

# Morphological innovation associated with the expansion of atelostomate irregular echinoids into fine-grained sediments during the Jurassic

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## ABSTRACT

The atelostomate and neognathostomate irregular echinoids are sister groups within the Microstomata. Extant atelostomates are common in fine-grained sediments, whereas the extant neognathostomates are generally confined to coarse-grained sediments. It is here argued that these differing environmental preferences are due at least in part to the contrasting morphology of the food-gathering tube feet. Specifically, the presence of specialized penicillate tube feet in the atelostomates makes them better able to feed in fine-grained sediments. Such tube feet are absent from the neognathostomates. Comparative analysis demonstrates that penicillate tube feet first appeared among Jurassic atelostomates. A statistical analysis compares the occurrence of Jurassic neognathostomate and atelostomate fossils with the areal extent of coarse- and fine-grained sedimentary rocks across England and France. The results suggest that Jurassic neognathostomates and early atelostomates occur most commonly in coarse-grained sedimentary rocks. However, those atelostomates with penicillate tube feet appear to be common only in fine-grained sedimentary rocks. The initial exploitation by atelostomates of fine-grained sediments coincides with the appearance of penicillate tube feet, suggesting that the two events are linked.

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## 1. Introduction

Today, the irregular echinoids are quantitatively abundant, taxonomically diverse and environmentally widespread. They comprise a substantial portion of the modern echinoid fauna (Smith, 2005), are known from sandy shore face environments (e.g. the Clypeasteroidea) to the deep-sea (e.g. the Holasteroidea), and occur at all latitudes.

Most irregular echinoids lie within the superorder Microstomata. This superorder is divided into two major clades, Neognathostomata and Atelostomata. The Neognathostomata is further divided into two clades, the paraphyletic Cassiduloidea and the monophyletic Clypeasteroidea (the latter arising from the cassiduloids in the Tertiary). The Atelostomata is divided into two monophyletic clades, Spatangoidea and Holasteroidea (Fig. 1).

Extant members of these clades, although of superficially similar morphology, differ in their environmental preferences. Specifically, the neognathostomates rarely occur in the fine-grained sediments occupied by the atelostomates. Extant cassiduloids are low in diversity (there are 30 or so living species: e.g. Mooi, 1990; Suter, 1994) and relatively rare. Of these living species, just ten are known in sufficient detail to determine their environmental preferences (Mooi, 1990). Nine of these are found within sandy or agitated sediments, just one

(*Studeria recens* Agassiz) occurs in muddy sediments. Seemingly, the cassiduloids are poorly adapted to exploit muds (e.g. Suter, 1994; Telford and Mooi, 1996). The clypeasteroids also occur in abundance in sandy sediments, although some burrow in muds (e.g. *Laganum* Link; Nebelsick, 1992). In contrast, the holasteroids and spatangoids (atelostomates) are common in fine-grained silts or muds as well as in sandy sediments (e.g. Telford and Mooi, 1996). Schinner (1993) found that the spatangoid *Schizaster canaliferus* (Lamarck) was confined to silt with at least 30% clay content, and did not occur in sands, in the Bay of Piran in the Adriatic Sea. Hollertz (2002) reported that the spatangoid *Brissopsis lyrifera* (Forbes) is common in clayey sediments. The extant holasteroids are exclusively deep marine, an area dominated by fine-grained sediments (e.g. Smith, 2003).

Morphological innovation governs the distribution of irregular echinoids. In the most general sense, it was the development of a dense coating of fine spines and the posterior migration of the periproct in the earliest irregular echinoids that enabled the group to exploit the infaunal niches that 'regular' echinoids cannot (e.g. Smith, 1978). It is therefore possible that morphological innovation explains the contrasting environmental preferences of neognathostomes and atelostomates. A number of studies have confirmed that morphology changes with substrate. A study of the Cenomanian echinoids of Charente-Maritime, France, found that the spatangoid *Hemiaster Desor* developed a more gibbous test as the substrate became finer grained (Néraudeau and Moreau, 1989). The same study found that the archiaciids, a family of neognathostomates, became more conical

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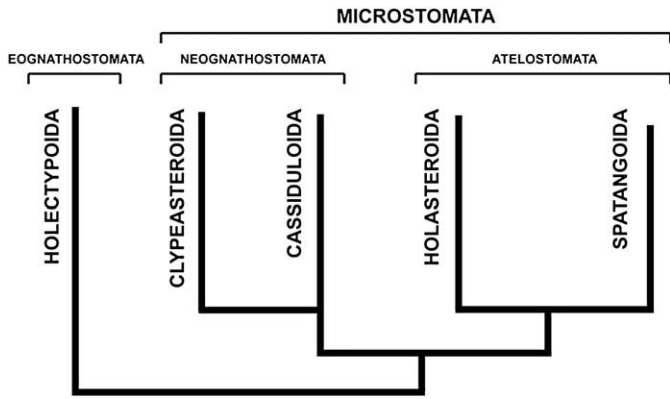


Fig. 1. Phylogenetic relationships between the major irregular echinoid clades.

in finer-grained sediments. François and David (2006) found variations in the size and morphology of the spatangoid *Toxaster* Agassiz in the Valanginian–Hauterivian sediments of Castellane Arc in south-east France. Specimens from more distal sediments were larger, and had a more anterior peristome. There is plenty of evidence that spatangoid fasciole patterns change in response to substrate particle size (Néraudeau et al., 1998 and references therein).

It is clear from this evidence that echinoids can adapt to changes in substrate, which makes the general absence of neognathostomates from fine-grained sediments all the more intriguing. It is likely that atelostomates possess certain traits that are absent from the neognathostomates which bestow on them an inherent advantage in fine-grained sediments. There are a number of morphological innovations unique to the spatangoids and holasteroids. Fascioles are dense bands of small, modified spines that are found only in spatangoids and holasteroids (e.g. Néraudeau et al., 1998). Their presence is a strong indication that the echinoid lived infaunally, as fascioles have important roles to play in terms of both respiration and maintaining burrow cleanliness. Spines within the fascioles are ciliated, producing currents that draw water into the burrow for respiration, and also secrete mucus that coats the echinoid, preventing small sediment particles from fouling the burrow (e.g. Smith and Stockley, 2005). However, fascioles do not occur universally among spatangoids and holasteroids and so cannot explain the general presence of these echinoids in fine-grained sediments.

There is one innovation shared by all extant atelostomates, but absent from the neognathostomates. Atelostomates possess penicillate tube feet, which are used to gather and manipulate food particles during feeding (e.g. De Ridder et al., 1987). The appearance of penicillate tube feet, and the accompanying changes in feeding strategy, may have contributed to the ability of atelostomates to exploit muds. This hypothesis is tested below.

## 2. Background

### 2.1. Feeding strategy in extant irregular echinoids

Most extant irregular echinoids are deposit feeders, using their podia (tube feet) to gather grains of sediment from the substrate, which are then passed towards the peristome and ingested, a feeding mode termed podial particle picking (Telford and Mooi, 1996). While the basic mechanism of food gathering is similar, neognathostomate podial particle picking differs in detail from atelostomate podial particle picking. Within the neognathostomates, clypeasteroids have evolved a highly sophisticated feeding strategy involving many thousands of podia. However, clypeasteroids appeared relatively recently, in the Palaeocene. The cassiduloids, holasteroids and spatangoids each have a much more ancient history, stretching back to the Jurassic. For simplicity, just these three groups are analysed.

#### 2.1.1. Cassiduloid podial particle picking

Specializations for podial particle picking fall into two categories: modifications to the spatial arrangement of food-gathering podia, and modifications to the structure of the food-gathering podia themselves. Cassiduloids are specialized for podial particle picking primarily through modifications to the spatial arrangement of food-gathering podia. Because the substrate is generally low in organic matter, it is necessary for deposit feeders to process vast quantities of sediment to obtain sufficient nutrition; Gladfelter (1978, p. 153) noted that the cassiduloid *Cassidulus caribaeorum* Lamarck feeds “more or less continuous[ly]”. Cassiduloids possess a key adaptation to bulk process sediment; immediately surrounding the mouth, the food-gathering podia are more densely packed than elsewhere on the test (Fig. 2a). These higher density areas of food-gathering podia are known as phyllodes. The larger number of podia within the phyllodes increases the rate at which the echinoid can feed; Higgins (1974) noted that the extant cassiduloid *Apatopygus recens* (Milne Edwards) processes so much sediment that there is a near continuous discharge of faecal waste.

However, the cassiduloid podia within the phyllodes (phyllodia) are similar in both size and structure to the podia beyond the phyllodes (accessory podia), which Telford and Mooi (1996) suggested is because accessory podia are also involved in feeding. Indeed, these authors (1996, p. 218) concluded that the podia were the “right equipment” for food gathering. The food-gathering podia have highly developed sensory capabilities to seek out sediment particles. Furthermore, there are secretory cells towards the terminal end of each podium, which produce adhesive substances necessary to hold the sediment particles. Finally, there is strong musculature in each podium to aid in manipulation of sediment particles towards the mouth (Telford and Mooi, 1996).

Nevertheless, the cassiduloid food gathering strategy is relatively crude (Higgins, 1974; Thum and Allen, 1976; Gladfelter, 1978; Telford and Mooi, 1996). Telford and Mooi (1996) found no conclusive evidence that cassiduloids are selective feeders; there were no consistent differences in the particle sizes within the gut compared to those in the surrounding sediments in *Cassidulus caribaeorum*. Elsewhere, however, it is suggested that very large particles may be under-represented in the cassiduloid gut, either because the peristome is too small to allow swallowing of such particles (Thum and Allen, 1976), or because very large particles are too difficult for the echinoid to hold and manipulate (Gladfelter, 1978).

More pertinently to the current question of environmental preferences, Thum and Allen (1976) suggested that very small particles are underrepresented in the gut of the cassiduloid *Echinolampas crassa* (Bell) because the animal lacks the ability to manipulate them.

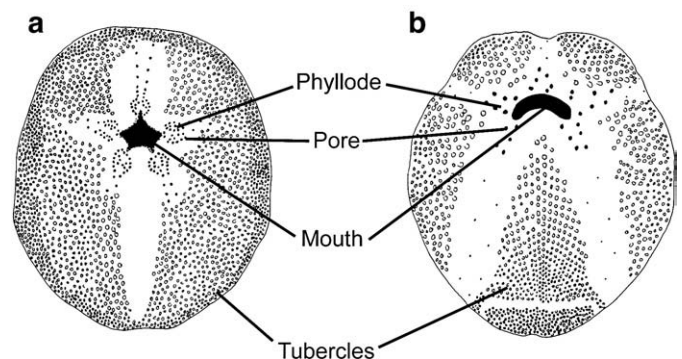


Fig. 2. Naked tests of two extant echinoids. Tubercles are the points of attachment of spines in life. Each pore was associated with a podium. a) Neognathostomate (cassiduloid) *Rhyncholampas pacificus* (Agassiz); NHM 41110; pores (and therefore podia) surrounding the mouth are small but densely packed into phyllodes. b) Atelostomate (spatangoid) *Brissopsis lyrifera* (Forbes); NHM 87.7.23; pores (and therefore podia) surrounding the mouth are large but not densely packed.

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