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Observations on the Light-Sensitive Tube Feet of the Burrowing Echinoid *Protenaster australis* (Gray, 1851)

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Abstract

Observations made on the burrowing spatangoid echinoid *Protenaster australis* (Gray, 1851) have revealed that it possesses light-sensitive tube feet. These have not previously been reported in irregular echinoids. At a white-light intensity of 8500-9000 lux the tube feet in ambulacrum III undergo positive phototaxis. Ambital sensory tube feet and phyllodal feeding tube feet also respond to light at this level of illumination, but undergo negative phototaxis. The same phototactic responses were observed with illumination by blue and green light, but not with red or yellow light in all three types of tube feet. The tube feet in ambulacrum III remain positively phototactic until a level of illumination of about 150-175,000 lux, whereupon they become negatively phototactic. It is considered that these tube feet play an important role in ensuring that the echinoid test remains completely covered by sediment during daylight. Night emergence of some spatangoids, such as *P. australis,* may be partly due to a lack of stimulation of light-sensitive tube feet.

Introduction

Tube feet, the external expression of the water vascular system in echinoderms, attain their greatest morphological and functional diversity in spatangoid echinoids. Tube feet on different parts of the test of an individual spatangoid may be adapted to a wide variety of functions. They may be respiratory or sensory, or they may be mucus-secreting and used for either feeding or funnel construction or both (Nichols 1959a, b; Chesher 1963; Smith 1980). Sensory tube feet in irregular echinoids have been ascribed either a chemosensory or a tactile function (Nichols 1962). On the spatangoid test sensory tube feet occur either adorally, in the periplastronal areas; ambitally, between the petals and phyllode; or, in some shallow-burrowing spatangoids, aborally in ambulacrum III (Nichols 1959c). Light-sensitive tube feet have been recorded in some regular echinoids, namely *Arbacia punctulata* (Holmes 1912), *Diadema antillarum* (Millot 1954), *Psammechinus miliaris* (Millott and Yoshida 1956) and *Lytechinus variegatus* (Millott 1955,

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1956). However, light sensitivity has not previously been reported in the tube feet of any irregular echinoids. It is the aim of this paper to report for the first time the presence of light-sensitive tube feet in an irregular echinoid and to discuss the functional significance of this particular sense to burrowing echinoids.

Materials and Methods

Protenaster australis is an uncommon echinoid which has been collected on the coasts of northern Tasmania (Gray 1851), Victoria (Clark 1946), South Australia (Cotten and Godfrey 1942) and south-western Australia (Clark 1938, 1946; McNamara in press). Until two specimens were collected *in situ* in January 1983 (McNamara and Bryce 1983) details of the natural habitat of this echinoid were not well known. Data with specimens in the collection of the Western Australian Museum indicate that the species inhabits depths from 25 fathoms off Mandurah, to intertidal sand, in Bunker Bay, where a specimen was found buried in sand amongst rocks, *Zostra* and *Cymadocea.*

The specimens collected in 1983 were found off Trigg Beach, Perth, Western Australia, only 30 m from shore living buried to a depth of 10 cm in fine calcareous sand in a pocket on a limestone reef platform. The water depth was only 1.8 m. The reef platform is exposed at low tides, but covered by about one metre of water at normal high tides. After transferal to an aquarium these two specimens survived for only a couple of days.

In January 1984, three further specimens were collected from the same sand pocket. They were buried with their apices just below the sediment/water interface. Prior to collection the burrowing activity of the echinoids was observed and a series of photographs recording their behaviour was taken. During observations of their behaviour following their removal to an aquarium, it was noticed that some of the tube feet responded to increasing levels of illumination. In order to study the response of the tube feet to varying levels of light intensity the echinoids were placed close to the side of an aquarium on a thin layer of fine-grained calcareous sand and illuminated from a distance of 3 cm with a white, cold-light source produced by a 150 watt Volpi Intralux fibre-optic light unit. Light intensity was varied from 0 to 200,000 lux by means of a diaphragm attached to the light unit. Variations in light intensity were measured using a light meter placed 3 cm from the source of the illumination.

Analysis of the effect of changing light intensity was initiated when the echinoid was at a low level of ambient illumination and was relaxed and actively feeding on the sediment surface, sensory and feeding tube-feet being extruded and active. Observations were made on two individuals more than twenty times and consistent reactions were noted. The main tube feet of concern were the aboral tube feet in ambulacrum III although observations were also made on the phyllodal and ambital tube feet. The tube feet in ambulacrum III, like all others in *P. australis,* are pale reddish-purple in colour, with closely spaced transverse darker

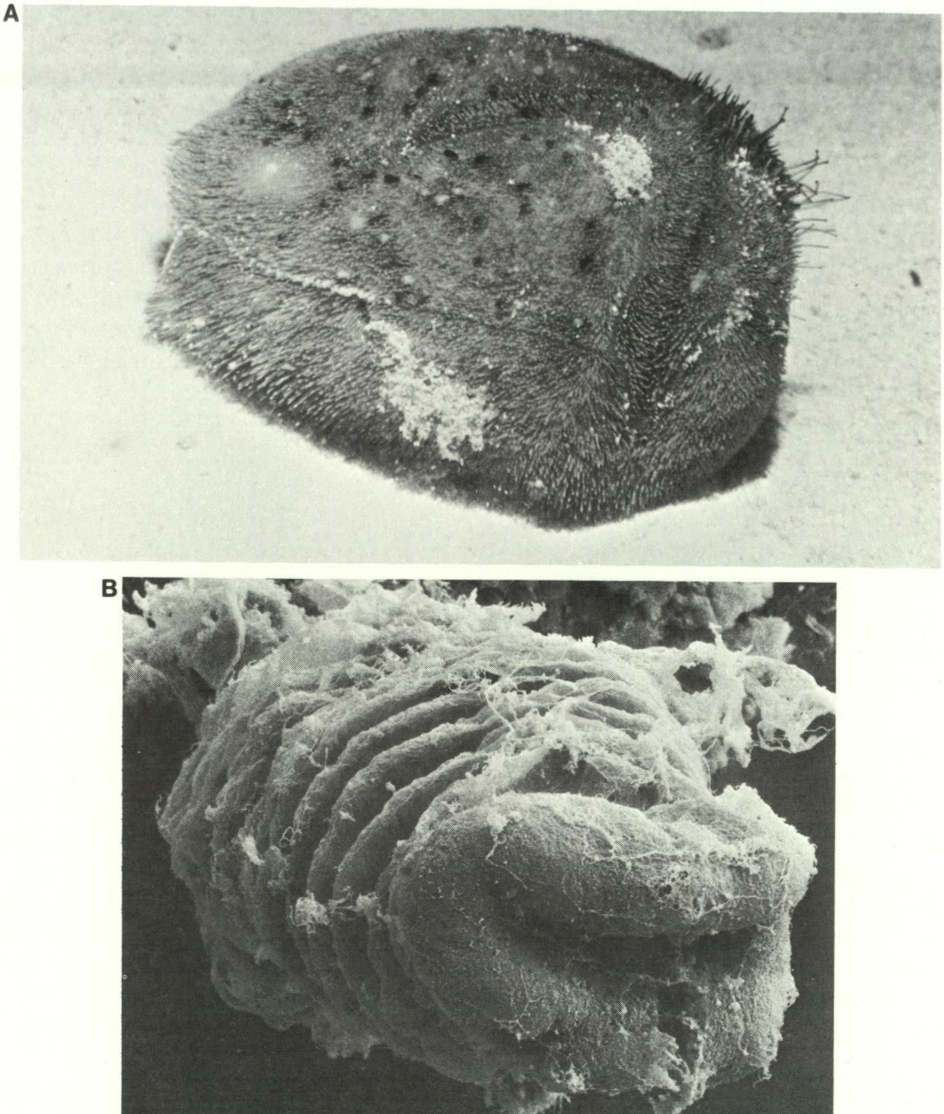


Figure 1 Light-sensitive tube feet in aboral ambulacrum III of *Protenaster australis* (Gray, 1851): (A) individual about twice natural size, photographed during daylight in water 1.8 m deep immediately after exhumation from the sediment and prior to burial. Note the positive phototactic response of the tube feet; (B) scanning electron micrograph of a freeze-dried tube foot from ambulacrum III in retracted condition. Note the simple light-sensitive terminal pad; bar equals 100μ.

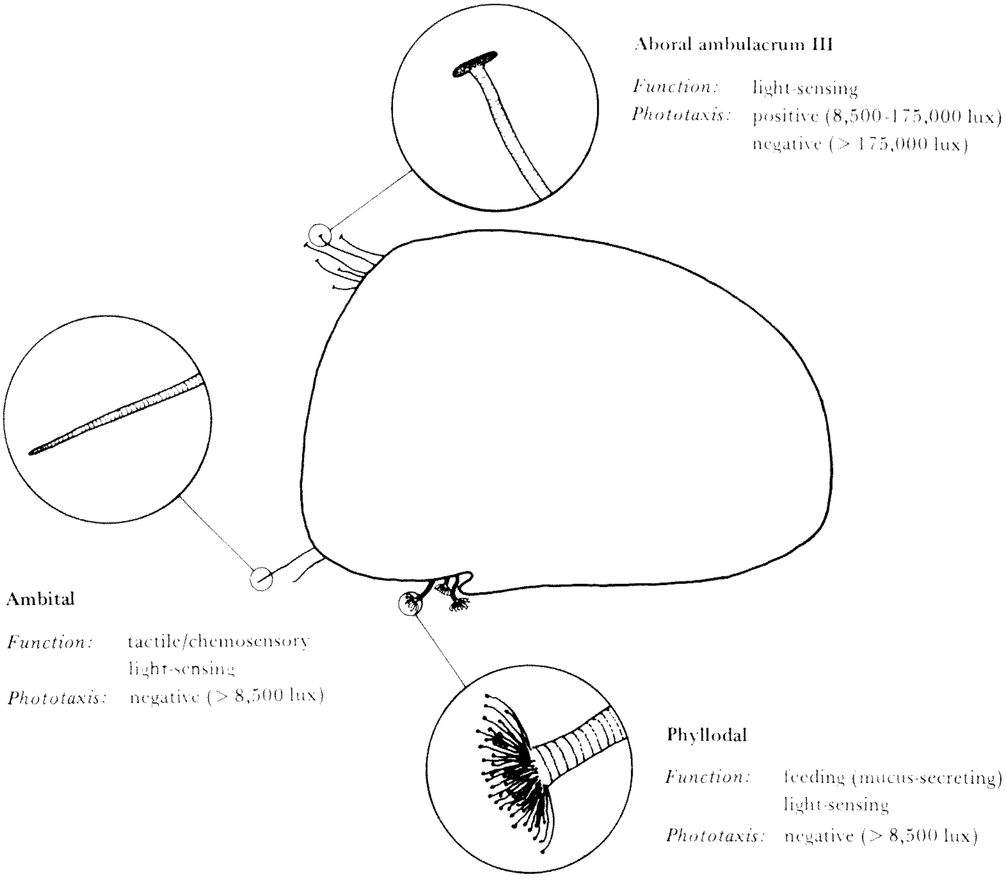
bands. They occur in the slightly sunken ambulacrum III between the apical system and the peripetalous fasciole. Each tube foot possesses a terminal pad (Figure 1B) which is half as wide again as the tube foot and has a dark reddish-purple outer-rim. The tube feet are extensile, extending up to about 20 mm in length in specimens 80 mm in test length, and are longest adapically. The associated pore pairs in ambulacrum III are isopores, separated by a prominent, raised interporal partition, and do not diminish appreciably in size adambitally.

It was only possible to keep the echinoids alive in the aquarium for one week, thus observations over an extended period were not possible. This species is an uncommon echinoid and subsequent attempts to locate further specimens have been unsuccessful. However, the consistent reactions which were repeatedly observed in the two specimens indicate that should further specimens be found, similar results to those described below are likely to be obtained.

Results

The light source was placed to one side of the test, pointing at the tube feet in ambulacrum III. When extruded at low levels of ambient illumination the tube feet were observed to move continuously in a random motion. The light intensity was gradually increased, until the tube feet were all observed to undergo a positive phototactic response. This occurred at a level of about 8500-9000 lux. The tube feet turned to the source of illumination by bending their top one-third, the lower section remaining nearly perpendicular to the test surface. The tube feet remained active, but continued to point toward the source of illumination for as long as it remained above 8500-9000 lux. On moving the light source to the front of the echinoid test and then to the opposite side, the tube feet followed the light source. Increasing the light intensity resulted in the tube feet becoming more agitated. They continued to point at the light source until a reading of 150,000-175,000 lux was reached, whereupon the tube feet retracted. Following the removal of the source of illumination the tube feet re-emerged almost immediately. However, after repeating the illumination three or four times in quick succession, tube feet re-emergence took longer. Response at the lower and upper light levels was relatively rapid, occurring in less than one second.

The adoral phyllodal tube feet and the ambital sensory tube feet were also subjected to illumination and found to be light sensitive. The mucus-generating penicillate tube feet of the phyllode (Figure 2) actively pick up the fine sediment and pass it to the mouth. The ambital tube feet simultaneously touch the sediment in front of the phyllode, either reacting to tactile or chemosensory stimuli. Although not possessing a terminal pad, the ambital tube feet also responded to light at the same threshold level of 8500-9000 lux as those in the aboral part of ambulacrum III. Moore (1921) considered that in echinoderms only those tube feet with a terminal pad are photosensitive. Clearly, this is not the case in *Protenaster*. Unlike the adapical tube feet the ambital tube feet displayed negative phototaxis, initially curling their apices into a spiral, and then withdrawing rapidly. The phyllodal tube feet likewise underwent negative phototaxis at this same threshold level and withdrew and ceased feeding. Positive phototaxis by the aboral tube feet in ambulacrum III did not cause any reciprocal response to the adoral and ambital tube feet. However, there was a marked increase in activity of the ambital and adoral interambulacral burrowing spines and the echinoid began burrowing into the sediment. With prolonged exposure to light above 8500-9000 lux the peripetalous fasciole secreted mucus in preparation for burrowing. A series of photographs taken of the echinoids *in situ* prior to collection shows that during burrowing activity the tube feet of ambulacrum III remain fully extended while exposed and show a positive phototactic response (Figure 1A).



Aboral ambulacrum III

Function: light-sensing
Phototaxis: positive (8,500-175,000 lux)
negative (> 175,000 lux)

Ambital

Function: tactile/chemosensory
light-sensing
Phototaxis: negative (> 8,500 lux)

Phyllodal

Function: feeding (mucus-secreting)
light-sensing
Phototaxis: negative (> 8,500 lux)

Figure 2 Outline of the test of *Protenaster australis* (Gray, 1851) showing distribution and detail of the three forms of light-sensitive tube feet. Test approximately natural size, expanded tube feet approximately x 10.

In addition to observing the responses of the tube feet to white light, blue, green, red and yellow filters were placed in front of the light source in order to assess the reaction of the tube feet to light of different wave lengths. When illuminated with blue and green light, the tube feet responded in the same manner as they did with white light, and at the same light intensities. However, illumination with red and yellow light elicited no response. The reaction to only blue and green light is not surprising as blue and blue-green light penetrates water most effectively (Utterbach 1936). The tube feet of *Psammechinus miliaris* react most strongly to blue-green light (Millott and Yoshida 1956). Although not specifically analysed, it would seem probable that the tube feet would react to ultraviolet radiation.

Discussion

Little is known of which pigments are responsible for photoreception in echinoderms, nor of how they function (Yoshida 1966). However, it is likely that the purple colour of all the light-sensitive tube feet in *Protenaster australis* is significant. Serial sections of the terminal disc of the adapical tube feet reveal dense clusters of cells in the periphery of the disc in areas that are the darkest purple. These cells appear dark when stained with haematoxylin (Figure 3), indicating either the presence of a large nucleus, and/or a strongly acidophyllic cytoplasm (J. Keesing, pers. comm.). It is quite probable that these cells are the light-sensitive cells and that similar cells occur concentrated in the purple bands in all three types of light-sensitive tube feet in *P. australis.*

A number of spatangoid echinoids, such as *Meoma ventricosa,* are known to emerge at night, but remain buried during the day. Chesher (1969) considered that this nocturnal emergence occurred in response to a reduction in oxygen content of the sediment. *Protenaster,* like many other spatangoids, possesses a peripetalous fasciole. When burrowed the upper half of the test of *Protenaster,* enclosing the petals, is enveloped by mucus secreted by the fasciole. An opening is created by a tuft of long spines around the apical system, to allow surface water to pass over the respiratory tracts in the petals. It seems unlikely that any changes in the oxygen content of the sediment would adversely affect the respiration rate of the echinoid. This rate is likely to be entirely controlled by the oxygen content of the sea water at the sediment/water interface.

Although it is not known whether *Protenaster* emerges at night, its morphological similarity to *Meoma,* the absence of funnel-building mucus-secreting tube feet in ambulacrum III, and its shallow mode of burrowing suggests that night emergence is quite likely. Furthermore, specimens kept in an aquarium in low levels of ambient illumination, below the lower threshold, fed quite actively on the sediment surface without attempting to burrow, whereas when they were originally collected and were placed on the sediment surface during daylight,

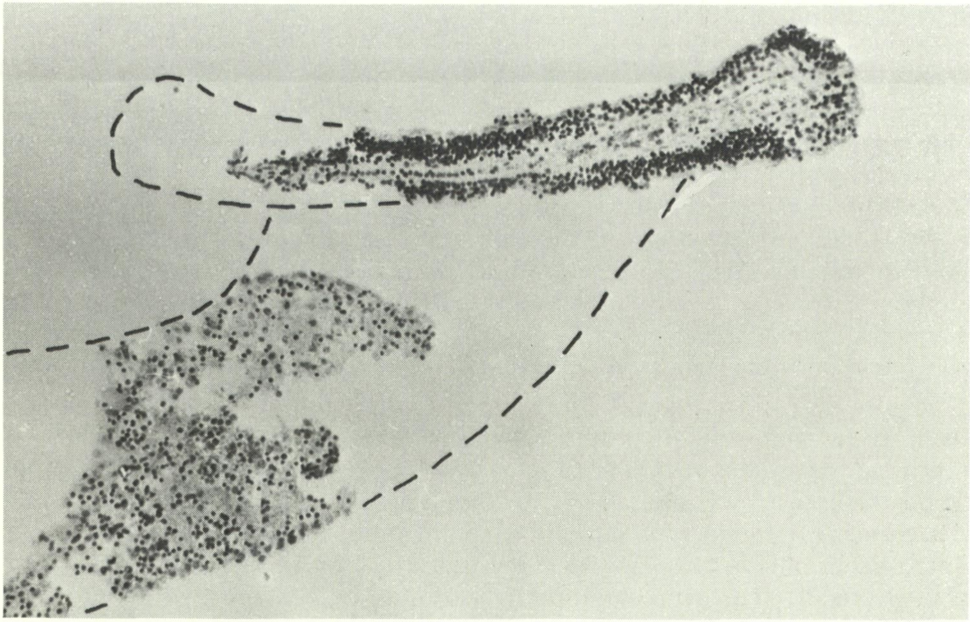


Figure 3 Longitudinal serial section through incomplete terminal pad and stem of a light-sensitive tube foot from the aboral part of ambulacrum III. The cells around the periphery of the pad, which have stained darkly with haematoxylin, are thought to be the light-sensitive cells; x 238.

they burrowed completely (C. Bryce, pers. comm.). Night emergence in *Protenaster* would be possible, given the absence of stimulation of the adoral light-sensitive tube feet at night. However, whether or not there is any particular advantage to be gained from surface feeding at night is questionable. Although there may be fewer vertebrate predators at night, the number of invertebrate predators is likely to be higher than during the day. The presence of light-sensitive tube feet in an adapical position may serve a more important function during the day in warning the echinoid of any exposure of the test to daylight. This is particularly important to *Protenaster* which is known to occur intertidally and to inhabit very shallow rock pools on a limestone reef.

In order to assess the significance of the two levels of light response in the tube feet of ambulacrum III, the ambient light intensity was measured at noon in Perth on a sunny day when the shade temperature was 32°C. With the sun nearly overhead, the light intensity was about 175,000 lux, while in the open shade the reading was about 8500 lux. The similarity of the ambient light levels in shade and sunlight to the levels of response of the tube feet in ambulacrum III argues for an important role for the tube feet in ensuring complete burial during the day. Some regular echinoids have a 'covering reaction' in response to high levels of illumination (Mortensen 1943a, b). This is accomplished by covering the test with opaque objects. Two of the four species of regular echinoids which have been shown to possess light-sensitive tube feet, *Lytechinus variegatus* and *Psammechinus miliaris,* are known to exhibit a 'covering reaction'. However, these, and other regular echinoids, also show dermal photosensitivity. *Protenaster* is unlikely to have such dermal sensitivity as the surface of the test is entirely covered by small spines, unlike regular echinoids where the larger, more sparsely distributed spines do not effectively shade the test. On detecting light above the lower threshold level, *Protenaster australis* may be considered to undergo a similar 'covering reaction', to regular echinoids, by burrowing into the sediment and completely covering the test with sand grains. In *Protenaster australis,* therefore, the adapical light-sensitive tube feet play an important role in controlling burrowing activity and ensuring complete coverage of the test by sediment during daylight.

The phyllodal and ambital tube feet play dual roles in being light-sensitive as well as carrying out other functions. The adaptive significance of light sensitivity in adoral tube feet in an echinoid which burrows in the sediment can only be fully realised if the animal was exhumed from the sediment during daylight and overturned. Immediate retraction of the tube feet would prevent damage by harmful ultra-violet rays in the very shallow water inhabited by the echinoid. Although relatively sheltered in their sand pocket on the reef platform, the environment is periodically one of very high hydrodynamic activity during high tides. In such a situation *Protenaster australis* is liable to be periodically dislodged during storms. Indeed, specimens of *Protenaster australis* in collections have mainly been derived from tests picked up on beaches inland from reefs, attesting to exhumation during the periods of high hydrodynamic activity.

In contrast to the phyllodal and ambital tube feet the adapical tube feet appear to carry out only a single function, that of light detection. Although the tube feet in ambulacrum III of some spatangoids are mucus-generating and used to establish a funnel to the surface when buried (Nichols 1959c; Chesher 1963), there is no evidence that the adapical tube feet in *Protenaster australis* also have a mucus-secretory function. Indeed, their very simple structure, consisting of a swollen light-sensitive terminal pad, contrasts with the structure of the more elaborate mucus-secreting tube feet found in ambulacrum III in spatangoids such as *Echinocardium, Moira, Aeropsis, Brissopsis,* and *Hemiaster.* In these genera the terminal disc extends from having a scalloped margin, as in *Brissopsis* and *Hemiaster,* to possessing a central pad margined by a ring of papillae, as in *Echinocardium* (Smith 1980).

The simple light-sensitive tube feet of *Protenaster australis* compare more closely with the simple tube feet of regular echinoids (Smith 1978). The corresponding pore pairs, unipores separated by a prominent interporal partition, likewise resemble those of many regular echinoids. Smith (1980) has suggested that tube feet, such as those in ambulacrum III in *Protenaster australis,* may, in spatangoids, be paedomorphic. However, rather than considering them to be of paedomorphic derivation, it may be more appropriate to consider them as being the only tube feet on the test not to have developed 'beyond' the simple ancestral structure of regular echinoid tube feet. In this regard the respiratory, ambital and phyllodal tube feet in spatangoids might more suitably be regarded as being peramorphic (*sensu* Alberch *et al* 1979) in origin.

Whether or not other spatangoids respond to light is not yet known, although night-emergent spatangoids such as *Meoma,* may well possess this facility. Light-sensitive tube feet in *Protenaster* are unlikely to have been phylogenetically recently derived not only because of their similar structure to those of regular echinoids, but also because of the long fossil history of *Protenaster.* Although *Protenaster* had until recently only been known from the living species *P. australis,* three fossil species are now known, which range back to the Late Eocene in Australia and New Zealand (McNamara in press). These fossil species possess adapical pore pairs in ambulacrum III which are structurally identical to those of *P. australis.* It is more likely that burrowing spatangoids such as *Echinocardium, Moira, Brissopsis* and *Schizaster,* which have adapical tube feet in ambulacrum III adapted to funnel construction, have probably lost the ability to respond to light and spend their entire lives within the sediment. However, confirmation is still required that these genera do not have light-sensitive tube feet. Hopefully, in the light of this paper, examination will be made in the future of the response of tube feet to light in spatangoids other than *Protenaster.*

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