

The evolution of pedicellariae in echinoids: an arms race against pests and parasites

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Keywords:

Echinoidea, phylogeny, taxonomy, cladistics, evolution, Mesozoic marine revolution, fossil record

Accepted for publication:

12 October 2010

Abstract

Coppard, S.E., Kroh, A. and Smith, A.B. (2010). The evolution of pedicellariae in echinoids: an arms race against pests and parasites. —*Acta Zoologica* (Stockholm) 00:1–24.

Sea urchins (Echinoidea) have evolved a diverse array of jawed appendages termed pedicellariae to deter pests and predators. Pedicellarial structure and function are reviewed and their distribution mapped in 75 extant genera. Using a phylogeny of echinoids at family level constructed from 353 skeletal characters scored across 162 extant and fossil taxa, the evolution of pedicellarial form and function is reconstructed. For much of the Palaeozoic echinoids possessed a very restricted pedicellarial armament. By the early Mesozoic a diverse array of pedicellarial types had become established, implying that the threat from predators and pests markedly increased at this time. Since the Triassic, echinoids have continued to improve their defensive capability by evolving more effective venom delivery in globiferous pedicellariae, developing spatulate-tips and curved blades for a more efficient grab in tridentate pedicellariae, and stouter, more robust valves with a stronger bite in ophicephalous pedicellariae to disable and remove ectoparasites. However, pedicellarial types are shown to be particularly prone to subsequent secondary loss, especially among infaunal echinoids, and thus have higher homoplasy levels than other phylogenetically useful skeletal structures.

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Introduction

All echinoids possess a series of mobile appendages for protection. Most obvious are the primary and secondary spines, which cover the surface of the animal (Fig. 1A) and provide a formidable defence against larger predators. In among the spines are a set of small stalked appendages, the pedicellariae (Fig. 1B). These are pincer-like structures used in defence and cleaning (Von Uexküll 1899). They are attached by muscles to a freely rotating joint on the surface of the test and consist of a stalk, a neck and valves, which form the jaws (Nichols 1962). These structures are functionally and structurally highly evolved and come in a bewildering array of different shapes (Fig. 2). Because of this variability, they have been widely used in taxonomy, especially at species and genus level (e.g. Mortensen 1928–1951; Coppard and Campbell 2006; Coppard 2008). Furthermore, characteristic pedicellarial types are restricted in their distribution, providing important phylogenetic markers for higher clades.

A similar sort of jaw-like appendage can be found in extant starfishes (Lambert *et al.* 1984; Lawrence 1987; Gale *in press*), and these are recorded as far back as the Silurian (Sutton *et al.* 2005). These serve the same overall role as echinoid pedicellariae, but are usually bivalved and are attached directly to underlying plates rather than being stalked. Their different structure suggests that they evolved from dermal spines independently from those of echinoids.

Surprisingly little is known about the evolutionary history of echinoid pedicellariae, and the fossil record provides relatively few clues. While the first pedicellariae are recorded from the late Ordovician (Nestler 1970), shortly after the earliest records of echinoid tests (Smith and Savill 2002), the small size and fragility of pedicellariae has meant that they are rarely preserved and even more rarely described. Furthermore, those few studies that have described pedicellariae are usually based on material found in sieved sediment samples that cannot be assigned to particular taxa with any degree of confidence (e.g. Geis 1936; Mostler 1972, 2009; Boczarowski 2001, 2004, 2005). The evolution of

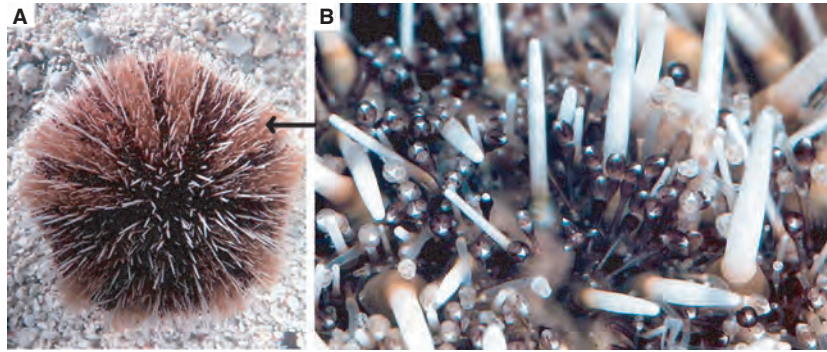


Fig. 1. —Pedicellariae among the spines of the regular echinoid *Tripneustes ventricosus* (Lamarck) from Carrie Bow Cay, Belize. —**A.** living animal in apical view; —**B.** detail showing large numbers of globiferous pedicellariae among the spines.

pedicellarial form and diversity thus can only be pieced together indirectly from an analysis of their distribution among extant echinoids.

Here we review how pedicellariae are distributed amongst crown-group echinoids and use this to reconstruct their evolutionary history of diversification. By pinpointing when and where important changes in form and function took place, we reconstruct how echinoids have been evolving to defend themselves against predators and pests.

Structure and Function of Echinoid Pedicellariae

Pedicellariae can be broadly categorized into four major types (see Fig. 2): globiferous (gemmiform), ophicephalous, triphyllous (trifoliolate) and tridentate (tridactylous) (Cavey and Märkel 1994). Often all four types can be found on the same individual, with clear spatial distribution differences, suggesting that their form and function are closely linked. All comprise a head, composed of between two and five valves, and a stalk, which is at least partially supported by a skeletal rod (Fig. 2A). Each valve is formed of a distal blade, the rim of which is often denticulate, and a proximal articulation surface with adductor muscle insertion regions (Fig. 2B). The valves are made of stereomic calcite, thus have a strong but lightweight construction, and are covered by a pigmented epithelium which often contains spicules. Large adductor muscles are present in most types of pedicellariae and are used to close the jaws, while abductor and flexor muscles open and manipulate the valves. The gripping power of the pedicellariae is not, however, limited to the muscles uniting the valves, as collagen fibres also link the stem formed of calcite rods to the valves (Campbell 1983). In life, pedicellariae can be observed opening and snapping closed their jaws. In most pedicellariae, this occurs after direct stimulation through an inbuilt reflex arc or through stimulation on the surface of the test through nerves under the skin (Campbell 1983). Such snapping of the pedicellarial jaws has been recorded at speeds of around 100 ms (Campbell 1976).

Globiferous pedicellariae

Globiferous pedicellariae are the most highly specialized of the four forms, with venom glands and valves that terminate in fangs or teeth designed to pierce the skin of predators and deliver their venom (Fig. 2A–M). The jaws have distal teeth and proportionally large adductor muscles that generate a strong grasping pressure. The valves typically have cilia on their inner surface forming a sensory hillock (Fig. 2Kii) of chemosensitive cells (Campbell and Laverack 1968; Chia 1970; Oldfield 1975). They only react to appropriate chemical stimulation (such as starfish tissue, see Cannone 1970) and respond to tactile stimulation by simply opening their jaws wider, thus further exposing the insides of the valves and the sensory hillock (Campbell 1983). This prevents the globiferous pedicellariae from prematurely releasing their venom when they come into contact with particulate matter or non-targeted organic material. The valves are sometimes enclosed in a muscular envelope and occur in a variety of forms that can be classed into three major types:

- *Fistulate* (Fig. 2A–D). The valves are tubular and terminate in a well-defined opening fringed by a series of small teeth designed to create puncture wounds (Fig. 2B). Venom glands lie internally in a glandular cavity housed within the body of the blade, and the venom is released through a subterminal opening, termed the foramen. In spatangoids, the distal part of the valve is extended and finger-like (Fig. 2C–D).
- *Fanged with external venom glands on the valves* (Fig. 2E–H). The valves can be either tubular or have an open blade, with large fangs distally that are surrounded by glandular tissue. The fangs are either solid or have a distal groove (Fig. 2G–H) and are designed to create puncture wounds, while the venom is released from the external glands.

- *Fanged with stalk glands* (Fig. 2K–M). The valves are tubular and terminate in a hypodermic-like fang, which creates a puncture wound into which the venom is directly released from a long narrow opening in the end of the tooth (Fig. 2Lii). The stalk glands are the source of the venom and are connected up through the neck to the distal fangs (Ghyoot *et al.* 1994).

In some highly derived globiferous pedicellariae combinations of both stalk and valve glands, and fistulate and valve glands can be present in the same pedicellaria (Fig. 2I–J). The role of the different glands is unknown; however, it seems likely that the stalk and fistulate venom glands produce venom that is released through the distal openings, while the valve glands release venom into the puncture wound, in some cases via a duct that goes directly to the underside of the fang (see Fig. 2I–J). The neck in fistulate forms is muscular (Fig. 2C) while in fanged forms it is short and typically attached to a short to mid-length stalk. The proportionally narrow neck in fanged types may be designed to rupture easily so that the head remains in the puncture site. This may prevent damage to the urchin from a predator and allow greater time for venom to be delivered from the glands. The venom, termed peditoxin (for more detail on the venom see Kuwabara 1994) has been recorded to have paralyzing effects on crustaceans, gastropods, octopus and fish, with unsubstantiated reports of fatalities in humans (Romanes 1883; Fujiwara 1935).

In epifaunal species of echinoids, the globiferous pedicellariae are predominantly found on the aboral surface (Coppard, pers. obs.), sometime at very large densities, providing a first line of defence against macropredators such as starfish (Dayton *et al.* 1977; Lawrence 1987, p. 235). In infaunal echinoids, particularly those that burrow in muddy sand, the globiferous pedicellariae are found in large numbers around the mouth and towards the posterior of the oral ambulacra near the periproct (Coppard 2008) (the vulnerable openings in the test) as a defence against nematodes, polychaetes and other smaller parasites and predators.

Ophicephalous pedicellariae

Ophicephalous pedicellariae have three denticulate valves, typically with blades that are short and broad, reaching their widest point two-thirds of the way down their length distally (Fig. 2P–Q). The valves can be simple or constricted and are characterized by having a large inward-projecting process beneath the articulating surface, referred to as ‘handles’ by Mortensen (1928–1951). This structure is reported to provide greater grasping pressure (Mortensen 1928–1951) and may well allow the jaws to hold onto objects for longer periods before the muscles fatigue. One valve has a large handle (Fig. 2Pii), in which sits the smaller handles of the second (Fig. 2Piii) and third valves (Fig. 2Piv), which are held in place by hinges on the lateral edges of the valves (see Fig. 2Pi). Handles were once thought to be unique to this

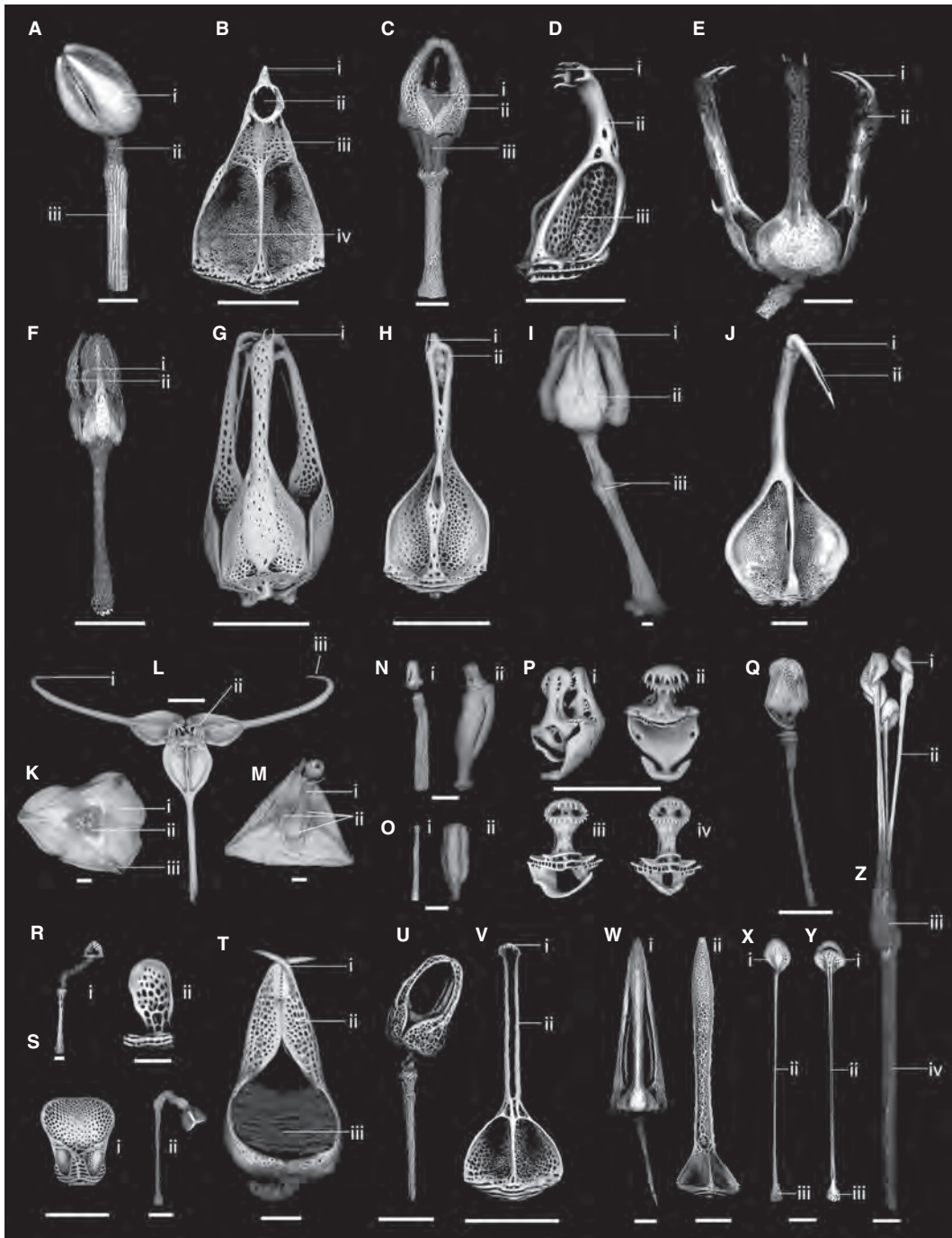
type of pedicellaria, however, they also occur in a much reduced form in some tridentate and triphyllous pedicellariae. Ophicephalous pedicellariae are held lowered on the test until alerted or stimulated, whereupon the stems are raised and their jaws are opened. Several ophicephalous pedicellariae then converge on the centre of tactile stimulation in a similar way to primary spines, the jaws snapping shut when an inner surface of a valve is touched (Campbell 1983). The skeletal ossicles of this type of pedicellaria being compact and denticulate are designed to hold onto struggling organisms for longer periods, providing that contact between the blades of the jaws and the organism is maintained (Campbell 1974). This type of pedicellaria is used to trap small moving organisms, e.g. ectoparasites, preventing them from settling on the test (Von Uexküll 1899; Campbell 1973; Campbell and Rainbow 1977).

In some groups (e.g. *Caenopedina*), the ophicephalous pedicellariae are distinctly differentiated orally and aborally. The aboral forms have more complex valves, with greater handle development and are abundant around the periproct, while the simpler oral ophicephalous pedicellariae form a defensive ring around the mouth.

Stalk venom glands are found in some ophicephalous pedicellariae (Fig. 2Ni, ii), with this type designated as claviform (club-shaped) by Mortensen (1928–1951). In this group, he also included a form that has a stalk, with large glands but which lacks valves (Fig. 2Oii). Agassiz (1883) stated that such sheathed pedicellariae recalled the sheathed secondary spines of the echinothurioid *Asthenosoma*; however, Mortensen was correct in stating that the microstructure of the stalks (Fig. 2Oi) is pedicellarial-like and quite unlike secondary spines. Mortensen proposed that this reduced form was most likely derived from ophicephalous pedicellariae with stalk venom glands but also suggested that they may have developed from a globiferous type, a view later supported by Lewis and Saluja (1967). Claviform ophicephalous pedicellariae occur in diadematoids where the ‘normal’ ophicephalous only occur in juveniles. Where they occur, they are found all over the test and probably function by releasing chemicals from the glands which repel fouling organisms, either after direct contact or through stimulation on the test surface.

Triphyllous pedicellariae

Triphyllous pedicellariae are the smallest of the four main types and are attached by a very long muscular neck to a long stalk (Fig. 2S). They have three small valves that meet along their lateral edges (Fig. 2Sii). The valves are usually rounded distally (Fig. 2Si) having either smooth blades or small interlocking teeth. In a few groups, the blades have a bilobed appearance creating a greater ‘bite’ area. These pedicellariae can be observed continually opening and closing their jaws, even after they have been removed from the living sea urchin for several hours (Coppard, pers. obs.). Their function



appears to be to clean bacterial plaque and small particulate matter from the test epithelium, which can be very detrimental to echinoids (Tajima *et al.* 1997; Nagelkerken *et al.* 1999; Bauer and Young 2000), and they occur in high abundance all over the test in most species. They are not sensitive to touch and only hold onto objects for short periods (Campbell 1983). A two-valved (biphylloous) form (Fig. 2R) is found in

some clypeasteroids, which has similar activity and performs an identical cleaning function.

Tridentate pedicellariae

Tridentate pedicellariae are the largest and most common type, with typically three long valves that have peripheral teeth

Fig. 2. —Major pedicellarial types showing morphological terms used in the text. —**A–B.** Cidaroid fistulate globiferous, **A:** (*Eucidaris*), i, valve with glandular cavity; ii, neck; iii, stalk; **B:** Valve ossicle (*Calocidaris*), i, terminal tooth; ii, denticulate foramen; iii, open blade with sensory pad; iv, adductor muscle insertion point. —**C–D.** Spatangoid fistulate globiferous, **C:** (*Paraster*), i, adductor muscles; ii, glandular cavity; iii, neck with adductor muscles; **D:** (*Brissalius*) valve ossicle, i, denticulate foramen; ii, glandular cavity; iii, adductor muscle insertion point. —**E.** spatangoid fanged with valve glands (*Brissopsis*), i, distal fangs; ii, valve glands. —**F–H.** camarodont (*Echinometra*) asymmetric fanged globiferous with external venom glands, **F:** i, venom valve glands (double per valve); ii, spicules; **G:** bleached whole head, i, primary fang duct; **H:** valve ossicle; i, primary fang with duct; ii, secondary fang. —**I–J.** camarodont (*Toxopneustes*) fanged globiferous with both stem and valve glands, —**I.** i, valve gland duct; ii, venom valve glands (double per valve); iii, stem glands (x3); **J:** valve ossicle; i, hooked fang; ii, distal opening in fang. —**K–M.** toxopneustid (*Toxopneustes*) fanged globiferous with stalk glands: **K:** dorsal view; i, skin between valves; ii, sensory hillock; iii, distal fang; **L:** bleached whole head; i, terminal barb on fang; ii, sensory hillock; iii, distal opening in fang; **M:** ventral view; i, stalk; ii, valve glands (x3 single). —**N.** diademmatid (*Astropyga*) glandular ophicephalous; i, bleached head & stalk; ii, whole, with valves & three stalk glands. —**O.** diademmatid (*Astropyga*) claviform (no valves); i, bleached stalk; ii, whole; with three stalk glands. —**P.** clypeasteroid (*Clypeaster*) ophicephalous; i, whole head; ii, valve ossicle 1; iii, valve ossicle 2; iv, valve ossicle 3. **Q.** arbacioid (*Coelopleurus*) opicephalous. —**R.** mellitid (*Mellita*) biphyllous: i, whole; ii, valve ossicle. —**S.** camarodont (*Toxopneustes*) triphyllous type: i, valve ossicle; ii, whole. —**T.** mellitid (*Encope*) scissor-like bidentate, i terminal tooth, ii valve ossicle, iii longitudinal muscle fibres. —**U–V.** spatangoid (*Brissopsis*) rostrate; **U:** whole; **V:** valve ossicle; i, fan of distal teeth; ii, rolled edge of valve. —**W.** pedinoid (*Caenopedina*) tridentate: i, whole; ii, valve ossicle. —**X–Z.** echinothurioid (*Araeosoma*) dactylous: **X:** valve ossicle (back of valve), i, blade; ii, shaft; iii, rod-like proximal region; —**Y.** valve ossicle (internal view), i, denticles; ii, groove in shaft; iii, rod-like proximal region of valve; —**Z.** whole, i, valve; ii, shaft; iii, gland; iv, stalk. Scale bars = 200 μm except R, S & V where scale bars = 20 μm .

(Fig. 2W). The head of the pedicellaria is often supported by a muscular neck, which allows free movement of jaws in all directions. The blades can be narrow (Fig. 2Wii), broad or spatulate with varying degrees of interlocking denticulation, ranging from forceps-like, the blades only meeting at their tips (Fig. 2Wi), to having a complete contact edge. They are found all over the test, but with longer, narrower valves aborally, and broader, squatter valves orally. In life, the tridentate pedicellariae are held closed and lowered in a resting position until alerted by tactile stimulation either directly, or on the test epithelium (Campbell 1983). Tridentate pedicellariae remove larger particulate matter from the surface of the test (Sladen 1880; Campbell 1973) and act as a deterrent against small invertebrate pests such as polychaete worms (Hamann 1887). They have also been observed to deter larvae such as barnacle cyprids from settling on the test (Campbell and Rainbow 1977).

Tridentate pedicellariae with highly curved lantern-shaped valves (Fig. 2U–V) are referred to as rostrate by some authors (Mortensen 1927; Campbell and Jensen 1993). These appear to function as a ‘grab’ and have a greater bite volume proportionally than other forms. The curvature of their valves suggests that they can grip and hold struggling organisms with greater force than straight-bladed tridentate pedicellariae.

A bidentate form of pedicellaria is found in some groups. The proximal regions of the valves are laterally compressed and have a large band of striated muscle connecting the valves (Fig. 2T). Peripheral teeth are present along the edges of the blades where they interlock. Bidentate pedicellariae can be subdivided into two forms, those with long narrow blades with large scissor-like distal teeth and those with squatter more beak-like blades that sometimes have distal fangs. Bidentate pedicellariae have a strong bite and a wide closure edge, allowing for a fast and broad capture.

A delicate type of pedicellaria termed dactylous (tetradactylous) by Mortensen (1928–1951) represents another distinctive subset of tridentate pedicellariae and is present only in a

few echinothurioid genera (Fig. 2X–Z). In *Araeosoma*, these occur in small numbers around the margin of the test. Dactylous pedicellariae have from three to five narrow, tubular valves with an expanded distal region that has an overhanging denticulate edge (Fig. 2Yi). The proximal regions of the valves are rod-like and lack adductor muscle insertion points (Fig. 2Yii). The muscles controlling the valves are very weakly developed suggesting that they have a very limited grasping ability. The valves sit directly on the stalk with no neck and have large glands lying at the base of the valves. Whether the glands contain venom is unknown, however, the stem of each valve has a groove that runs along the shaft from the gland to the blade providing a means for potential venom release.

The Fossil Record of Pedicellariae

The fossil record of pedicellariae is rather poorly known largely because pedicellariae are small and fragile and fall off soon after the sea urchin dies. Fossil pedicellariae are therefore found intact and associated with the preserved test only in cases of exceptional preservation and are rarely reported from the microfossil record. The oldest known echinoid pedicellariae are isolated valves that come from the late Ordovician Boda Limestone (Nestler 1970) and the late Silurian Hemse Beds (Kutscher and Reich 2001) of Gotland. These already have a clearly differentiated basal muscle pad for connecting the valves together and controlling the snapping movement. However, simpler and more primitive pedicellariae have been described *in situ* from well-preserved examples of *Palaeodiscus* and *Echinocystites* from the late Silurian of England by Blake (1968). These consist of three slender spines attaching to a single tubercle on the surface of the plate, strongly suggesting that pedicellariae originated as clusters of small spines that became functionally united at their base. The few fossil pedicellariae known from the Lower Palaeozoic have spinate-blades that are similar to the tridentate pedicellariae that we see today but with more rounded, spine-like blades (Philip

1963; Haude 1998). An important study on pedicellariae from the Middle Devonian of Poland was published by Boczarowski (2001). Unfortunately all his material was picked in isolation from sediment samples and is thus of uncertain taxonomic attribution. While there are clear spinate-valved tridentate pedicellariae (tentatively assigned to the echinoid *Albertechinus*), the remainder resemble pedicellariae of Palaeozoic starfish (cf. Sutton *et al.* 2005; Hotchkiss and Glass 2010). Tridentate pedicellariae recovered from the Upper Devonian *Nortonechinus* consisted only of two valves (Kier 1968). In later echinoids the spinate-blades appear to have flattened, eventually becoming open and concave on the inner surface. This flattening of the blades may have aided in gripping hold of material (Haude 1998).

The morphological diversity of pedicellariae increased in the late Palaeozoic. In the Lower Carboniferous archaeocidarid *Archaeocidaris whatleyensis* (Lewis and Ensom 1982), there are just two forms of pedicellariae, a large tridentate type whose valves are straight and meet along most of their length (cidarid-style straight forceps) and a much smaller, squatter, more bulbous form that might be a primitive globiferous type or a stubby tridentate type (unfortunately no internal view of the valves is available to provide confirmation). Because there is excellent preservation of the fine secondary spine canopy on both oral and aboral surfaces in these specimens, we are confident that other pedicellarial types are genuinely absent and not just missing through lack of preservation. By the late Upper Carboniferous, however, a more diverse assemblage of pedicellariae is known to exist. Geis (1936) and Hoare and Sturgeon (1984) described a number of isolated pedicellariae from the late Upper Carboniferous of Texas, Illinois and Missouri, USA, identifying tridentate, globiferous and ophicephalous morphologies. The tridentate pedicellariae were of two forms, one with longer spinate-type valve blades and a second with shorter subtriangular valves. In both, the valves lack denticles and meet along their entire length. All globiferous pedicellariae are incomplete, but it is clear that they lack an internal cavity for housing venom glands. They have a large bulbous base and a narrow tubular blade with a sagittal groove. In shape, they resemble the ‘group 1’ fanged pedicellariae described by Mostler (2009) from the late Triassic. Whether these really are globiferous pedicellariae is impossible to tell, but they are clearly different from the fistulate and fanged globiferous pedicellariae of crown-group echinoids. The supposed ophicephalous pedicellariae described and illustrated by Hoare and Sturgeon (1984) are ophiuroid lateral arm plates. However, Geis (1936) described some bona fide well-preserved ophicephalous pedicellariae complete with characteristic large handles. These have valves with a long neck and spoon-shaped tip, and are very similar in appearance to ophicephalous pedicellariae of basal euechinoids such as *Caenopedina*. However, they differ from any modern ophicephalous pedicellariae in having imperforate handles.

Crown-group echinoids had evolved by the early Permian, around 260 million years ago (Smith *et al.* 2006), with two

evolutionary lines of echinoids surviving the Permian-Triassic boundary and giving rise to the modern day cidaroids and euechinoids (Smith and Hollingworth 1990; Smith 2007). Euechinoids subsequently underwent a spectacular radiation in the late Triassic and Jurassic to give rise to the diverse forms that we see today (Smith *et al.* 2006; Kroh and Smith 2010). Permian echinoid pedicellariae tentatively attributed to *Eocidaris* by Spandel (1898) are misidentified goniodonts of ophiocystoids (Reich 2007). An important study of isolated pedicellariae from the late Triassic by Mostler (2009) has documented an impressive range of pedicellarial forms, including straight forceps and non-forceps tridentate pedicellariae, ophicephalous pedicellariae and various fanged and fistulate globiferous pedicellariae. There are also two additional types of pedicellariae, termed folifere and dentifer, although as these were all found disassociated, their echinoid affinities remain speculative. Unfortunately, while pedicellariae are occasionally reported in post-Triassic echinoids (e.g. Groom 1887; Geis 1936; Mortensen 1937; Philip 1962; Zankl 1965; Nestler 1966, 1978, 1979; Hess 1971, 1972, 1973, 1975; Kozur and Mostler 1973; Smith and Wright 1989; Krainer *et al.* 1994; Reich and Frenzel 2002), especially in Pleistocene ones (Borghini 1993, 1994, 1995, 1997a,b, 1998, 1999; Néraudeau *et al.* 1998), there has been no attempt to synthesize this fossil information and no modern SEM studies on their structure.

Tracing Pedicellarial Evolution

Tree construction

While the fossil record of pedicellariae remains extremely sparse and poorly documented, the only practical way to reconstruct their evolution over geological time is through adopting a phylogenetic approach. Pedicellariae present in the type genus of the 75 extant families of echinoid ever formally proposed were surveyed using published descriptions, especially Mortensen (1903–1907, 1928–51) and our own scanning electron microscopical examination of both dried and bleached specimens. Table 1 lists the species studied and the source of data used. A number of additional species and genera within some families were also studied but were not formally included in the phylogenetic analysis. From this database, we scored for 50, mostly binary presence/absence, characters that referred to significant anatomical features that could be consistently scored, and which were usually invariant among congeneric species. Pedicellarial types, if present in species other than the type of the genus, were scored irrespective of whether they were found in the type species or not. As outgroup we used the late Palaeozoic fossil *Archaeocidaris*, known from two very well preserved species with spines and pedicellariae (Lewis and Ensom 1982; Schneider *et al.* 2005). Appendix 1 lists the characters and their states and provides the pedicellarial character scores for the 76 taxa.

To construct a phylogenetic tree, we have combined our 50 pedicellarial characters with the 303 test and spine characters

Table 1 List of taxa studied and the sources of information used when scoring their pedicellariae

Major	clade Family	genus scored (*type)	source of data	
Arbacioida	Arbaciidae	* <i>Arbacia</i>	specimens; (Mortensen 1935)	
	Coelopleuridae	* <i>Coelopleurus</i>	specimens	
Aulodonta	Aspidodiadematidae	* <i>Aspidodiadema</i>	specimens; (Mortensen (1940)	
	Diadematidae	* <i>Diadema</i>	specimens; (Mortensen (1940)	
	Micropygidae	* <i>Micropyga</i>	specimens; Mortensen (1940)	
Camarodonta	Echinidae	* <i>Echinus</i>	specimens; Mortensen (1903–1907)	
	Echinometridae	* <i>Echinometra</i>	specimens; Mortensen (1943b)	
	Parasalenidae	* <i>Parasalenia</i>	Mortensen (1935)	
	Parechinidae	* <i>Parechinus</i>	Mortensen (1943b)	
	Strongylocentrotidae	* <i>Strongylocentrotus</i>	specimens; Mortensen (1943b); Mortensen (1903–1907)	
	Temnopleuridae	* <i>Temnopleurus</i>	Mortensen (1943b)	
	Toxopneustidae	* <i>Toxopneustes</i>	specimens; (Mortensen (1943a); Mortensen (1903–1907)	
	Trigonocidaridae	* <i>Trigonocidaris</i>	Mortensen (1903–1907)	
	Neognathostomata	Apatopygidae	* <i>Apatopygus</i>	Baker (1983)
	Cassiduloida	Cassidulidae	* <i>Cassidulus</i>	specimens; Mortensen (1948a)
Echinolampadoida	Echinolampadidae	* <i>Echinolampas</i>	Mortensen (1948a)	
	Neolampadidae	* <i>Neolampas</i>	Mortensen (1948a)	
Cidaroida	Cidaridae	* <i>Cidaris</i>	specimens; Mortensen (1903–1907)	
	Ctenocidarinae	* <i>Ctenocidaris</i>	Mortensen (1903–1907, 1928–1951)	
	Goniocidaridae	* <i>Goniocidaris</i>	Mortensen (1928)	
	Histocidaridae	* <i>Histocidaris</i>	specimens; Mortensen (1928)	
	Phyllacanthini	* <i>Phyllacanthus</i>	specimens; Mortensen (1928)	
	Poriocidarini	* <i>Poriocidaris</i>	Mortensen (1928)	
	Psychocidaridae	* <i>Psychocidaris</i>	specimens; Ikeda (1939)	
	Stereocidaridae	* <i>Stereocidaris</i>	specimens; Mortensen (1928); Mortensen (1903–1907)	
	Stylocidarinae	* <i>Stylocidaris</i>	specimens; Mortensen (1928)	
	Clypeasteroida	Ammotrophinae	* <i>Ammotrophus</i>	Mortensen (1948b)
Arachnoididae		* <i>Arachnoides</i>	Mortensen (1948b)	
Astriclypeidae		* <i>Astriclypeus</i>	Mortensen (1948b)	
Clypeasteridae		* <i>Clypeaster</i>	specimens; Mortensen (1948b)	
Dendrasteridae		* <i>Dendraster</i>	Mortensen (1948b)	
Echinarachniidae		* <i>Echinarachnius</i>	Mortensen (1948b)	
Echinocyamidae		* <i>Echinocyamus</i>	Mortensen (1903–1907)	
Fibulariidae		* <i>Fibularia</i>	Mortensen (1948b)	
Laganidae		* <i>Laganum</i>	specimens; Mortensen (1948b)	
Mellitidae		* <i>Mellita</i>	specimens	
Rotulidae		* <i>Rotula</i>	Mortensen (1948b)	
Taiwanasteridae		* <i>Taiwanaster</i>	Wang (1984)	
Echinoneoida		Echinoneidae	* <i>Echinoneus</i>	Westergren (1911)
Echinothurioida		Echinothuriidae	<i>Araeosoma</i>	specimens; Mortensen (1935)
	Hygrosomatinae	* <i>Hygrosoma</i>	Mortensen (1935)	
	Kamptosomatidae	* <i>Kamptosoma</i>	Mortensen (1935)	
	Paraphormosomatinae	* <i>Paraphormosoma</i>	Mortensen (1935)	
	Phormosomatidae	* <i>Phormosoma</i>	specimens; Mortensen (1935)	
	Sperosomatinae	* <i>Sperosoma</i>	Mortensen (1935)	
	Holasteroida	Calymnidae	* <i>Calymne</i>	Saucède <i>et al.</i> (2009)
	Camarechininae	* <i>Camarechinus</i>	Mironov (1978, 1993)	
Holasteroida	Corystidae	* <i>Corystus</i>	de Meijere (1904); Mooi and David (1996)	
	Plexechinidae	* <i>Plexechinus</i>	Mortensen (1951a); Mooi and David (1996)	
	Pourtalesidae	* <i>Pourtalesia</i>	Mortensen (1903–1907); Mironov (1995)	
	Urechinidae	* <i>Urechinus</i>	Mooi and David (1996); Mortensen (1903–1907); Mironov (1978)	
	Pedinoida	Pedinidae	<i>Caenopedina</i>	specimens
	Salenioida	Saleniidae	<i>Salenia</i>	Mortensen (1935)

Table 1 (continued)

Major	clade Family	genus scored (*type)	source of data
Spatangoida	Salenocidarini	* <i>Salenocidaris</i>	Mortensen (1935)
	Aeropsidae	* <i>Aeropsis</i>	Mortensen (1903–1907)
	Breyntinae	* <i>Breyntia</i>	specimens; Mortensen (1951)
	Brisasterinae	* <i>Brisaster</i>	specimens; Mortensen (1903–1907)
	Brissidae	* <i>Brissus</i>	specimens
	Brissopsidae	* <i>Brissopsis</i>	specimens
	Cyclasterinae	* <i>Cyclaster</i>	Baker (1969)
	Echinocardiidae	* <i>Echinocardium</i>	specimens; Mortensen (1903–1907)
	Eupatangidae	* <i>Eupatagus</i>	Mortensen (1903–1907)
	Eurypataginae	* <i>Eurypatagus</i>	Mortensen (1903–1907)
	Hemiasteridae	* <i>Hemiaster</i>	Mortensen (1903–1907)
	Loveniidae	* <i>Lovenia</i>	specimens; Mortensen (1951)
	Maretiidae	* <i>Maretia</i>	Mortensen (1951)
	Palaeostomatidae	* <i>Palaeostoma</i>	Mortensen (1951)
	Palaeotropidae	* <i>Palaeotropus</i>	Mortensen (1950); Mironov (2006)
	Paleopneustidae	* <i>Paleopneustes</i>	Mortensen (1950)
	Pericosmidae	* <i>Pericosmus</i>	Mortensen (1951)
	Prenasteridae	<i>Saviniaster</i>	Chesher (1968)
	Schizasteridae	* <i>Schizaster (Ova)</i>	specimens; Mortensen (1903–1907)
	Spatangidae	* <i>Spatangus</i>	specimens; Mortensen (1903–1907)
Stem group	Archaeocidaridae	* <i>Archaeocidaris</i>	specimens
Stomopneustoida	Glyptocidaridae	* <i>Glyptocidaris</i>	Mortensen (1935)
	Stomopneustidae	* <i>Stomopneustes</i>	specimens; Mortensen (1935)

for the same taxa previously published by Kroh and Smith (2010) to create a data matrix comprising 353 characters for 162 Recent and fossil taxa (see electronic supplementary Data S1). For all fossil taxa except *Archaeocidaris*, pedicellarial character states were scored as unknown. All pedicellarial characters were treated as unordered except character P21, which was ordered as it refers to an ontogenetic series. Non-pedicellarial characters were treated as ordered or unordered exactly as in Kroh and Smith (2010). The data matrix was run in the phylogenetic program PAUP* (Swofford 2002) with all characters given equal weight. A heuristic search was carried out and the characters then reweighed by their maximum rescaled consistency index. A second heuristic search was carried out with 100 random additions. To calculate approximate bootstrap support values for nodes, we ran 100 000 fast heuristic searches on the reweighted matrix, sampling all characters at random but applying weights and omitting all fossil taxa.

Pedicellarial characters were optimized onto the maximum parsimony tree using the accelerated transformation option, which favours secondary loss over independent evolution. While the choice of optimization has a major impact on how pedicellarial characters are assigned to fossil taxa (whose pedicellariae are unknown), it has little effect on Recent taxa, where almost all character states are known. The distributions of individual pedicellarial characters were therefore mapped onto the cladogram, after having removed all fossil taxa, using the program MacClade (Maddison and Maddison 2005).

We have taken a total evidence approach by combining pedicellarial characters with other skeletal characters to

construct the best overall supported phylogenetic hypothesis. While this could have compromised our approach by introducing some degree of circularity, mapping pedicellarial character state changes onto cladograms constructed from just independent test-plus-spine (Kroh and Smith 2010) or molecular (Smith *et al.* 2006) characters results in much the same outcome. We therefore feel confident that the history of pedicellarial characters that we outline below is robust. An advantage of our approach is that it provides a ready means of dating events in the history of pedicellarial evolution. Although fossil echinoids are very rarely preserved with any of their complement of pedicellariae attached and the record of fossil pedicellariae is very patchy and difficult to interpret, we can still date nodes on our cladogram, and thus the timing of events in the evolution of pedicellariae, on the basis of associated test characters.

Analysing the 75 extant echinoids on the basis of their 50 pedicellarial characters alone led to many more than 65 000 equally parsimonious solutions (upper memory limit) and produced little resolution. Reweighting characters by their retention index generated a topology in which none of the traditional groupings was identified (not shown) suggesting that homoplasy and secondary loss in pedicellarial characters is rife.

A heuristic search of the full data matrix for all 162 Recent and fossil taxa and the full 353 test and appendage characters given equal weights again found 65 300 equally parsimonious trees 1888 steps in length. Trees had a low consistency index (0.27) but a high retention index (0.78), and a strict consensus retained a great deal of phylogenetic structure. After

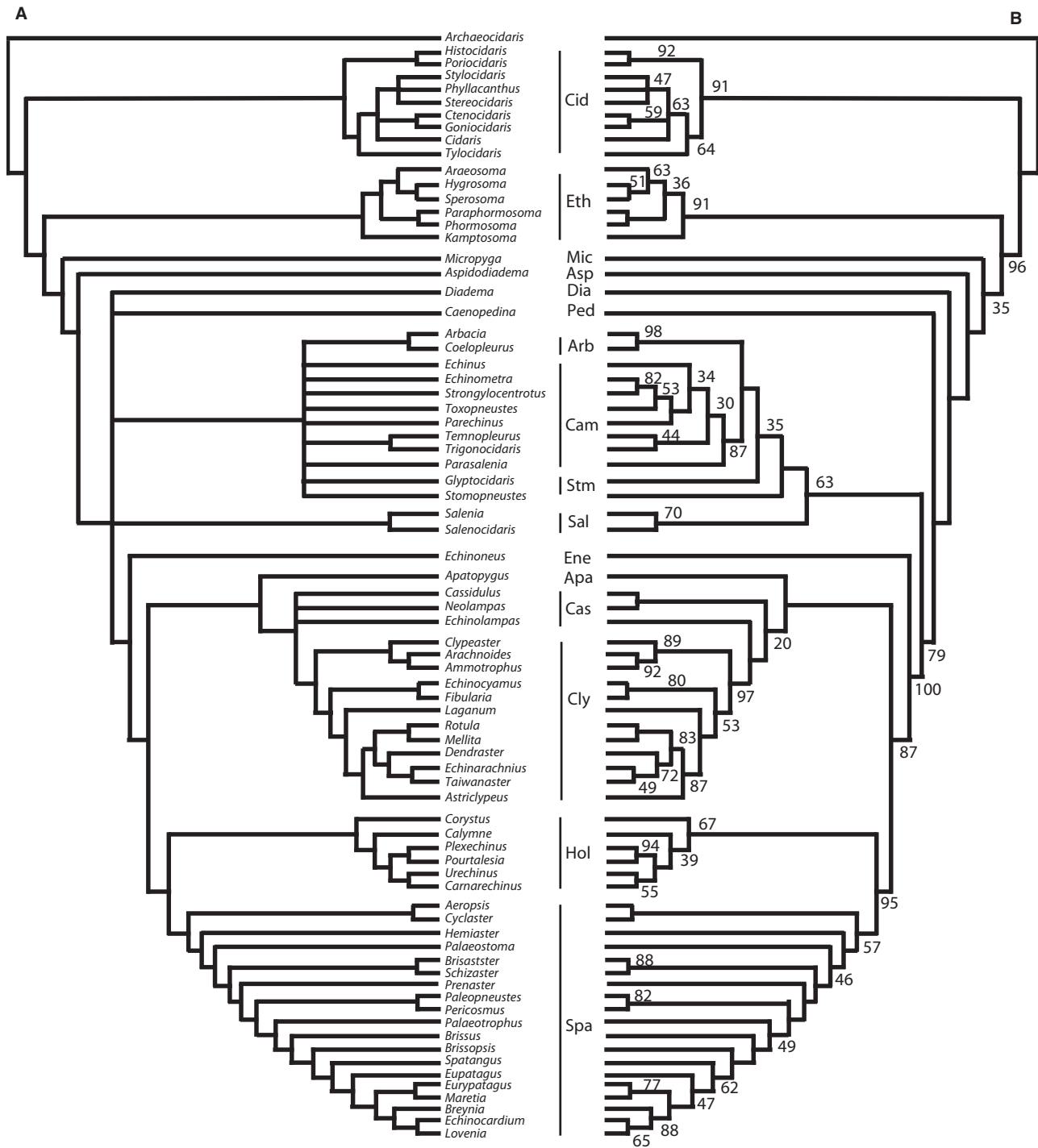


Fig. 3. —**A.** strict consensus for just extant taxa of the 130 equally parsimonious trees 1888 steps in length recovered with all characters given equal weight. —**B.** strict consensus for just extant taxa of the 9 equally parsimonious trees, with a length of 351.967 steps recovered after reweighting characters by their mean rescaled consistency index. Figures in B are bootstrap values based on 100 000 fast heuristic searches of a datamatrix of just Recent taxa. Out, outgroup; Cid, Cidaroida; Eth, Echinothurioida; Mic, Micropygoida; Asp, Aspidodiadematoidea; Dia, Diadematoidea; Ped, Pedinoida; Arb, Arbacioida; Cam, Camarodonta; Stm, Stomopneustoida; Sal, Salenioida; Ene, Echinoneoida; Apa, Apatopygidae; Cas, Cassiduloida; Cly, Clypeasteroida; Hol, Holasteroida; Spa, Spatangoida.

removing the fossil taxa and condensing to remove all duplicate trees just 130 equally parsimonious trees remained (Fig. 3A). Characters were reweighed by their mean rescaled consistency index and the analysis rerun with the full data matrix, 2187 equally parsimonious trees resulted with a length of 351.967, a consistency index of 0.48 and a retention index of 0.89. After removing the fossil taxa and removing duplicate topologies, there were just nine equally parsimonious trees. A strict consensus of these trees after removing all fossil taxa is shown in Fig. 3B. While this is closely similar to the topology found by Kroh and Smith (2010) using just test features, it is not identical. The tree differs in the following four areas: (1) the genera *Glyptocidaris* and *Stomopneustes* no longer group together as a clade, based on the very primitive structure of the globiferous pedicellariae in *Stomopneustes* and their advanced, camarodont-like structure in *Glyptocidaris*. (2) The position of *Aspidodiadema* is now more basal than that of the pedinoids or diadematids and *Caenopedina* is now the closest living relative to the combined Echinacea, Calycina and Irregularia clade. However, these nodes are very weakly supported and pedicellarial characters provide no convincing clues as to the precise branching order of these primitive groups. (3) *Astriclypeus* is now basal to the Scutellina clade, which reflects the primitive three-valved nature of the pedicellariae in *Astriclypeus* compared with other members all of which have bivalved pedicellariae. (4) The paedomorphic *Taiwanaster* now groups with *Echinarachnius* rather than falling at the base of the Scutellina, in keeping with the findings of Mooi (1990b). It is onto the topology shown in Fig. 3B that pedicellarial characters are optimized and from which we deduce the evolutionary histories of the different pedicellarial morphologies.

Globiferous pedicellariae

Pedicellariae that secrete venom are widely distributed across the Echinoidea (Fig. 4) and must have been present in the latest common ancestor of all modern echinoids. Fistulate globiferous pedicellariae without fangs clearly represent the primitive form, being found in both cidaroids (Fig. 4A–B) and the primitive irregular echinoids *Echinoneus* and *Apatopygus* (Fig. 4D–E). These have a large fistula with a distal foramen that is surrounded by a ring of small teeth. In *Apatopygus* and *Echinoneus* the fistula forms almost the entire blade. Their forerunner may have been the narrow-bladed pedicellarial type described by Geis (1936) from the late Carboniferous and Mostler's 'group 1, type 3' globiferous pedicellariae from the Triassic (Fig. 4C). This distinctive pedicellaria clearly lacked an internal cavity for housing venom-secreting cells, but these may have resided in the prominent sagittal groove of the blade. It would then be only a small evolutionary step to partially enclose this groove creating the fistulate globiferous pedicellariae of crown-group echinoids.

The presence of a distal fang in the fistulate globiferous pedicellariae of some Cidarinae (Fig. 4B) is a later derived

character that arose no earlier than the Cretaceous. The fistulate globiferous pedicellariae of spatangoids represent a more derived version in which the distal part of each valve is developed as a tubular finger-like extension with a distal denticulate foramen (Fig. 4J–M), possibly giving a stronger bite. A trend in this form is for the distal teeth to become more fang-like (Fig. 4N–O) and this is taken to extremes in the spatangoid genera *Brisaster* (Fig. 4P), *Palaeostoma* and *Palaeobrissus* where each valve ends in a single large fang and the venom opening is reduced to a small pore. Interestingly, fistulate globiferous pedicellariae with denticulate opening and tubular neck very similar to those of extant atelostomates are found in the late Triassic (Mostler 2009: pl. 3, fig. 4) and Late Cretaceous (Nestler 1966: pl. 4, fig. 2 and pl. 5, fig. 5).

Fanged globiferous pedicellariae with venom glands housed outside the valves must have evolved early in the Mesozoic as they are present in *Caenopedina* (Fig. 4F–G) and in a range of stirodons and camarodons (Figs 2G–M and 4H–I). This places their origin as no later than the Norian in the late Triassic. The primitive condition in these fanged pedicellariae is for venom glands to be distributed in the thicken skin of the valves themselves and for there to be a small number of distal fangs (Fig. 2E). This is the condition seen in *Caenopedina* and *Stomopneustes* and in the atelostomates among the spatangoid *Brisopsis* (Fig. 4K) and holasteroid *Pourtalesia*. In such cases, the venom gland is either positioned on the back of the distal region of the valve where venom is released through pores at the base of the fangs or where the venom gland surrounds the fangs, venom is released directly into the puncture wound. In some members, the blade has become partially open.

An important innovation is found in *Glyptocidaris* and all camarodons where a characteristic groove runs along the top of the fang (Fig. 2G–H) delivering venom to the tip of the needle-like blade. This must have arisen by at least the early Cretaceous and possibly earlier. In some camarodons, such as the echinometrids the tip of the valve is asymmetric (with double venom glands on each valve); on one side there is a large fang with a large groove, on the other a secondary smaller fang that lacks a groove (Fig. 2H). In one clade of more derived Camarodons, the venom glands have shifted in position to the stalk and there form well defined sacks, and there is only a single needle-like terminal fang (Fig. 2K–M). The stalk venom sacks are primitively double in *Parasalenia* and *Glyptocidaris* but single (Fig. 2M) in more derived members. The strong similarity between the fanged pedicellariae of camarodons and the stirodont *Glyptocidaris* points to them being sister groups. Fanged globiferous pedicellariae have apparently evolved independently in the clypeasteroid *Fibulariella* (figured in Mooi, 1989: fig. 23), a taxon not included in our analysis. Originally included as a subgenus of *Fibularia* by Mortensen (1948b), *Fibulariella* is now thought to be closer to the laganids (Mooi et al. 2001).

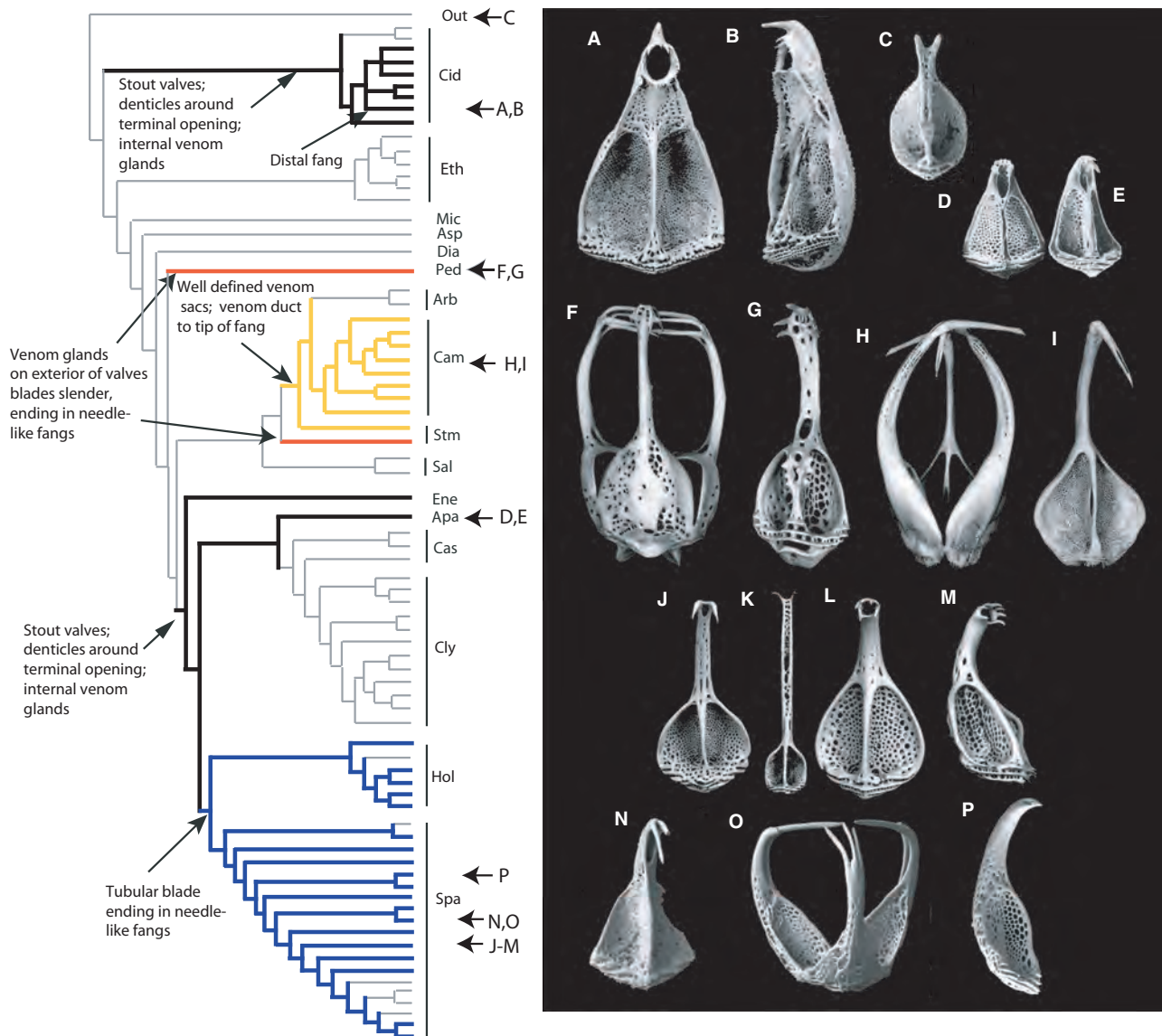


Fig. 4. —Strict consensus of the 9 equally parsimonious trees found in the analysis showing the major events in globiferous pedicellarial evolution. Globiferous pedicellariae as follows: —**A, B.** *Calocidaris* fistulate pedicellarial valve: **A**, interior; **B**, lateral. —**C.** ‘group 1, type 3’ valve interior (from Mostler 2009; pl. 3, fig. 7): Norian, Upper Triassic of Austria. —**D, E.** *Apatopygus* fistulate pedicellarial valve (from Baker 1983): **D**, interior; **E**, oblique profile. —**F, G.** *Caenopedina* fanged pedicellaria: **F**, head; **G**, valve interior. —**H, I.** *Toxopneustes* fanged pedicellaria: **H**, head; **I**, valve interior. —**J–M.** spatangoid fistulate pedicellarial valves: **J–L.** *Brissopsis*, interior; **M.** *Brissalius*, oblique lateral. —**N, O.** *Amphipneustes* fistulate pedicellaria: **N**, valve interior; **O**, head. —**P.** *Brisaster*, fistulate pedicellarial valve, lateral. Coloured clades indicate major morphological groups; light grey thin lines – pedicellariae of this type absent. Not to scale. For abbreviations see Fig. 3.

Globiferous pedicellariae have been secondarily lost numerous times in evolution: at least three times in spatangoids, once in holasteroids and from all cassiduloids and clypeasteroids except *Fibulariella* noted above. Among regular echinoids, they have been lost at least once in cidaroids and are absent from all echinothurioids, salenioids, arbacioids and most aulodonts (except *Caenopedina* and *Centrostephanus*).

While this raises the possibility that globiferous pedicellariae evolved independently in the cidaroids, irregular echinoids and pedinoid + stirodont + camarodont clade, this seems unlikely, given the similarity between those of cidaroids and primitive irregular echinoids. Figure 4 summarizes the major evolutionary changes that have occurred to globiferous pedicellariae in post-Palaeozoic echinoids.

Ophicephalous pedicellariae

Ophicephalous pedicellariae are absent from the outgroup *Archaeocidaris* and from all cidaroids but are present in many echinothurioids at the base of the euechinoid clade, and so must have evolved in stem-group euechinoids (Fig. 5). The

record of ophicephalous pedicellariae from the Silurian (Mostler 2009) is surely erroneous. However, this form of pedicellaria had definitely evolved by the late Upper Carboniferous (Geis 1936) and had diversified into several discrete forms by the late Triassic (Mostler 2009: pl. 1, figs. 6–7). This suggests either that ophicephalous pedicellariae were present in late

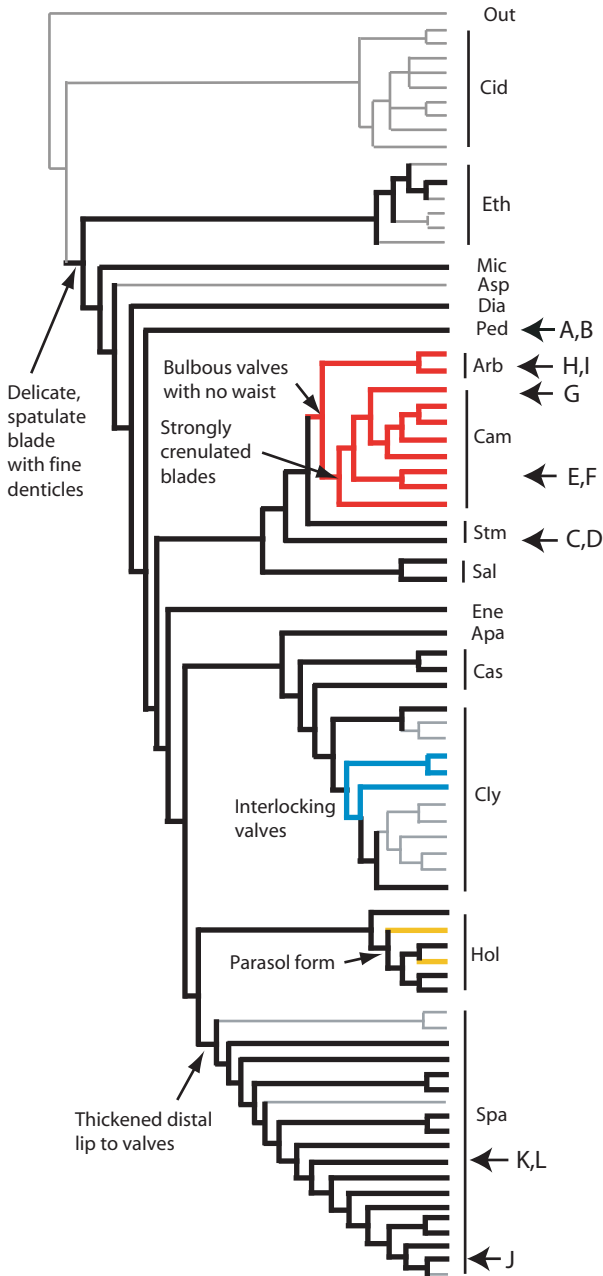


Fig. 5. —Strict consensus of the 9 equally parsimonious trees found in the analysis showing the major events in ophicephalous pedicellarial evolution. Ophicephalous pedicellariae (all from the aboral surface) as follows: — **A, B.** *Caenopedina*: **A**, valve interior; **B**, head. — **C, D.** *Stomopneustes*: **C**, valve interior; **D**, head. — **E, F.** *Temnopleurus*: — **E**, valve interior; — **F**, head. — **G.** *Echinus*, head. — **H, I.** *Coelopleurus*, valve interiors. — **J.** *Echinocardium*: valve interior. — **K, L.** *Brissopsis*: **K**, head; **L**, valve interior. Not to scale. For abbreviations see Fig. 3.

stem group echinoids and were lost in the line leading to modern Cidaroida or that cidaroids and euechinoids had diverged by the late Upper Carboniferous. Both aboral and oral ophicephalous pedicellariae, once evolved, remained remarkably conservative in appearance, but were repeatedly lost, particularly in infaunal clades (at least three times each in clypeasteroids and spatangoids). Interestingly, in all primitive groups (echinothurioids, aspidodiadematids, micropygids and some diadematids) ophicephalous pedicellariae are present only in juvenile stages, whereas in all more derived groups they are retained into adulthood. Furthermore, the ophicephalous pedicellariae in aspidodiadematids and some diadematids are unique in being invested with glandular tissue (Fig. 2Nii) as well as having the valveless claviform type (Fig. 2Oii). Despite this conservatism, aboral ophicephalous pedicellariae did undergo some limited morphological change. More robust aboral ophicephalous pedicellariae with stronger bite evolved in one clade of regular echinoids, in the immediate outgroup to arbaciods and camarodonts. These pedicellariae (Fig. 5E–I) have stout valves that have lost their proximal waist so that the valves meet along their entire length. Further modifications to ophicephalous pedicellariae have occurred among the irregular echinoids. In the Eocene both laganid and fibulariid clypeasteroids evolved ophicephalous pedicellariae whose individual valves became so strongly interlocking that they remain tightly articulated even after death (Mooi 1990a: fig. 7a). These solid valves must be particularly effective at holding struggling prey. Another distinctive modification occurs in the ophicephalous pedicellariae of *Clypeaster* and the cassiduloid *Echinolampas* and its close relatives (*Planilampas*, *Conolampas*). Here the proximal part of the blade has become tubular and the distal part an ovate, denticulate foramen with an inturned distal edge (Fig. 2i–iv). However, the most highly derived ophicephalous pedicellariae are the so-called parasol pedicellariae that are found in the deep-sea holasteroids *Calymne* and *Pourtalesia* (see Saucède et al. 2009). In these taxa, the blade is long and slender and terminates in an overhanging head with a palmate fan of downward-facing teeth. How these function has never been observed.

Triphyllous pedicellariae

As triphyllous pedicellariae are absent from *Archaeocidaris* and all cidaroids, we deduce that they evolved once in the stem group of the Euechinoidea, in the Triassic or latest Permian. Within euechinoids, they have only occasionally been secondarily lost, in a couple of infaunal irregular echinoid clades (Fig. 6). The primitive shape of valves is conical with a distinct neck, as seen in echinothurioids (Fig. 6A–B) and various aulodont taxa, but they evolved to become smaller and flatter in more derived groups (Fig. 6C–M). Bilobed valves evolved twice independently, once in cassiduloids and once in camarodonts. In mellitid and dendrasterid scutellines, this form of pedicellaria has given rise to the biphyllous pedicellariae, where there are just two valves (Fig. 6H–J).

Tridentate pedicellariae

These encompass the largest morphological range in diversity of our four major pedicellarial types (Figs 7 and 8) and are the only one widely found in Palaeozoic echinoids. Their presence is thus plesiomorphic for crown-group echinoids. Straight, slender-bladed tridentate pedicellariae with open blades that meet along most of their length is the most primitive morphology encountered (Fig. 7J–K). This form is present in the Palaeozoic outgroup and in cidarids (Fig. 7J–K), echinothurioids (Fig. 7L–M, Q–S) and aspidodiadematids. In more derived members, the blades tend to be separated proximally and touch only towards their tips (Fig. 7A–G). In irregular echinoids, the tips of the blades are usually spatulate (Fig. 7H–I), whereas in most regular echinoids they are primitively tapered to a point (Fig. 7C–G). Another innovation occurred in holasteroids, and independently in the echinothurioid *Kamptosoma*, when the shaft of the blade became tubular rather than open and U-shaped, thus strengthening the valve. These large pedicellariae have been secondarily lost along numerous branches (once each in cidaroids, clypeasterines, scutellines, holasteroids, trigonocidarids, glyptocidarids and twice in spatangoids and echinothurioids).

A second form of tridentate pedicellariae with short, stubby blades commonly accompanies forceps-like tridentates. The primitive morphology is for blades to be open and meeting along the majority of their length, being just stubby versions of the larger form. However, in more advanced euechinoids (camarodonts (Fig. 7N–O), stirodons and irregular echinoids (Fig. 7T–Y)) contact of blades is typically reduced. The beaked form of bidentate pedicellariae in scutelline clypeasteroids (Fig. 7Z–FF) is almost certainly derived from this form (Fig. 7), with the development of elongated distal teeth in some species (Fig. 7EE–FF). It is quite common in spatangoids for the edges of the valves of the tridentate pedicellariae to be highly denticulate (Fig. 7T–U). Once again this form of pedicellaria has been lost several times independently.

Lantern-like (rostrate) tridentate pedicellariae (Fig. 8) primitively occur with a partially enclosed proximal region of the blade as seen in echinothurioids (e.g. *Kamptosoma* and *Araeosoma* Fig. 8A–C). Rather broad, open curved blades, are seen in aspidodiadematids, pedinoids (Fig. 8H–I), diadematids (Fig. 8D–E) and primitive irregulars. They are also present in the camarodonts *Loxechinus* (Fig. 8F–G), *Echinus* and *Echinometra*, and some clypeasteroids but are absent from all stirodons. Whether these are all truly homologous is questionable as curved tridentate blades may have evolved several times independently: their scattered distribution suggests multiple origins. Atelostomates evolved a rather distinctive form of rostrate pedicellaria with narrow, well-defined blades terminating in short fans of teeth (Fig. 8J–M). Secondary loss of rostrate pedicellariae is again prevalent in spatangoids and holasteroids. The record of rostrate pedicellariae from the Carboniferous (Mostler 1971) and the Norian (Mostler

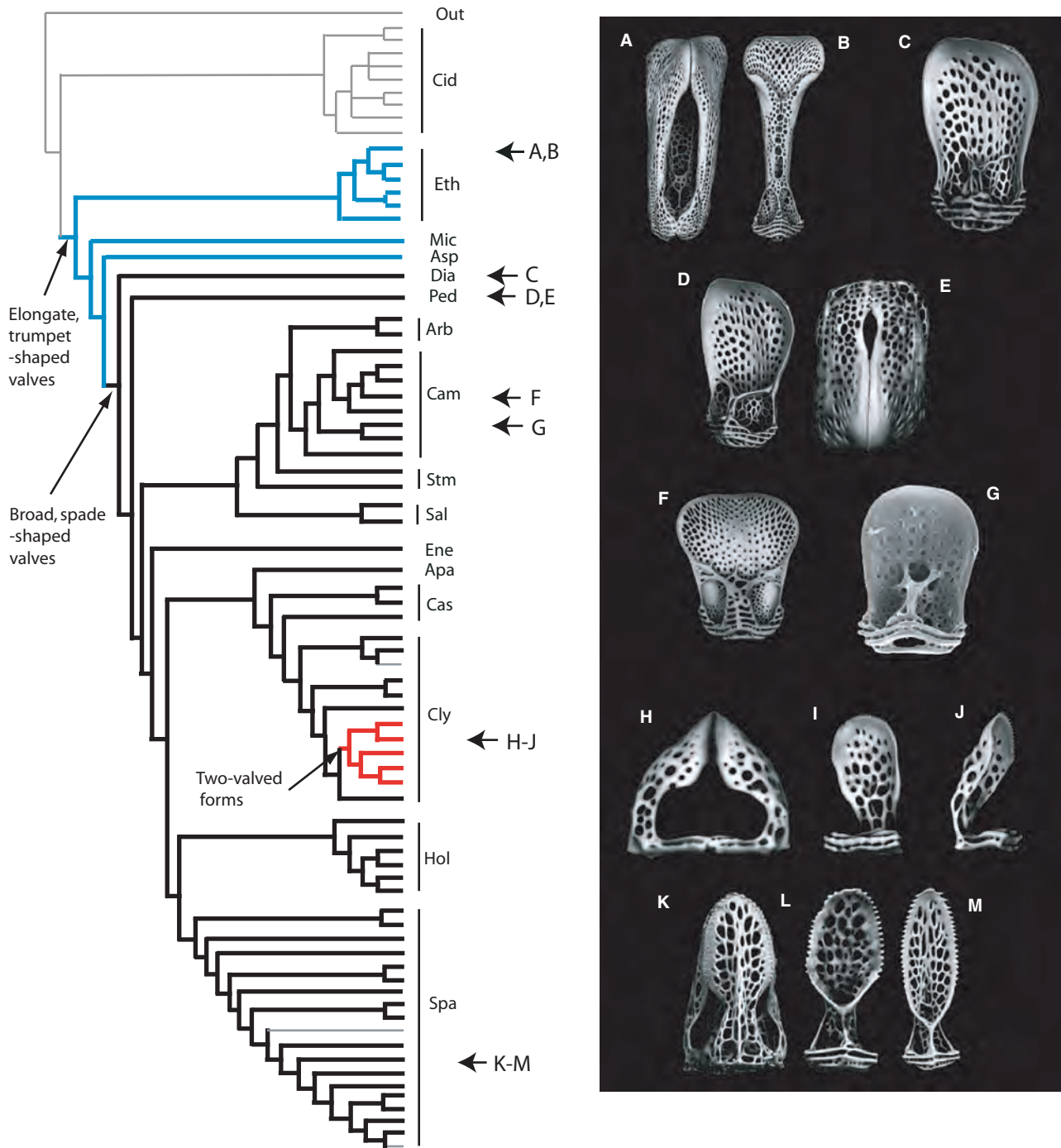


Fig. 6. —Strict consensus of the 9 equally parsimonious trees found in the analysis showing the major events in triphyllous pedicellarial evolution. Triphyllous pedicellariae as follows: — **A–B.** *Araeosoma*; **A**, head; **B**, valve interior. — **C.** *Echinothrix*: valve interior. — **D–E.** *Caenopedina*: **C**, valve interior; **D**, head. — **F.** *Toxopneustes*, valve interior. — **G.** *Tennopleurus*, valve interior. — **H–J.** *Mellita* bidentate form: — **H.** head; — **I.** valve interior; — **J.** valve lateral. — **K–L.** *Brissopsis*; — **K.** head, — **L.** valve interior. — **M.** *Brissalius*, valve interior. Not to scale. For abbreviations see Fig. 3.

1968) are both highly doubtful. The oldest unambiguous ros-trate pedicellariae reported so far come from the Late Creta-ceous (Nestler 1966: pl. 3, figs. 6–7).

Dactylous pedicellariae are only present in deep-water echi-nothurioids of the genera *Araeosoma* (Fig. 2X–Z) and *Hapalo-soma*, being absent from both the Palaeozoic outgroup and all

other crown-group echinoids. The rod-like structure of the proximal regions of the valves that sit directly on the stalk and the lack of well-defined adductor and abductor muscles clearly differentiate this type of pedicellaria from all other modern forms, and they most closely resemble early spinate pedicellariae. They may therefore represent the most primitive pedicellarial morphology to be found in extant forms, one that has been superceded by functionally better designs in other living taxa.

Discussion

The evolutionary arms race against pests and predators

Late stem-group echinoids were equipped with just two kinds of pedicellariae, a large straight forceps-type tridentate form and a much smaller, possibly primitive globiferous form. Yet by the Jurassic echinoids had evolved a multiplicity of types and all four major structural types were clearly established. The evolution in the late Palaeozoic of the first primitive globiferous pedicellariae along with the first ophicephalous pedicellariae suggest that echinoids were facing a significantly increased level of threat from predators and ectoparasites at this time. Globiferous pedicellariae are employed to disable or kill small pests and deter the larger predators such as starfishes while ophicephalous pedicellariae offer a formidable defence against ectoparasites and other small pests that move through the spine canopy. The marked diversification of pedicellarial forms in the early Mesozoic and the shift to better, more effective delivery of venom to puncture points in globiferous pedicellariae point to a significant step-up in the defensive armament of echinoids presumably in response to the Mesozoic marine revolution (Vermeij 1977). Another indication of the rising threat from ectoparasites is the evolution in cidaroids at this time of flattened secondary spines forming a palisade-like protective barrier around the large muscles at the base of primary spines and above the rows of tube-feet. Furthermore, fouling of the epithelium by bacterial plaque and fine detritus must also have become a significant problem at this time as echinoids evolved small triphyllous pedicellariae specifically designed to cleanse the test surface.

The evolutionary trend towards better, more effective armament continued through the Mesozoic and into the Tertiary with globiferous pedicellariae in particular becoming progressively better adapted for their role of deterring pests and predators. The mechanical design of globiferous pedicellariae evolved to provide ever more effective delivery of venom. Whereas the most primitive forms had rather stout valves with only small denticles surrounding a relatively large opening to deliver venomous secretions, in more advanced forms the venom secreting cells multiplied and formed distinct glands, at first in the head but later moving to the top of the stalk. There is also a move towards a more effective bite, presumably to cope with warding off predators with

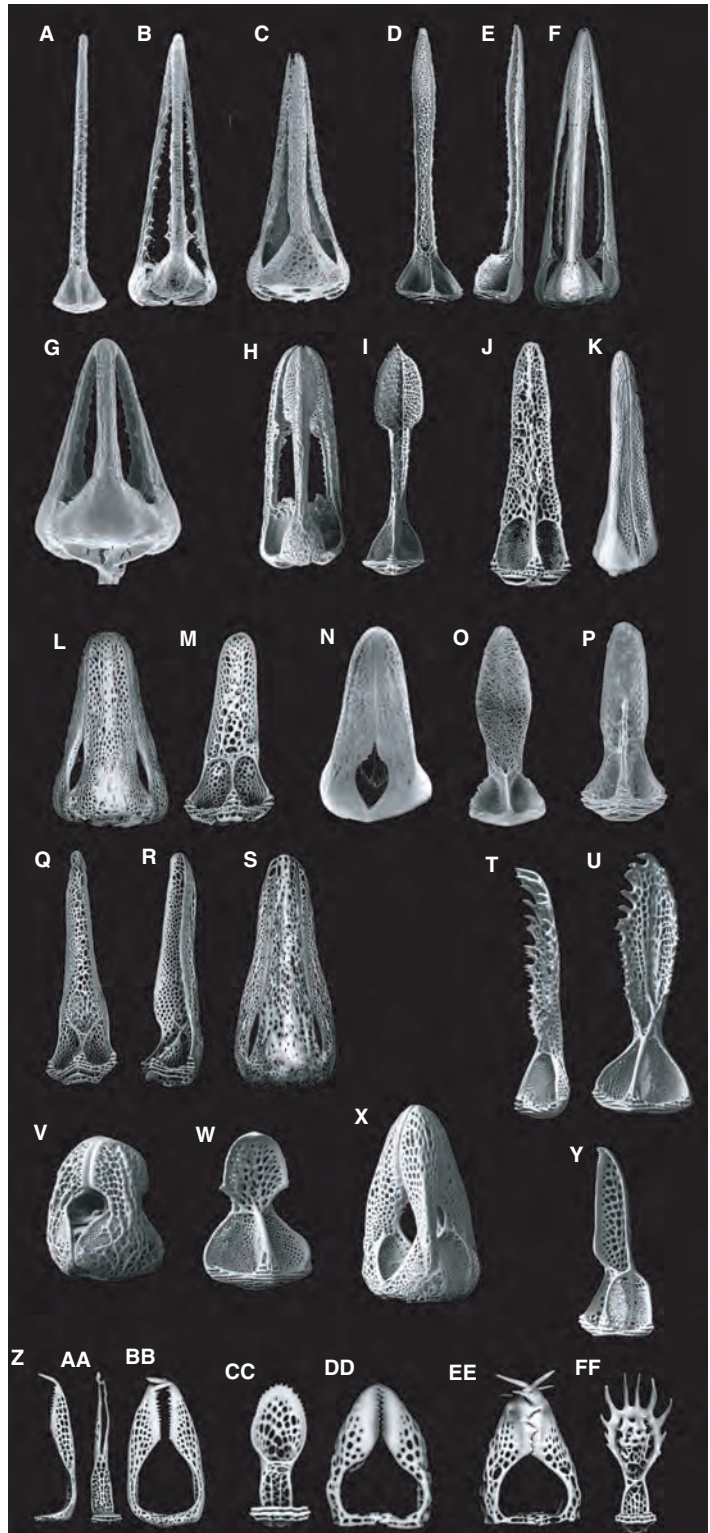
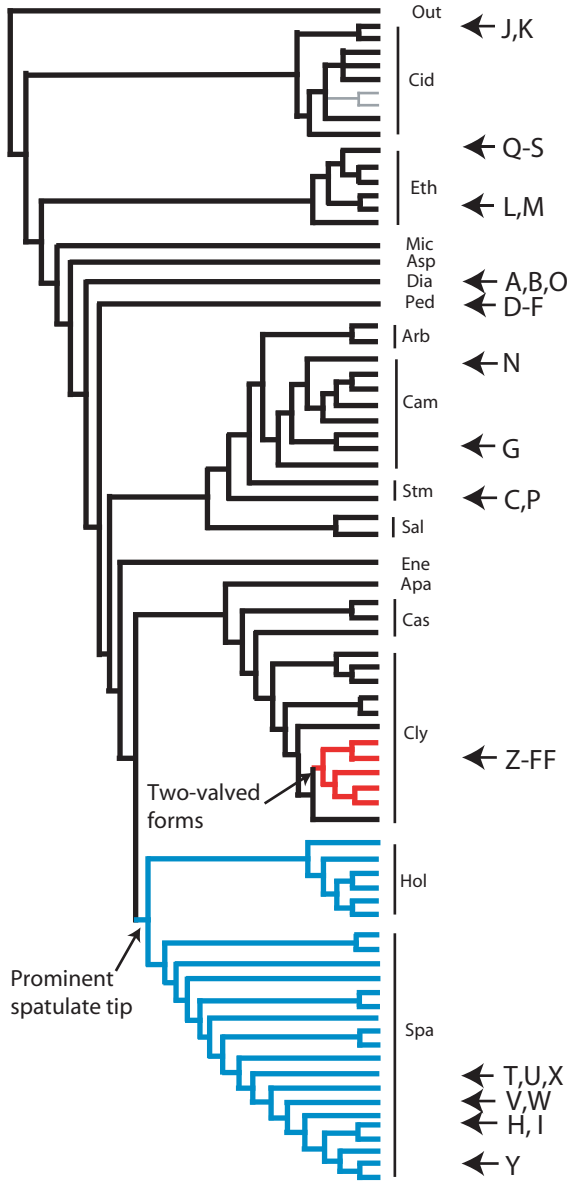
thicker skin or better protection. This has occurred three times independently. In cidaroids, one derived clade has evolved a single stout fang at the tip of its fistulate globiferous pedicellariae to increase its piercing power. In spatangoids, there is a tendency along at least two lines to replace the fan of small distal teeth with a smaller number of large fangs. A similar trend is also seen in the line leading to camarodonts, with more primitive stirodons such as stomopneustids having a fan of smaller teeth, which in the more derived *Glyptocidaris* and camarodonts is replaced by a single fang. Finally the valves become lighter and stronger by evolving more tubular blades, and this occurred at least twice, once in the fanged and once in the fistulate forms. Globiferous pedicellariae reached the peak of their evolution in the Neogene toxopneustids where the valves have hooked tips with a barb (see Fig. 2L). This is clearly designed to remain in the predator to increase venomation time. Camarodonts have also evolved stronger more sturdy ophicephalous and rostrate pedicellariae able to grip and hold struggling prey more effectively. There has thus been continual selection pressure on echinoids to improve their defensive armament against pests and predators and this has been most pronounced in shallow water, epifaunal clades.

With this extended history of evolution, pedicellariae might therefore be expected to provide good phylogenetic markers. Yet cladistic analysis of pedicellarial characters on their own generates a very unexpected tree topology in which none of the well-defined and long-established groupings are supported. This is in marked contrast to phylogenies derived from test and spine characters (Kroh and Smith 2010) or molecular data (Smith *et al.* 2006). This apparent lack of phylogenetic signal from pedicellarial characters arises largely because of the extensive number of secondary losses that have taken place over time. While a few morphologies are clearly clade specific and provide excellent synapomorphies, most show a patchy distribution. Furthermore, our phylogenetic analysis suggests that all four major pedicellarial types had evolved before the end of the Triassic and that their current patchy distribution has arisen through multiple independent secondary loss. This leads pedicellarial characters to show disproportionately high levels of homoplasy (average homoplasy index for all 49 characters = 0.51). When compared with the average homoplasy levels encountered in characters drawn from various categories of test and spine morphology (Fig. 9), it is clear that pedicellariae show higher levels of homoplasy than any other set of skeletal characters. Only interambulacral features of the test reach almost the same levels, with an important source of homoplasy coming from variation in detailed tuberculation patterns.

Secondary loss of defensive pedicellariae in epifaunal echinoids occurs in a few groups and can be explained by the greater development of defensive spines and the migration of species to deeper water, where there are fewer fouling organisms (particularly larvae) and a reduced frequency of contact with larger predators. Aulodonts, echinothurioids, salenioids

and coelopleurid arbacioids have all migrated to deeper water over time and have lost their globiferous pedicellariae, relying on their long, needle-like primary spines to ward off larger predators. Among their shallow water members, diadematis

evolved primary spines that contain venom in the skin as well as glandular ophicephalous pedicellariae, while both deep and shallow water echinothurioids developed venomous glandular spines.



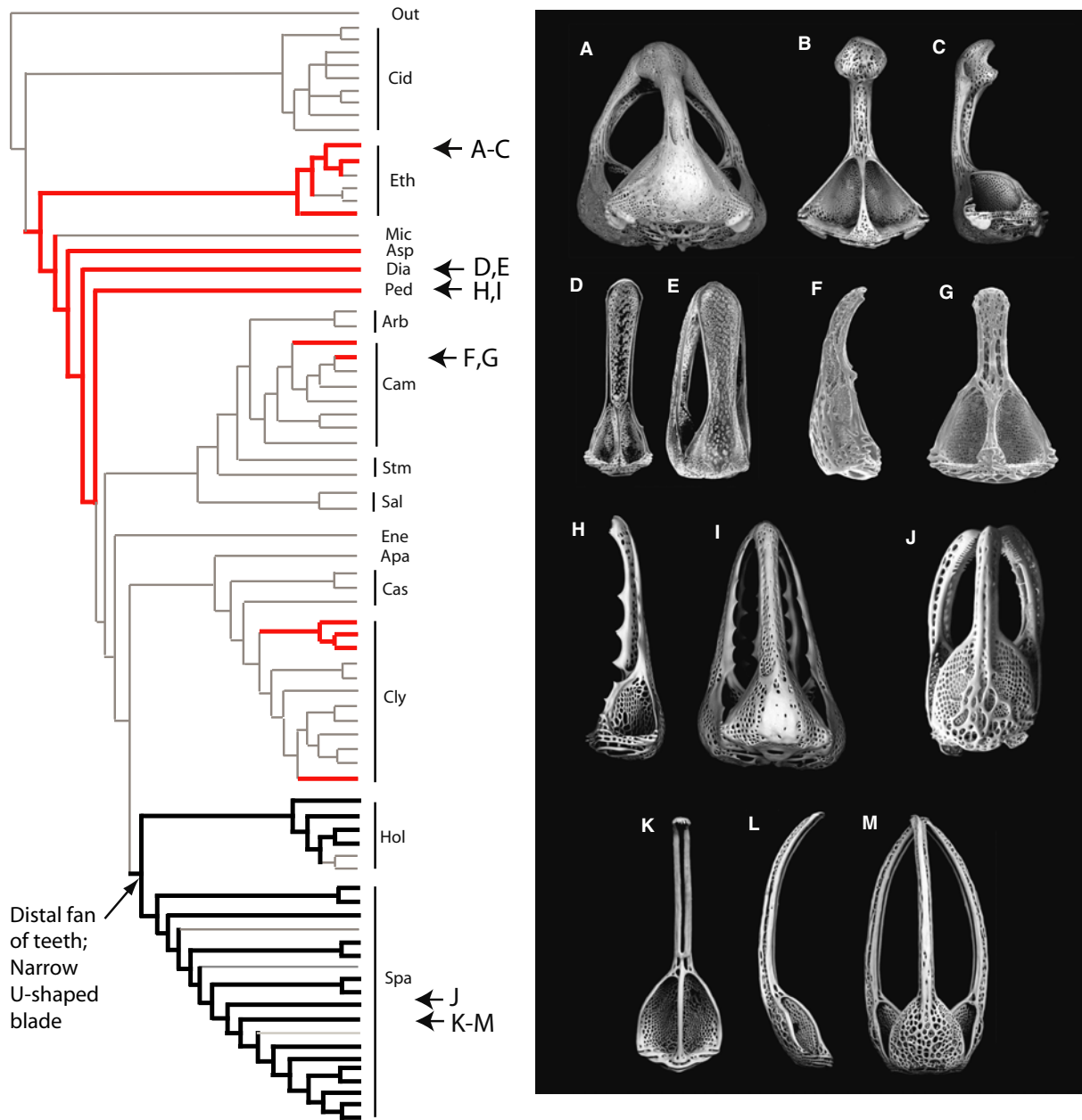


Fig. 8. —Strict consensus of the 9 equally parsimonious trees found in the analysis showing the major events in rostrate pedicellarial evolution. Rostrate pedicellariae as follows: — **A–C.** *Araeosoma*: **A**, head; **B**, valve interior; **C**, valve in oblique profile. — **D, E.** *Echinothrix*: **D**, valve interior; **E**, head. — **F, G.** *Loxechinus*: **F**, valve in lateral profile; **G**, valve interior. — **H, I.** *Caenopedina*: — **H**, valve in lateral profile; **I**, head. **J**, *Spatangus*, head. — **K–M.** *Brissalius*: **K**, valve interior; **L**, valve in lateral profile; **M**, head. Not to scale. For abbreviations see Fig. 3.

Fig. 7. —Strict consensus of the 9 equally parsimonious trees found in the analysis showing the major events in tridentate pedicellarial evolution: — **A–I.** forceps-like pedicellariae; — **J–Y.** beak-like pedicellariae; — **Z–FF.** bidentate pedicellariae. Pedicellariae as follows: — **A–B.** *Diadema*: **A**, valve interior; **B**, head. — **C.** *Stomopneustes*, head. — **D–F.** *Caenopedina*: **D**, valve interior; **E**, valve lateral; **F**, head. — **G.** *Temnopleurus*, head. — **H–I.** *Linopneustes*: **H**, head; **I**, valve interior. — **J–K.** *Histocidaris*: — **J**, valve interior; **K**, head. — **L–M.** *Phormosoma*: **L**, head; **M**, valve interior. — **N.** *Echinus*, head. — **O.** *Diadema*, valve interior. — **P.** *Stomopneustes*, valve interior. — **Q–S.** *Araeosoma*. **Q**, valve interior; **R**, valve profile; **S**, head. — **T–U.** *Brisaster*: **T**, valve in profile; **U**, valve interior. — **V–W.** *Spatangus*: **V**, head; **W**, valve interior. — **X.** *Amphipneustes*: head. — **Y.** *Echinocardium*: valve in lateral profile. — **Z–BB.** *Encope*: **Z**, valve in lateral view; **AA**, valve interior; **BB**, head. **CC–DD.** *Mellita*: **CC**, valve interior; **DD**, head. — **EE–FF.** *Encope*: **EE**, head; **FF** valve interior. Not to scale. For abbreviations see Fig. 3.

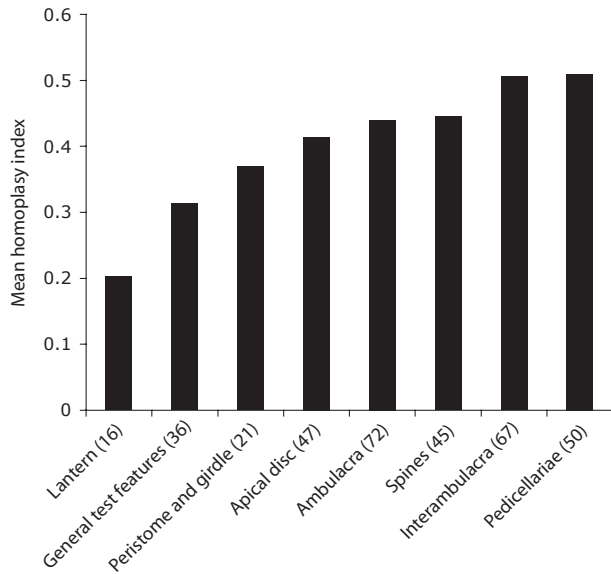


Fig. 9. —Plot of homoplasy indices for different groups of skeletal-based characters. Number of characters from which homoplasy index is calculated is given in brackets for each suite.

Secondary loss of pedicellariae seems to be particularly prevalent among irregular echinoids, especially those living infaunally within rather coarse, well-ventilated sands. Cassiduloids, echinoneoids and most clypeasteroids generally have relatively few types of pedicellariae. Only ophiocephalous pedicellariae occur in large numbers, and in the flattened clypeasteroids these are concentrated around the margin of the test, presumably forming a defensive barrier against small ectoparasites that might invade the spine canopy where it is least dense because of the strong curvature of the test surface. On the other hand, although there is abundant secondary loss of globiferous pedicellariae in atelostomates that live in coarse granular sand, there is a concurrent increase in the diversity of other pedicellariae, particularly tridentate forms. In mud-dwelling atelostomates that build well-defined burrows such as *Brissopsis*, the globiferous pedicellariae are richly developed with both fistulate and fanged forms occurring on the same individual. This may reflect the greater prevalence of nematodes and other small infaunal parasites of echinoids burrowing in these finer sediments.

Acknowledgements

We thank Jorge Ceballos (STRI) for his help with SEM and Mike Reich for pointing out important papers that we might otherwise have missed. Simon Coppard was funded by SENACYT (Secretaría Nacional de Ciencia, Tecnología e Innovación, Panamá) as part of project COL08-002. We are particularly grateful to Rich Mooi and an anonymous referee for their very helpful and constructive comments that have improved this paper.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Data S1. Data matrix used for the phylogenetic reconstruction in nexus format.

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Appendix. List of characters and character states used in the phylogenetic analysis

Globiferous pedicellariae

- P1.** Globiferous pedicellariae bearing venom glands: absent (0); present (1).
- P2.** Globiferous pedicellariae fanged and lacking distal foramen (Fig. 2J–M): no (0); yes (1).
- P3.** Fanged globiferous pedicellariae: fine (straight-valved) type (Fig. 2J) (0); coarse, globular (curved-valved) type (Fig. 2E) (1).
- P4.** Fanged globiferous pedicellariae with well-differentiated venom sacs beneath jaw set (Fig. 2Iii): no (0); yes (1).
- P5.** Fanged globiferous pedicellariae with double venom sacs beneath jaw set: no (0); yes (1).
- P6.** Fanged globiferous pedicellariae with stalk glands (Fig. 2Iiii): no (0); yes (1).
- P7.** Fanged globiferous pedicellariae: blade terminates as a single tooth (Fig. 2J) (0); blade terminates as 2–3 long teeth (Fig. 4F) (1).
- P8.** Fanged globiferous pedicellariae with: no lateral teeth directly beneath distal fang (Fig. 2J) (0); asymmetric lateral tooth beneath distal fang (Fig. 2H) (1); paired lateral teeth beneath distal fang (2).

P9. Fanged globiferous pedicellariae: fang with venom sac furrow (Fig. 2Gi): no (0); yes (1).

P10. Fanged globiferous pedicellariae: blade clearly differentiated as a closed, rounded shaft (Fig. 4L) (0); open, U-shaped blade (1).

P11. Fanged globiferous pedicellariae: stalk longer than length of valves: no (0); yes (1).

P12. Fanged globiferous pedicellariae with projecting rods around the base of the stalk: no (0); yes (1).

P13. Fistulate globiferous pedicellariae with enclosed venom gland and distal opening (Fig. 2A–D): absent (0); present (1).

P14. Fistulate globiferous pedicellariae, distal opening: more or less ringed by small uniform teeth (Fig. 2B) (0); with a few well-developed fang-like teeth (Figs 2D; 4J–O) (1).

P15. Fistulate globiferous pedicellariae with separate end-tooth (fang) above opening (Fig. 4B): no (0); yes (1).

P16. Fistulate globiferous pedicellariae, blade: clearly differentiated as a rounded shaft partially or completely closed by cross-beams (Fig. 4J–L) (0); broad subtriangular blade beneath distal opening (Fig. 2B) (1); no distinct blade between distal opening and proximal muscle (Fig. 4D–E) (2).

P17. Rudimentary, non-fistulate and non-fanged globiferous pedicellariae: absent (0); present (1).

Triphyllous/biphyllous pedicellariae

P18. Triphyllous pedicellariae (Fig. 6): absent (0); present (1).

P19. Triphyllous pedicellariae, number of valves: two (0); three (1).

P20. Triphyllous pedicellariae: valves flat and rounded or tapering distally (Fig. 6C–G) (0), cone-shaped (constricted proximally, flaring distally) (Fig. 6A–B) (1), bilobed (2).

Ophicephalous pedicellariae

P21. Ophicephalous pedicellariae (Fig. 5): absent (0); present (1).

P22. Ophicephalous pedicellariae, valves tightly bound together by a locking loop so that the three valves do not fall apart (see Mooi 1990a; fig. 7A): no (0); yes (1).

P23. Ophicephalous pedicellariae with parasol-like blades (broad, highly rounded, overlapping): no (0); yes (1).

P24. Ophicephalous pedicellarial blade ending in a closed denticulate foramen (Fig. 2P): no (0); yes (1).

P25. Ophicephalous pedicellariae with stalk longer than length of valves: no (0); yes (1).

P26. Claviform ophicephalous pedicellariae (clear stalk with expanded distal region, large stalk glands, but no valves – Fig. 2O): absent (0); present (1).

Tridentate pedicellariae

P27. Tridentate pedicellariae (Figs 7 and 8): absent (0); present (1).

P28. Straight-bladed tridentate pedicellariae (Fig. 7): absent (0); present (1).

P29. Straight-bladed tridentate pedicellariae with open, very narrow, forceps-like blades (Fig. 7A–H): no (0); yes (1).

P30. Straight bladed tridentate pedicellariae with open, beak-like blades (Fig. 7J–Y): no (0); yes (1).

P31. Rostrate tridentate pedicellariae (Fig. 8): absent (0); present (1).

P32. Forceps-like straight-bladed tridentate pedicellariae: blades meet for <25% of their length (Fig. 7G) (0); 26–50% (Fig. 7H–I) (1); >50% (2).

P33. Forceps-like straight-bladed tridentate pedicellariae with spatulate tips (Fig. 7H–I): no (0); yes (1).

P34. Forceps-like straight-bladed tridentate pedicellariae with central ridge running down the centre of the valves: no (0), yes (1).

P35. Forceps-like straight-bladed tridentate pedicellariae with proximal region of blade clearly differentiated as: a predominantly closed, rounded shaft (0); an open blade (Fig. 7D) (1).

P36. Beak-like straight-bladed tridentate pedicellariae,

blades meet for <25% of their length (0); 26–50% (Fig. 7X) (1); >51% (Fig. 7M) (2).

P37. Beak-like straight-bladed tridentate pedicellariae with spatulate tips (Fig. 7O, W): absent (0); present (1).

P38. Beak-like straight-bladed tridentate pedicellariae with stalk longer than length of valves: no (0); yes (1).

P39. Beak-like straight-bladed tridentate pedicellariae with proximal region of blade clearly differentiated as: a predominantly closed, rounded shaft (0); an open blade (Fig. 7Q) (1).

P40. Rostrate tridentate pedicellariae: blades meet for <25% of their length (0); 26–50% (1).

P41. Rostrate tridentate pedicellariae with blade clearly differentiated as: a closed, rounded shaft (Fig. 8J) (0); an open blade (Fig. 8D) (1).

P42. Rostrate tridentate pedicellariae with fan of teeth distally (Fig. 8K): no (0); yes (1).

P43. Rostrate tridentate pedicellariae with valve ending in a terminal tooth: no (0); yes (1).

P44. Rostrate tridentate pedicellariae with stalk longer than length of valves: no (0); yes (1).

Bidentate pedicellariae

P45. Bidentate pedicellariae (Fig. 7Z–FF): absent (0); present (1).

P46. Large tridentate-type bidentate pedicellariae (Fig. 7EE–FF): absent (0); present (1).

P47. Small triphyllous-type bidentate pedicellariae (Fig. 7X–BB): absent (0); present (1).

P48. Tridentate-type bidentate pedicellariae with distal teeth (Fig. 7EE–FF): no (0); yes, with one or more teeth (1).

P49. Tridentate-type bidentate pedicellariae with stalk longer than length of valves: no (0); yes (1).

Dactylous pedicellariae

P50. Dactylous pedicellariae (Fig. 2X–Z): absent (0), present (1).

Data matrix (a = 0&1; b = 1&2; – , not applicable; ?, character state unknown)

<i>Archaeocidaris</i>	00—	—	–0—	–00—	0—	01101	020?1	2000-	—0	00–0
<i>Histocidaris</i>	00—	—	–0—	–00—	0—	01111	02001	2001-	—0	00–0
<i>Poriocidaris</i>	00—	—	–0—	–00—	0—	01101	0—	2001-	—0	00–0
<i>Stylocidaris</i>	10—	—	–100	100–	0—	01110	01001	—	—0	00–0
<i>Cidaris</i>	10—	—	–101	100–	0—	01110	02001	—	—0	00–0
<i>Ctenocidaris</i>	10—	—	–100	100–	0—	00000	0—	—	—0	00–0
<i>Gonicidaris</i>	10—	—	–100	100–	0—	00000	0—	—	—0	00–0
<i>Phyllacanthus</i>	10—	—	–100	100–	0—	01111	02001	10?1-	—0	00–0
<i>Tylocidaris</i>	10—	—	–0—	–00—	0—	01110	00001	—	—0	00–0
<i>Stereocidaris</i>	10—	—	–100	100–	0—	01110	02001	—	—0	00–0
<i>Araeosoma</i>	00—	—	–0—	–0111	0—	01111	12011	20110	00010	00–1
<i>Hygrosoma</i>	00—	—	–0—	–0111	10001	01111	0110a	10111	00010	00–0
<i>Kamptosoma</i>	00—	—	–0—	–1111	0—	01110	10100	—0	10010	00–0
<i>Paraphomosoma</i>	00—	—	–0—	–0111	0—	01101	0—	?011-	—0	00–0
<i>Phormosoma</i>	00—	—	–0—	–011a	0—	01111	02001	2011-	—0	00–0
<i>Sperosoma</i>	00—	—	–0—	–0111	0—	01101	0—	?0?1-	—0	00–0
<i>Aspidodiadema</i>	00—	—	–0—	–0111	00001	01111	12001	20110	00010	00–0
<i>Diadema</i>	00—	—	–0—	–0110	1000a	11111	10001	10110	10010	00–0
<i>Micropyga</i>	00—	—	–0—	–0111	10001	01111	00001	2011-	—0	00–0
<i>Caenopedina</i>	11100	01000	100–	–0110	10001	01110	10001	—0	10010	00–0
<i>Salenia</i>	00—	—	–0—	–0110	10000	11111	00001	1011-	—0	00–0
<i>Salenocidaris</i>	00—	—	–0—	–0110	10000	01111	00001	1a11-	—0	00–0
<i>Arbacia</i>	00—	—	–0—	–0110	10000	01111	0?001	2011-	—0	00–0
<i>Coelopleurus</i>	00—	—	–0—	–0110	10000	01111	02001	2011-	—0	00–0
<i>Glyptocidaris</i>	11111	00010	110–	–0110	10000	01101	0—	1111-	—0	00–0
<i>Stomopneustes</i>	11100	01001	000–	–0110	10000	01110	01001	—	—0	00–0
<i>Echinus</i>	11110	00210	100–	–0112	10000	01111	10001	10110	10010	00–0
<i>Echinometra</i>	11111	a0110	100–	–011c	10000	01111	10001	10110	10010	00–0
<i>Parasalenia</i>	11111	10010	100–	–0110	10000	01110	01001	—	—0	00–0
<i>Parechinus</i>	11110	00211	100–	–0110	10000	01111	00001	1111-	—0	00–0
<i>Strongylocentrotus</i>	11110	00010	100–	–0112	10000	01111	00001	1011-	—0	00–0
<i>Toxopneustes</i>	11110	10010	100–	–0110	10000	01110	00001	—	—0	00–0
<i>Trigonocidaris</i>	11110	1011a	100–	–0110	10000	01101	0—	0011-	—0	00–0
<i>Temnopleurus</i>	11111	0011a	100–	–0110	10000	01111	00001	0011-	—0	00–0
<i>Echinoneus</i>	10—	—	–100	20110	10001	01111	01101	2111-	—0	00–0
<i>Calymne</i>	00—	—	–0—	–0110	10101	01000	1—	—0	110?0	00–0
<i>Corystus</i>	10—	—	–100	20110	1000a	01110	11100	—1	01010	00–0
<i>Plexechinus</i>	10—	—	–100	20110	10001	01101	1—	00110	10110	00–0
<i>Pourtalesia</i>	11000	01000	??0–	–0110	10101	01101	1—	10??1	11010	00–0
<i>Urechinus</i>	10—	—	–110	00110	10000	01111	0b100	2011-	—0	00–0
<i>Aeropsis</i>	00—	—	–0—	–0110	0—	01101	1—	20110	10010	00–0
<i>Paleopneustes</i>	00—	—	–0—	–0110	10001	01111	11101	11111	00010	00–0
<i>Cyclaster</i>	10—	—	–110	00110	0—	01111	11001	10?10	110?0	00–0
<i>Palaeostoma</i>	11100	00000	100–	–0110	10001	01110	0a101	—	—0	00–0
<i>Pericosmus</i>	10—	—	–100	00110	10001	01111	11101	20?00	110?0	00–0
<i>Schizaster</i>	10—	—	–100	00110	10001	01111	11001	10110	11010	00–0
<i>Hemiaster</i>	10—	—	–100	00110	10001	01111	11001	20110	11010	00–0
<i>Brisaster</i>	10—	—	–110	00110	10001	01101	1—	11100	11010	00–0
<i>Brissopsis</i>	11100	01000	11110	00110	10001	01111	10101	11110	11010	00–0
<i>Eupatagus</i>	00—	—	–0—	–0110	10001	01011	1—	11?10	11010	00–0
<i>Palaeotrophus</i>	10—	—	–110	000–	10001	01111	11101	1a?10	11010	00–0
<i>Breyntia</i>	00—	—	–0—	–0110	10001	01110	11101	—0	10010	00–0
<i>Brissus</i>	10—	—	–100	00110	10001	01111	11101	20110	11010	00–0
<i>Echinocardium</i>	10—	—	–110	00110	10001	01111	11101	10111	10010	00–0
<i>Eurypatagus</i>	00—	—	–0—	–0110	10001	01111	10001	10111	11010	00–0
<i>Lovenia</i>	10—	—	–01?	–0110	0—	01111	10101	10110	110?0	00–0
<i>Maretia</i>	00—	—	–0—	–0110	10001	01110	10001	—?0	11010	00–0
<i>Prenaster</i>	10—	—	–100	00110	0—	01111	10101	11?10	100?0	00–0

<i>Spatangus</i>	00—	——	—0—	-0110	10001	01111	01101	2011-	—0	00-0
<i>Camarechinus</i>	10—	——	-110	0011?	10001	01101	0-?-	1011-	—0	00-0
<i>Apatopygus</i>	10—	——	-100	20112	10001	01111	01101	10?1-	—0	00-0
<i>Cassidulus</i>	00—	——	—0—	-0110	10001	01101	0—	1011-	—0	00-0
<i>Echinolampas</i>	00—	——	—0—	-0110	10011	01111	01101	1111-	—0	00-0
<i>Neolampas</i>	00—	——	—0—	-0112	10001	01101	0—	10?1-	—0	00-0
<i>Clypeaster</i>	00—	——	—0—	-0110	10011	01111	10101	1a110	100?0	00-0
<i>Ammotrophus</i>	00—	——	—0—	-00-	0—	01100	1—	—0	100?0	00-0
<i>Arachnoides</i>	00—	——	—0—	-0110	0—	01100	1—	—0	100?0	00-0
<i>Echinocyamus</i>	00—	——	—0—	-0110	11001	01101	0—	b011-	—0	00-0
<i>Fibularia</i>	00—	——	—0—	-0100	11001	00000	0—	——	—0	00-0
<i>Laganum</i>	00—	——	—0—	-0110	11001	01111	00101	1010-	—0	00-0
<i>Rotula</i>	00—	——	—0—	-00-	0—	00000	0—	——	—1	10010
<i>Astriclypeus</i>	00—	——	—0—	-0110	10001	01100	1—	—0	100?0	00-0
<i>Dendraster</i>	00—	——	—0—	-00-	0—	00000	0—	——	—1	11100
<i>Echinarachnius</i>	00—	——	—0—	-00-	0—	00000	0—	——	—1	101?0
<i>Mellita</i>	00—	——	—0—	-00-	0—	00000	0-?-	——	—1	11100
<i>Taiwanaster</i>	00—	——	—0—	-00-	0—	00000	0—	——	—1	10??0