltis*, *Dubarechinus* or *Cottaldia*.

3. Aboral tubercles highly reduced or absent

Although not all modern arbaciids have a strong oral–aboral differentiation in tubercle pattern, this is a distinctive feature of many. *Pygmaeocidaris*, *Dialithocidaris*, *Habrocidaris*, *Podocidaris*, *Arbaciella* and some modern species of *Coelopleurus* all have tubercles confined to the oral surface—their upper surface is devoid of all tubercles and spines. Tubercles in other *Coelopleurus* species and in *Arbacia* and *Tetrapygus* continue aborally, but there is often a wide, median, naked zone and the tubercle pattern differs strongly between the oral and aboral surfaces in *Coelopleurus*. No other extant regular echinoid group ever develops such a clear oral–aboral demarcation in tuberculation pattern.

Of the fossil members only *Gymnodiadema*, *Codiopsis* and possibly *Dubarechinus* entirely lack aboral tubercles. *Glypticus*, *Pleiocyphus* and *Brochechinus*, however, show a sharp change in tuberculation pattern, with well-developed tubercles below the ambitus and only very much reduced primary tubercles continuing to the apex. There is also an obvious, but less drastic change in tuberculation pattern at the ambitus in *Magnosia* and *Eucosmechinus*. In *Acropeltis*, *Goniopygus*, *Mimiosalenia* and *Glyphopneustes* tubercles show no clear oral–aboral differentiation being well developed on all plates: tubercles are largest at the ambitus and decrease in size gradually both adorally and adapically.

4. Presence of well-developed epistroma covering the surface of plates

Epistroma is the term given to dense wart-like projections developed on the outer surface of plates. In extant arbaciids, this takes two forms, as glassy tubercles or papillae composed of imperforate calcite that project from the test-like stumpy spines, and as lower, more irregular series of bumps and nodes termed epistroma which generally retain stereom perforations. Glassy papillae occur in some irregular echinoids (echinoneioids, clypeasteroids) but are otherwise restricted to arbaciids amongst the modern fauna. They are developed aborally in all the modern deep-sea forms, where they are either organized into well-defined horizontal rows (*Pygmaeocidaris*, *Dialithocidaris*, *Podicidaris*, *Arbaciella*) or lie irregularly scattered over the plates (*Habrocidaris*). Glassy papillae are also found in some *Coelopleurus* where they are often arranged as two columns, one on either side of the broad naked interradiial zone that is developed adapically. The test surface in *Coelopleurus*, *Arbacia* and *Tetrapygyus* has a fine ornament of epistroma wherever there are no tubercles.

Glassy papillae are well developed in *Codiopsis* and *Gymnodiadema* where they lie scattered over the plate surface, as in *Habrocidaris*. Poor preservation makes it impossible to tell whether *Dubarechinus* has these also, but they are definitely absent from all other genera. A very coarse epistroma is developed over the entire aboral surface in *Glypticus*, *Pleiocyphus* and *Brochechinus* giving these taxa a very distinctive appearance. A fine epistroma is present in *Noetlingaster* giving the plates a distinctive reticulate ornamentation (Smith 1995). Epistroma is rarely present along the interradiial suture of supra-ambital plates in *Magnosia* and is completely absent from *Acropeltis*, *Goniopygus*, *Mimiosalenia*, *Atopechinus* and *Glyphopneustes*.

5. Apical disc dicyclic and free of tubercles

In extant arbaciids, the apical disc is always firmly bound to the corona and plating is mostly dicyclic (it becomes

hemicyclic in adult *Tetrapygyus* and rarely in *Arbacia*). Furthermore, the disc is distinctive in being completely tubercle free, which is in marked contrast with those of most other regular echinoids.

Noetlingaster, *Codiopsis*, *Gymnodiadema*, *Magnosia*, *Eucosmechinus*, *Glypticus*, *Pleiocyphus* and *Brochechinus* also have dicyclic apical discs devoid of tubercles. In contrast, while the discs of *Acropeltis*, *Goniopygus*, *Mimiosalenia* and *Glyphopneustes* are dicyclic and firmly bound to the corona, these all bear tubercles. *Acropeltis* has a single primary tubercle central on each genital plate while the others have perianal tubercles usually situated in pits around the rim of the periproct. *Arbia* and *Cottaldia* discs are unusual in having scattered secondary tubercles.

Another aspect of the apical disc is the presence of sutural pits. These are absent from all extant arbacioids, but are developed in *Goniopygus*, *Mimiosalenia* and *Glyphopneustes*. Superficially, the disc of *Glypticus*, *Pleiocyphus* and *Brochechinus* also appears pitted, but this ‘pitting’ is created by the thick epistromal overgrowth, not by excavation into the plate surface.

6. Anal opening covered by 4–6 valve-like plates

This is a feature seen in all extant arbaciids, but unfortunately is rarely preserved and remains unreported from any fossil arbacioid taxa.

7. Tubercles in ambulacral and interambulacral zones similar in size; interambulacral zones with rows of subequal tubercles

The arrangement of tubercles in extant arbaciids is rather consistent. Those in ambulacral and interambulacral zones are developed to the same extent and those on interambulacral plates are set into rows. This is the case in *Tetrapygyus* and *Arbacia* where there are many tubercles to a row. In the deep-sea forms, there are typically just two subequal tubercles on adoral plates. *Coelopleurus* can have just a single primary tubercle on adoral plates, but usually has two.

Well-developed rows of subequal tubercles are developed in *Noetlingaster*, *Codiopsis*, *Arbia*, *Magnosia*, *Eucosmechinus* and *Gymnodiadema*. However, *Dubarechinus*, *Glypticus*, *Acropeltis*, *Brochechinus*, *Pleiocyphus*, *Goniopygus*, *Mimiosalenia* and *Glyphopneustes* only ever have a single primary tubercle on interambulacral plates. Furthermore, in *Goniopygus*, *Mimiosalenia* and *Glyphopneustes*, the ambulacral tubercles are always considerably smaller than those in a similar position in interambulacral zones. The fossil *Murravechinus* (Philip 1965), a subgenus of *Coelopleurus*, is unusual in having ambulacral tubercles very much larger than interambulacral tubercles.

8. Tubercles imperforate and non-crenulate

Although by no means unique to arbaciids, all extant members have imperforate and non-crenulate tubercles. The same is true for most of the fossil genera under discussion with the exception of *Gymnodiadema*, *Dubarechinus* and *Cottaldia*. *Gymnodiadema* has perforate tubercles with a clear non-crenulate parapet surround the mamelon (Fig. 4f), while tubercles of *Dubarechinus* are both perforate and crenulate. The tubercles in *Cottaldia* are, for the most part, imperforate and non-crenulate, but the oral tubercles in large individuals are definitely perforate (Smith and Wright 1996, text-fig. 113).

9. Oral and aboral tube-feet are strongly differentiated

Unlike camarodonts, arbacioids often show a strong differentiation between oral and aboral tube feet that is also matched in the morphology of their pore-pairs. In *Arbacia*, the aboral tube-feet are broad and morphologically specialized for gaseous exchange, whereas their oral tube-feet are highly muscular and suckered (Smith 1978). These differences are reflected in the morphology of the pore-pairs, with aboral pore-pairs being broad with a wide interporal partition, and oral pore-pairs being small, circular and with a wide periporal muscle attachment area. Large phyllodes (expanded adoral zones of tube-feet) are developed in *Arbacia* and *Tetrapygyus* but not in *Coelopleurus* or any of the deep-sea forms. Only *Sexpyga* is reported to have weak phyllodes. Tube-feet and pore-pairs are clearly differentiated around the test in *Arbacia*, *Tetrapygyus* and *Coelopleurus*. However, in the other modern deep-sea forms, all tube-feet remain small and undeveloped and no differentiation is apparent.

Amongst fossil taxa, there is a clear differentiation of pore-pairs evident in *Noetlingaster*, *Codiopsis*, *Gymnodiadema*, *Magnosia*, *Glypticus*, and possibly *Arbia*. Strong phyllodes are developed in *Codiopsis*, *Gymnodiadema*, *Magnosia* and *Eucosmechinus*, weak phyllodes are present in *Dubarechinus*, *Glypticus*, *Pleiocyphus*, *Brochechinus* and *Acropeltis* and are absent in *Noetlingaster* and *Arbia*.

10. Ambulacral compounding in the arbaciid style

Arbacia has trigeminate plate compounding with a large middle element and upper and lower elements reduced to small demiplates and this is what is typically taken as arbaciid-style compounding. Exactly the same pattern is evident in *Coelopleurus* and *Tetrapygyus*, although in that taxon, there are four elements (three demiplates) to a compound plate. Plate compounding in deep-sea forms is less developed, possibly because of their small size, and often a simple plate alternates with a pair of elements bearing a primary tubercle (Mortensen 1935).

Ambulacral plate compounding is diverse amongst fossil representatives. *Codiopsis* has true arbaciid plate compounding throughout, as does *Noetlingaster*, although one of its demiplates often becomes entirely occluded. However, *Magnosia*, *Goniopygus*, *Acropeltis* and *Glypticus* have plate compounding in which only the lower element is a demiplate while the upper element is reduced in size but not cut off from the perradius. *Gymnodiadema* and *Dubarechinus* are unique in having entirely simple plating aborally.

Cladistic analysis of the principal arbacioid taxa

It is clear from the discussion above that the taxa currently placed in the arbacioids vary tremendously in the degree to which they display crown-group arbaciid characters. Some, like *Noetlingaster* and *Codiopsis*, share with the crown-group a large number of derived characters, others, such as *Goniopygus* and *Glyphopneustes*, share almost none. To clarify relationships amongst the various genera previously assigned to the Arbacioida I carried out a cladistic analysis. Included were the genera *Acropeltis*, *Arbacia*, *Arbia*, *Baueria*, *Brochechinus*, *Codiopsis*, *Coelopleurus*, *Cottaldia*, *Dubarechinus*, *Eucosmechinus*, *Glyphopneustes*, *Glypticus*, *Goniopygus*, *Gymnodiadema*, *Magnosia*, *Mimosalenia*, *Noetlingaster*, *Panglyptus*, *Pleiocyphus* and *Tetrapygyus*, all of which were scored on material that had been examined personally. Five taxa, *Arbaciella*, *Pygmaeocidaris*, *Dialithocidaris*, *Podocidaris* and *Sexpyga* were also included, but scored based on the descriptions in Döderlein (1906), Agassiz and Clark (1908), Mortensen (1935) and Shigei (1975). Genera that have not personally been examined, or which are based on such poor material as to remain poorly known, such as *Acrosaster* and *Atopechinus*, are excluded from the analysis. To root the tree I included three outgroups, a primitive pedinoid, *Hemipedina*, a primitive pseudodiadematid, *Stereopyga*, and a primitive stomechinid, *Psephechinus*. A description of the characters used together with the data matrix is given in the appendix. Table 1 lists the sources of data used for assembling the data matrix.

The data matrix was analysed using the program PAUP* (Swofford 2005) with all characters given equal weight. A heuristic search was carried out with 100 random addition replicates, which generated 35 equally parsimonious trees of length 82. All 100 random addition replicates found the same island of trees. A strict consensus of these trees is shown in Fig. 9b. The characters were then reweighed by their mean rescaled consistency index and the analysis repeated. This resulted in two trees, whose strict consensus is shown in Fig. 9a, and which differs only in being slightly more resolved, placing *Podocidaris* as sister group to

Table 1

Genus	Species	Source of data
<i>Acropeltis</i>	<i>aequituberculata</i> (Agassiz, in Agassiz & Desor, 1846)	MNHN A20351
<i>Arbacia</i>	<i>lixula</i> (Linnaeus, 1758)	NHM EE8657
<i>Arbaciella</i>	<i>elegans</i> Mortensen, 1910	Mortensen (1935), Smith (2005)
<i>Arbia</i>	<i>aldrichi</i> (Clark, 1915)	Cooke (1959)
<i>Atopechinus</i>	<i>cellensis</i> Thiery, 1928	MNHN J00915
<i>Baueria</i>	<i>rousseli</i> (Cotteau, 1886)	ULPC EM40589
<i>Brochechinus</i>	<i>elizae</i> Lambert and Thiery, 1908	MNHN L16.49
<i>Codiopsis</i>	<i>doma</i> (Desmarest, 1825)	NHM 57861
<i>Coelopleurus</i>	<i>exquisitus</i> Coppard and Schultz, 2006	NHM 2006_599; MNHN EcEh 1282; Coppard and Schultz (2006)
<i>Cottaldia</i>	<i>benettiae</i> (Koenig, 1820)	NHM E1595, MNHN L19572
<i>Dialithocidaris</i>	<i>gemmifera</i> Agassiz, 1898	Mortensen (1935)
<i>Dubarechinus</i>	<i>despujolsi</i> Lambert, 1937	NHM EE76732a-f
<i>Eucosmechinus</i>	<i>decoratus</i> (Agassiz, in Agassiz & Desor, 1847)	MNHN R65697
<i>Glyphopneustes</i>	<i>hattaensis</i> Ali, 1992	NHM EE3945
<i>Glypticus</i>	<i>hieroglyphicus</i> (Goldfuss, 1826)	NHM E79157
<i>Goniopygus</i>	<i>peltatus</i> Agassiz, 1838	MNHN R65689
<i>Gymnodiadema</i>	<i>hessi</i> sp. nov.	NHM EE13923-13927
<i>Habrocidaris</i>	<i>scutata</i> (Agassiz, 1880)	Mortensen (1935)
<i>Hemipedina</i>	<i>etheridgei</i> (Wright, 1855)	NHM E1593
<i>Magnosia</i>	<i>termieri</i> Lambert, 1931	NHM EE139238-13929
<i>Mimiosalenia</i>	<i>quinquetuberculata</i> Smith, 1995	NHM EE3981
<i>Noetlingaster</i>	<i>sphericus</i> (Ali, 1992)	NHM EE3710, EE3659
<i>Panglyptus</i>	<i>douvillei</i> (Lambert, 1905)	ULPC EM12138
<i>Phymopedina</i>	<i>marchamensis</i> (Wright, 1855)	NHM 75923
<i>Pleiocyphus</i>	<i>regularis</i> (Etallon, 1858)	MNHN collections
<i>Pleurodiadema</i>	<i>sturtzi</i> (Moesch, 1867); <i>gauthieri</i> Cotteau, 1875	MNHN J06035, J01518
<i>Podocidaris</i>	<i>sculpta</i> Agassiz, 1869	Agassiz (1872), Mortensen (1935)
<i>Psephechinus</i>	<i>quoniami</i> Gauthier, 1903	NHM EE14013-14019
<i>Pygmaeocidaris</i>	<i>prionigera</i> (Agassiz, 1879)	Mortensen (1935)
<i>Sexpyga</i>	<i>soyoae</i> Shigei, 1975	Shigei (1975)
<i>Stereopyga</i>	<i>moorei</i> (Wright, 1854)	NHM E1056
<i>Tetrapygyus</i>	<i>niger</i> (Molina, 1782)	Smith (2005), Mortensen (1935)

Habrocidaris and identifying the clade (*Dialithocidaris* + *Sexpyga* + *Pygmaeocidaris*). Bremer support values, however, were low for the entire tree with only two clades, the Glypticiidae and the Acropeltidae remaining in the consensus of trees just one step longer.

The phylogenetic analysis suggests that the living Arbaciidae form a well-defined clade characterized by the shared possession of sphaeridial pits situated medially in the ambulacra. The more basal members of this group lack aboral tubercles and spines, with *Arbacia* and *Tetrapygyus* as derived members. The late Cretaceous *Noetlingaster* falls within this crown-group as sister taxon to *Arbacia* and *Tetrapygyus*. This places crown group divergence as latest Cretaceous and suggests that the deep-water lineages split from their shallow water counterparts sometime in the late

Cretaceous. *Arbia* is another possible crown-group member, although the presence of sphaeridial pits in this taxon has yet to be confirmed and it has an aberrant apical disc tuberculation.

The immediate outgroup to crown-group arbacioids is the Cretaceous *Codiopsis*, which shares with crown-group members' derived arbacioid-style ambulacral plating. Arbacioid-style plate compounding is absent from all clades lower than *Codiopsis* in the cladogram. The Jurassic sister-group to *Codiopsis* is *Gymnodiadema*, which resembles *Codiopsis* in many details, including tuberculation pattern and the development of glassy papillae. However, it is primitive in having perforate rather than imperforate tubercles and in having simple ambulacral plating aborally. This clade shares with *Magnosia* and its

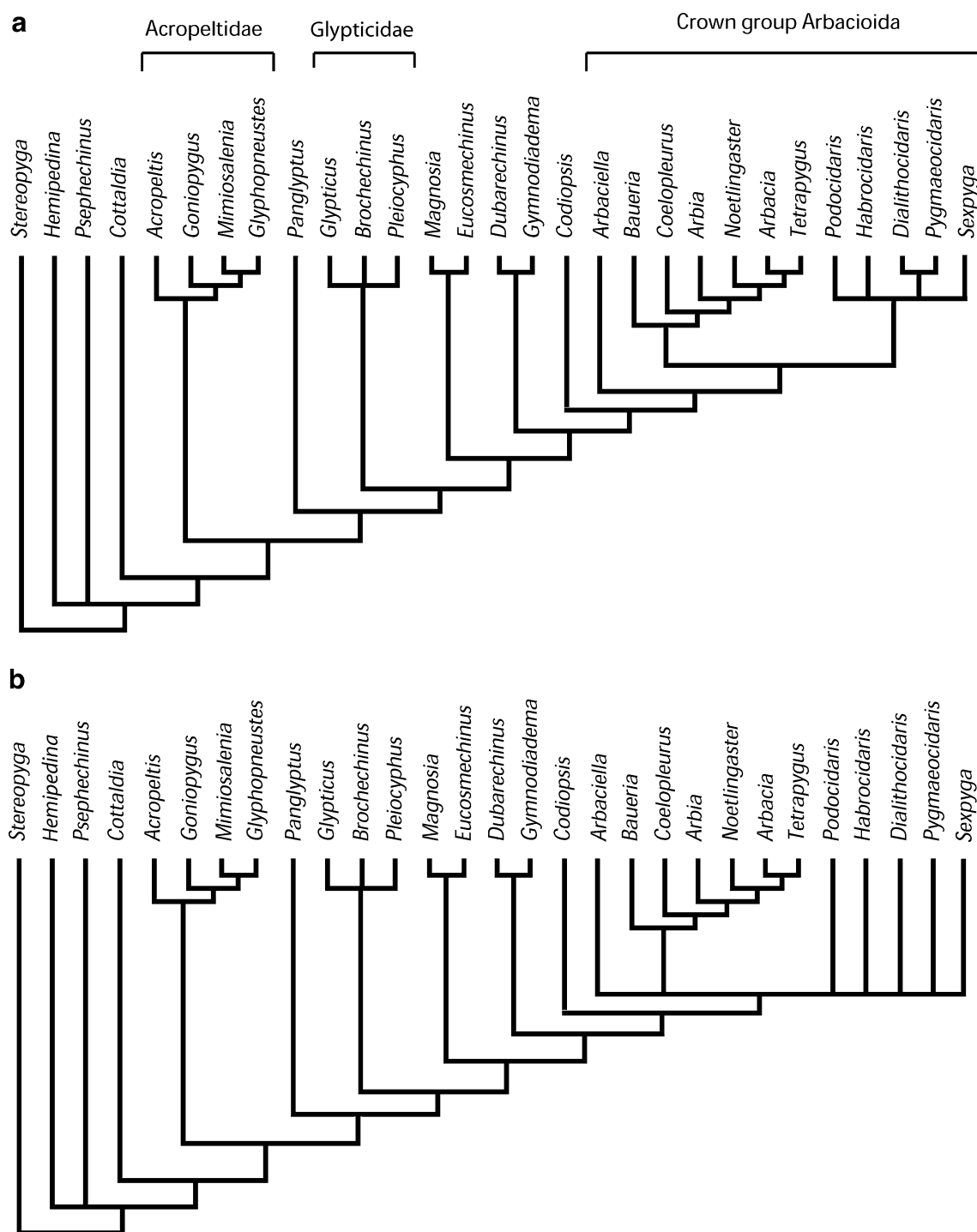


Fig. 9 **a** Strict consensus of the two equally parsimonious trees of length 32.53 derived from the 29-taxa and 31-character matrix given in the appendix after reweighting characters by their maximum retention index. **b** Strict consensus of the 35 trees, length 82 steps,

consistency index of 0.49, a retention index of 0.77 and a rescaled consistency index of 0.38, obtained from analysis of the equal-weighted data matrix

relatives the derived retention of a basicoronal plate, which was the first of the crown-group arbacioid synapomorphies to evolve. *Dubarechinus*, with its slender basicoronal plate suggests that arbaciids may extend back well into the Lower Jurassic. In this analysis, it is paired with

Gymnodiadema, both lacking aboral tubercles and both having perforate tuberculation. However, without more information on how widely developed the retention of a thin basicoronal plate is amongst other primitive regular echinoids from the Lower Jurassic, *Dubarechinus* can only

tentatively be associated with arbacioids at present as it has a very different pattern of tuberculation.

More basal groups may or may not be stem group members of the Arbacioida, but without much greater taxon sampling it is impossible to say which group they are more closely related to. This includes *Cottaldia* and the Acropeltidae, which both lack even a single diagnostic arbacioid character. In the Kroh and Smith (2010) analysis, Acropeltidae did group with Glypticidae and Arbaciidae rather than with any non-arbacioid taxon, and so may well represent a very early branch of their stem group.

Finally, the cladogram shows that arbacioids, like several other echinoid groups with deep-water representatives, could only have begun moving into the deep-sea from the late Cretaceous onwards. Stem group representatives are primarily shallow water forms, with *Gymnodiadema*, for example, being found in shallow patch-reef settings. The most crownward outgroup, *Codiopsis* is widely distributed in the Cretaceous and is found in peri-reefal habitats during the Lower Cretaceous, but moved into deeper water shelf chalks during the Upper Cretaceous. *Podocidaris mortenseni* (Lambert 1911) is the oldest fossil representative of the deep-water group and is found in shelf settings of early Middle Eocene in the Aude department of France. It is only, therefore, since the end of the Mesozoic that arbacioids have been able to move into deeper water settings, mirroring the situation seen in other echinoid groups such as holasteroids (Smith 2004; Smith and Stockley 2005).

Systematic palaeontology

Order Arbacioida Gregory, 1900

Stem group Arbacioida Gregory, 1900

Genus *Gymnodiadema* de Loriol, 1884, p. 4

Type species: *Gymnodiadema choffati* de Loriol, 1884, p. 606; Middle Jurassic (Callovian) of Portugal (see also de Loriol 1890, p. 100)

Other species: *G. hessi* sp. nov.; Bajocian, Middle Jurassic of Morocco (Central Atlas region)

Gymnodiadema hessi sp. nov. (Figs. 2, 3, 4).

Etymology: In honour of Hans Hess for his contribution to our understanding of Jurassic echinoids.

Types: Holotype NHM EE13923, paratypes NHM EE13924–13927, housed in the Natural History Museum, London, UK.

Occurrence: All material comes from a patch reef of late Bajocian age at Enjil, north of Midelt, Central Atlas Mountains, Morocco (Fig. 1; 33°15′31.4 N 004°31.10.8 W).

Diagnosis: A species of *Gymnodiadema* that has interambulacral tubercles arranged as transverse rows close to the peristome that do not form two clearly defined marginal columns running parallel with the ambulacra.

Description: Tests up to 46 mm in diameter and globular in shape with a circular outline. Test height only slightly less than test diameter (87–91% of diameter); ambitus at about mid-height. Apical disc small, 20% of test diameter at its widest point; plates firmly bound into the corona and flush with its surface. Plating dicyclic with large seven-sided genital plates that project interradially and much smaller pentagonal ocular plates (Fig. 3a–c). The periproct is about one-third of the apical disc diameter and is rounded pentagonal in outline. The genital plates each have an ovate gonopore situated on the outer projecting part of the plate. Genital plates are all very similar in size and hydropores are scattered over three or four of the genital plates. The ocular plates have a small perforation close to their outer edge and may also house some hydropores.

Ambulacral zones are straight and narrow, forming about 9% of the test diameter at their widest point. From the subambital region adapically, they consist entirely of simple plates devoid of tubercles. The perradial suture is a simple zig-zagged boundary. Pore-pairs are relatively large with no obvious peripodial muscle attachment zone and with a broad, low, interporal partition that is about as wide as a single pore. Below the ambitus every second plate carries a small tubercle, and adorally the ambulacra expand to form broad phyllodes. Here plating is in triads with a primary tubercle overlying two of the elements and a third element with just a small granule (Figs. 3d, 4d). Each triad has the central element as the largest and both upper and lower elements reach the perradius (Fig. 3e). There are about 18–20 pore-pairs per column in the phyllode arranged three abreast; these pore-pairs are smaller than those above and have a large, circular peripodial muscle attachment platform surrounding them. Close to the peristome the tubercles reduce in size and leave a narrow naked perradial zone that has a short row of granules, one per compound plate.

Interambulacral zones are wide. From the subambital region adapically plates are relatively tall and devoid of tubercles, covered instead in minute glassy granules scattered irregularly across the surface. Individual plates have a slightly tumid centre. Below the ambitus plates become lower and wider and start to bear small tubercles. These are at first confined to the adradial margins but quickly spread to cover the entire plate giving the oral surface a distinct U-shaped band of tuberculation. There are up to six subequal tubercles abreast on these adoral plates. Closer still to the peristome a naked zone appears leading to each buccal notch, with tubercles confined to adradial and interradiial zones. A single primordial interambulacral plate, bearing a single median tubercle, borders the peristome (Fig. 3f). In the best-preserved specimen, tubercles have a large and distinct perforate mamelon and no real surrounding

platform (Fig. 4f). Buccal notches are well developed, forming obvious U-shaped indentations to the margin, and have a distinct rim.

Spines, pedicellariae and lantern all unknown.

Remarks: The type species *G. choffati* is housed in the collections of the Museu Geológico, Lisbon, Portugal while a plastercast of this specimen is available in the de Lorient collection at the Museum d'Histoire Naturelle, Geneva, Switzerland; accession number 26022. This damaged specimen provides only incomplete information on its morphology, making detailed comparison with this species difficult. However, the pattern of oral tubercles immediately separates the two species. In *G. choffati*, the tubercles form a long double column along the adradial sutures and there is a gradual decrease in size of tubercles towards the interradius (see Smith 2005 for an illustration).

Appendix: characters used in the cladistic analysis

1. Test shape: subglobular; ambitus at mid height no (0); yes (1).
2. Apical disc: monocyclic (0); hemicyclic (1); dicyclic (2).
3. Apical disc tuberculation: absent (0); present (1).
4. Genital plates with only a single tubercle to each genital plate: no (0); yes (1).
5. Perianal tubercles developed in pits bordering the periproct: no (0); yes (1).
6. Sutural pits present: no (0); yes (1).
7. Position of gonopore: subcentral on genital plate (0); at extreme outer tip of genital plate (1).
8. Distribution of hydropores: scattered over the surface of G2 (0); confined to outer edge of G2 forming a U-shaped band (1).
9. Disc: flush (0); raised above corona (1).
10. Disc with coarse epistomal ornament: no (0); yes fine epistroma (1); yes, coarse knobbly rugosities (2).
11. Ambulacral plating above ambitus: simple (0); compound (1).
12. Ambulacral plate compounding: diadematid (0); goniopygid (single demiplate present) (1); arbaciid (both upper and lower elements small demiplates) (2).
13. Number of plates in compound element: 2 (2); 3 (3); 4 (4).
14. Aboral pore-pairs differentiated—larger and wider than adoral pore-pairs; no (0); yes (1).
15. Oral pores expanded into broad phyllode: no; oral pore-pairs small and rudimentary (0); yes weak (1); yes very strong (2).
16. Ambulacral tubercles absent above ambitus: no (0); yes (1).

17. Sphaeridial in pit: no (0); yes single (1); yes series of pits (2).
18. Interambulacral basicoronal plate: absent (0); present (1).
19. Basicoronal plate with central primary tubercle: no (0); yes (1); 3 tubercles (2).
20. Tubercles above ambitus normal—changing only slightly in size around the ambitus (0); reduced in size markedly and obviously smaller than oral tubercles (1); absent above ambitus (2).
21. Tubercles on subambital interambulacral plate: single (0); two subequal tubercles (1) rows of multiple subequal tubercles (2).
22. Ambital tubercles: occupy full plate height (0); occupy only part of the plate height (1).
23. Epistroma: absent (0); fine epistroma (1) coarse granular (2).
24. Papillae: absent (0); present (1).
25. Papillae: scattered over plate (0); forming well-defined rows (1).
26. Tubercles: perforate (0); imperforate (1).
27. Tubercles: non-crenulate (0); crenulate (1).
28. Ambulacral tubercles similar in size to interambulacral tubercles: no (0); yes (1).
29. Interambulacral plates at ambitus more than three times as wide as tall: no (0); yes (1).
30. Median naked zone: absent (0); present as a narrow strip (1); present as a broad band (2).
31. Buccal notches with tag: no (0); yes, forming a distinct flange (1).

Data matrix

<i>Stereopyga</i>	02100 00000 10301 000-0 0100-01100 0
<i>Panglyptus</i>	02000 00000 1?311 000-0 0120-10000 0
<i>Hemipedina</i>	02100 00000 10301 000-0 0100-00000 0
<i>Psephechinus</i>	02100 00000 10301 000-0 2100-10100 0
<i>Cottaldia</i>	12100 00000 11301 000-0 2100-00110 0
<i>Magnosia</i>	02000 00000 11312 00111 20?0-10111 0
<i>Eucosmechinus</i>	02000 0000? 11302 00111 20?0-10111 0
<i>Dubarechinus</i>	12000 00000 00311 10102 01??? 01100 0
<i>Codiopsis</i>	12000 00001 12312 10112 10110 1010-0
<i>Gymnodiadema</i>	12000 0000? 00312 10112 20?10 0010-0
<i>Arbacia</i>	02000 00001 12312 01100 2010-10112 1
<i>Tetrapyrgus</i>	01000 00001 12412 01100 2010-10112 1
<i>Arbia</i>	02100 00001 1?3?0 0???0 1010-10102 0
<i>Coelopleurus</i>	02000 00001 12310 02111 10111 10102 1
<i>Dialithocidaris</i>	02000 0?001 11301 01111 10111 1010-0
<i>Sexpyga</i>	02000 00001 1?301 101?2 10111 1010-0
<i>Baueria</i>	02000 00001 12? ?0 12??2 10111 1010-1
<i>Arbaciella</i>	02000 00001 12312 11112 10111 1010-1
<i>Noetlingaster</i>	02000 00001 12310 02110 2110-10112 0
<i>Glypticus</i>	02000 00002 11311 000-1 0020-10100 0
<i>Brochechinus</i>	02000 00002 11311 000-1 0020-10100 0

<i>Pleocyphus</i>	02000 01002 11301 000-1 0020-10100 0
<i>Acropeltis</i>	02110 01000 11311 000-0 0000-10100 0
<i>Pygmaeocidaris</i>	02000 07001 11301 11112 10111 1010-0
<i>Habrocidaris</i>	02000 00001 11300 11112 10110 1010-0
<i>Podocidaris</i>	02000 00001 17300 11112 10111 1010-0
<i>Goniopygus</i>	02111 11110 11311 000-0 0000-10000 0
<i>Mimiosalenia</i>	02111 11110 10201 000-0 0000-10000 0
<i>Glyphopneustes</i>	02111 11110 11301 000-0 0000-10000 0

References

- Agassiz, A. (1872). Revision of the Echini. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 3, pt. 1–2, i–xii, 1–378, pls. 1–49.
- Agassiz, A., & Clark, H. L. (1908). Hawaiian and other Pacific Echini. The Saleniidae, Arbaciidae, Aspidodiadematidae and Diadematidae. *Memoirs of the Museum of Comparative Zoology Harvard*, 34(3), 43–134. (pls. 45–59).
- Baumeister, J. G., & Koch, I. (1998). *Arbaciella elegans* (Echinoidea: Arbaciidae) aus dem Thyrrenischen Meer. *Stuttgarter Beitrage zur Naturkunde. Serie A (Biologie)*, 568, 1–6.
- Cooke, C. W. (1959). Cenozoic echinoids from Eastern United States. *Geological Survey USA Professional Papers* 321 (106 pp), 43 pls.
- Coppard, S. E., & Schultz, H. A. G. (2006). A new species of *Coelopleurus* (Echinodermata: Echinoidea: Arbaciidae) from New Caledonia. *Zootaxa*, 1281, 1–19.
- de Loriol, P. (1884). Notes pour servir à l'étude des Echinodermes. *Recueil Zoologique Suisse*, 1(4), 603–638. pls. 31–35.
- de Loriol, P. (1890). *Description de la faune Jurassique du Portugal. Embranchement des Echinodermes. I. Echinides réguliers ou endocycliques* (179 pp.). Lisbonne: Commision des Travaux géologiques du Portugal, 29 pls.
- Döderlein, L. (1906). Die Echinoiden der deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*, 5(2), 61–290, pls. 9–50.
- Durham, J. W., & Melville, R. V. (1957). A classification of echinoids. *Journal of Paleontology*, 31, 242–272.
- Fell, H. B., & Pawson, D. L. (1966). Echinacea. In R. C. Moore (Ed.), *Treatise on Invertebrate Paleontology. Part U, Echinodermata* 3 (pp. U367–U436). The Geological Society of America and the University of Kansas Press, Boulder, Co.
- Gordon, I. (1926). The development of the calcareous test of *Echinus miliaris*. *Philosophical Transactions of the Royal Society, London*, B, 214, 259–312.
- Gray, J. E. (1855). An arrangement of the families of Echinida, with descriptions of some new genera and species. *Proceedings of the Zoological Society, London*, 1855, 35–39.
- Gregory, J. W. (1900). Echinoidea. In E. R. Lankester (Ed.), *A Treatise on Zoology. Part III: The Echinodermata* (pp. 282–332). London: Adams & Charles Black.
- Kroh, A., & Smith, A. B. (2010). The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology*, 8, 147–212.
- Lambert, J. (1911). Notes sur quelques Échinides Eocéniques des Corbières septentrionales. *Annales de la Université du Lyon, N.S. I Fasc.*, 30, 1–24.
- Lambert, J. (1931). Etude sur les Échinides fossiles du Nord d'Afrique. *Mémoires de la Société géologique du France, n.s. Paléontologie* 7, fasc. 2–4, *Mémoire*, 16, 1–228, pls. 1–8.
- Lambert, J. (1933). Échinides fossiles du Maroc. *Notes et Mémoires du servir des Mines et de la Carte géologique du Maroc*, 27, 1–89, pls. 1–3.
- Lambert, J. (1937). Échinides fossiles du Maroc. *Notes et Mémoires du Service Géologique du Maroc*, 39, 1–110.
- Lambert, J., & Thiéry, P. 1914 (in 1909–1925): *Essai de Nomenclature Raisonnée des Echinides*. L. Ferrière, Chaumont, fasc. 1, i–iii, 1–80, pls. 1–2 (March 1909); fasc. 2, 81–160, pls. 3–4 (July 1910); fasc. 3, 161–240, pls. 5–6 (May 1911); fasc. 4, 241–320, pls. 7–8 (March 1914); fasc. 5, 321–384, pl. 9 (Sept. 1921); fasc. 6–7, 385–512, pls. 10–11, 14 (Dec. 1924); fasc. 7–8, 513–607, pls. 12, 13, 15 (Feb. 1925).
- Mortensen, T. (1935). *A Monograph of the Echinoidea. II. Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta* (647 pp). Copenhagen: C. A. Reitzel
- Petitot, M.-L. (1967). Contribution à l'étude des échinides fossiles du Maroc (Jurassique et Crétacé). *Notes et Meoirs du Service géologique du Maroc*, 146, 183 pp.
- Philip, G. (1965). The tertiary echinoids of South-eastern Australia. III Stirodonta, Aulodonta, and Camarodonta (1). *Proceedings of the Royal Society of Victoria*, 78, 181–196. pls. 26–29.
- Schultz, H. (2005). *Sea urchins*. Hemdingen: HPSP Publications.
- Shigei, M. (1975). A new species of a new genus of the arbaciid sea-urchins (Echinoidea: Arbacioida) from the North Pacific, off Hachijo Island. *Journal of the Faculty of Science, Tokyo University, Section 4 Zoology*, 13, 329–332.
- Smith, A. B. (1978). A functional classification of the coronal pores of regular echinoids. *Palaeontology*, 21, 759–789.
- Smith, A. B. (1995). Late Campanian-Maastrichtian echinoids from the United Arab Emirates–Oman border region. *Bulletin of the Natural History Museum London (Geology)*, 51, 121–240.
- Smith, A. B. (2004). Phylogeny and systematics of holasteroid echinoids, and their migration into the deep-sea. *Palaeontology*, 47, 123–150.
- Smith, A. B. (2005). The echinoid directory. World Wide Web electronic publication, available at <http://www.nhm.ac.uk/research-curation/research/projects/echinoid-directory/>.
- Smith, A. B., Pisani, D., Mackenzie-Dodds, J. A., Stockley, B., Webster, B. L., & Littlewood, D. T. J. (2006). Testing the molecular clock: molecular and paleontological estimates of divergence times in the Echinoidea (Echinodermata). *Molecular Biology and Evolution*, 23, 1832–1851.
- Smith, A. B., & Rader, W. L. (2009). Echinoid diversity, preservation potential and sequence stratigraphical cycles in the Glen Rose Formation (early Albian, Early Cretaceous), Texas, USA. *Palaeobiodiversity and Palaeoenvironments*, 89, 7–52.
- Smith, A. B., & Stockley, B. (2005). The geological history of deep-sea colonization by echinoids: roles of surface production and deep water ventilation. *Proceedings of the Royal Society B*, 272, 865–869.
- Smith, A. B., & Wright, C. W. (1996). British Cretaceous echinoids. Part 3, Stirodonta 3 (Phymosomatidae, Pseudodiadematidae) and Camarodonta. *Monographs of the Palaeontographical Society*, 150(602), 268–341. pls. 93–114.
- Stanley, R. G. (1981). Middle Jurassic shoaling of the central High Atlas Sea near Rich, Morocco. *Journal of Sedimentary Research*, 51, 895–907.
- Swofford, D. L. (2005). *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*, Version 4.0b10. Sunderland: Sinauer Associates
- Vadet, A., & Nicolleau, P. (2005). Les oursins Domériens de la Région de Rich (Maroc). *Annales de la Société d'Histoire Naturelle du Boulonnais*, 5(1), 1–36.
- Wright, T. (1851). On the Cidaridae of the Oolite, with descriptions of some new species of that family. *Annals and Magazine of Natural History Series*, 2(8), 241–279.