TOOTH STRUCTURE OF THE PYGASTEROID SEA URCHIN *PLESIECHINUS*

by ANDREW B. SMITH

ABSTRACT. The fine structure of a tooth thought to belong to the Jurassic pygasteroid *Plesiechinus ornatus* (Buckman) is described and the tooth elements are reconstructed. The tooth is quite distinct from contemporary and Recent keeled teeth of regular echinoids but has a structure similar to that of known teeth of irregular echinoids. The discovery that pygasteroids have teeth constructed like other irregular echinoid teeth so far described strengthens the view that irregular echinoids are a monophyletic group.

PYGASTEROIDS have long been recognized as primitive irregular echinoids, but the exact relationship of pygasteroids to the other irregular echinoids has, however, been disputed. Early workers considered pygasteroids and holectypoids to be closely related and for many years the family Pygasteridae was classified within the Holectypoida. The first serious attack on this view was made by Mortensen (1948), who considered that pygasteroids arose independently from other holectypoids. This view was accepted by Durham and Melville (1957), who erected the order Pygasteroida to accommodate them, principally on the assumption that pygasteroids would prove to have grooved teeth in contrast to the 'keeled' teeth they had described in *Holectypus*.

In 1961 Melville published the first description of a pygasteroid lantern. He showed that *Pygaster trigeri* Cotteau had stout, triangular teeth and pyramids with a very deep V-shaped foramen magnum. Melville argued that the unique shape of pygasteroid teeth proved that pygasteroids were unrelated to other irregular echinoids. However, Melville had apparently overlooked Hawkins's (1909) work on holectypoid teeth, where stout, diamond-shaped teeth were illustrated, and based his argument on a misinterpretation of the teeth of *Holectypus*. Critical re-examination of the specimen of *Holectypus*, from which Durham and Melville (1957) described and illustrated teeth, has shown that the teeth are stout and triangular in cross-section rather than keeled (Kier 1974; Smith 1981) and similar observations on another specimen have been made by Hess (1971). I have recently argued that Pygasteroids and Holectypoids are sister groups and form a monophyletic group Eognathostomata (Smith 1981).

The purpose of this paper is to describe the ultrastructure of teeth thought to belong to the pygasteroid *Plesiechinus ornatus* (Buckman) from the Lower Bajocian (Middle Jurassic) of the Cotswolds. This allows critical comparison to be made with tooth structure in other groups of echinoid, since Melville's original material is not available for SEM study.

Methods and materials

The Pea Grit (Crickley Oncolite lithofacies of Mudge 1978) is a horizon famed for its fossil echinoid fauna. It belongs to the *murchisonae* Zone of the Bajocian, Middle Jurassic, and over the years bed-by-bed collections of the echinoid fauna have been made. Sievings taken from a marly horizon in the Crickley Oncolite at Crickley Hill, near Cheltenham by Dr. C. R. C. Paul proved to contain quantities of lantern elements. Collection from this unit has yielded some 200 specimens of echinoid. *P. ornatus* (Buckman) is the commonest species, making up 42% of the echinoid fauna. The echinaceans *Trochotiara depressus* (Agassiz) (31%), *Acrosalenia lycetti* Wright (10%), and *Psephechinus deslongchampsi* (Wright) (4%) are also important. The rest of the fauna is composed of echinoids with grooved teeth—the pedinoid *Hemipedina perforata* Wright (6%) and cidarids (5%)—together with the irregular *Galeropygus agariciformis* (Forbes) (2%) that has no lantern.

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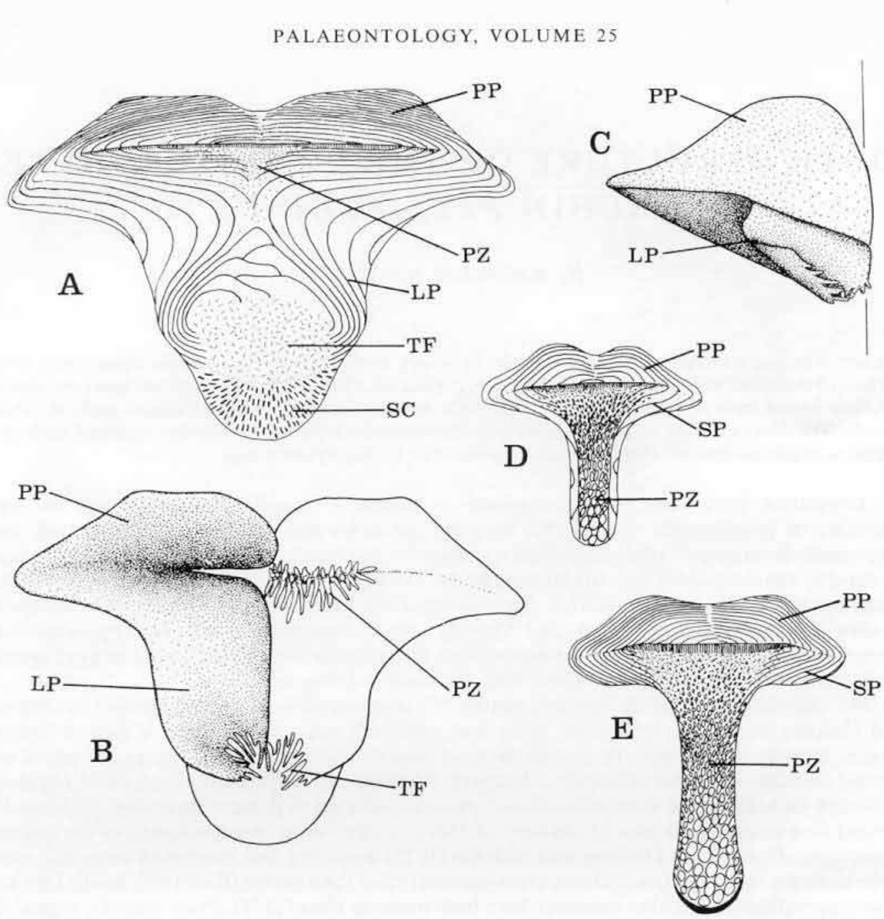


TEXT-FIG. 1. A–C, tooth of *Plesiechinus* (BMNH E 76938). A, cross-section, slightly restored from Plate 98, fig. 1. B, C, reconstruction of a single tooth element: B, apical view showing left-hand element in detail (prisms restored in only the right-hand element for clarity); C, adaxial view of left-hand element—vertical line marks the mid-line of the tooth. D, cross-section of a keeled tooth from an unknown echinacean collected from the Pea Grit of Crickley Hill, Cotswolds (Bajocian) (BMNH E 76940). E, cross-section of the tooth of *Acrosalenia pustulosa* from the White Limestone (Bathonian) at Northbrook Farm, Oxfordshire. (BMNH E 76939). LP = lateral plate; PP = primary plate; PZ = prism zone; SC = secondary calcite crust; SP = secondary plate; TF = terminal fibres.

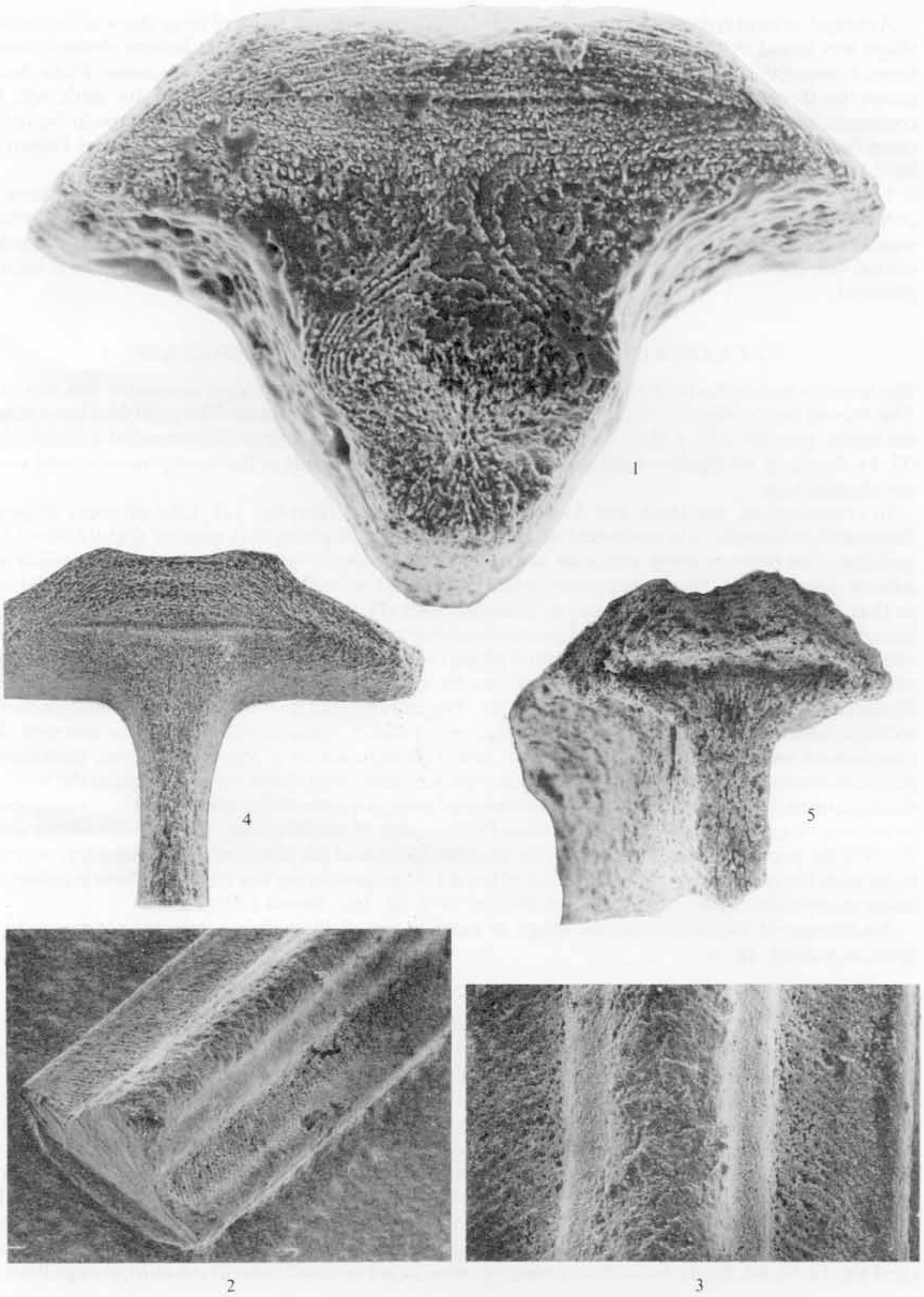
EXPLANATION OF PLATE 98

Figs. 1–3. Tooth of *Plesiechinus ornatus* (Buckman). 1, cross-section, abaxial edge to the top, × 200. 2, oblique view of adaxial face, × 60. 3, adaxial face, × 120. BMNH E 76938.

Fig. 4. Tooth of *Acrosalenia pustulosa* Forbes, cross-section, abaxial edge to the top, × 100. BMNH E 76939.

Fig. 5. Keeled tooth of an unknown echinacean in cross-section, abaxial adge to the top, × 100. BMNH E 76940.

All figures are SEM photomicrographs (details of specimens in text-fig. 1).



SMITH, echinoid teeth

Amongst several typically echinacean (keeled) teeth one different tooth of large size and distinctive shape was found. Although it is impossible to prove just which species these lantern elements come from, it seems fairly certain that the large and distinctive tooth belongs to *Plesiechinus*. *Plesiechinus* grows to three or four times the size of any of the regular echinoids and its teeth will be correspondingly larger. More importantly, the tooth described here is identical in shape to the tooth described by Melville (1961) from a pygasteroid. Only pygasteroids and holectypoids are known to have teeth of this shape and no holectypoid has ever been collected from these beds.

Echinoid teeth were etched in E.D.T.A. (ethylene diamine tetracetic acid) for about one hour in order to develop the stereom microstructure. This had little effect on the tooth of *Plesiechinus* which was then etched for twenty seconds in 10% HCl to reveal stereom. Specimens were mounted and gold-coated for the SEM. All specimens are now in the collections of the British Museum (Natural History).

ULTRASTRUCTURE OF THE TOOTH OF *PLESIECHINUS*

The tooth, which lacks both the aboral plumula and the oral chewing edge, is more or less straight. The abaxial face is broad and relatively flat with a marked median groove. The axial face has a stout, triangular process with a clear convex ridge on either side and a smoothly-rounded adaxial edge (Pl. 98, figs. 2, 3). Obliquely-running plates can be seen on either side of the stout process as well as on the abaxial face.

In cross-section, the tooth has a very distinctive outline (text-fig. 1A). Like all teeth of post-Palaeozoic echinoids, it is composed of two vertical series of plates that overlap slightly along the mid-line. The primary tooth plates lie abaxially and are steeply inclined. Lateral plates, which are adaxial extensions of the primary plates, make up most of the tooth. They are folded and set obliquely so that, in cross-section, they appear as S-shaped lines (Pl. 98, fig. 1; text-fig. 1A). The two series of lateral plates overlap and this zone of overlap becomes more pronounced adaxially towards their free end. The line separating primary and lateral plates is well marked across most of the tooth. The prism zone is poorly differentiated. Small prisms can be seen between the lateral plates centrally but no distinct zone of prismatic stereom is developed. The adaxial edge is smoothly rounded and, in cross-section, consists of dense, radially aligned stereom. Lateral plates do not extend into this area. By comparison with teeth of other echinoids, this is interpreted as a secondary calcite thickening, probably composed of polycrystalline calcite. Similar radial crusts have been reported in the teeth of diadematoids (Märkel 1970*a*). Beneath this adaxial crust is a zone of fine fibrous stereom interpreted as an area of terminal fibres extending from the free ends of lateral plates. The position of this zone distal to the primary plates and enclosed by the abaxial ends of the lateral plates shows it has nothing to do with the prism zone. Distal splitting of lateral plates producing fine terminal fibres is known to occur in several irregular echinoids (see Märkel 1978, fig. 10*a*; Jensen 1979, fig. 3).

An attempt at reconstructing the shape of tooth plates of *Plesiechinus* from the cross-section is given in text-fig. 1B, C.

COMPARISON WITH OTHER TEETH

The structure of the tooth described above is fundamentally different from any keeled tooth known from regular echinoids. The ultrastructure of keeled teeth of Recent regular echinoids has been reviewed by Märkel (1969) and, for comparison, the ultrastructure of keeled teeth of the Bathonian echinacean *Acrosalenia pustulosa* Forbes and an unknown echinacean tooth from the Pea Grit are illustrated (Pl. 98, figs. 4, 5; text-fig. 1D, E). These teeth have a sharp, narrow keel formed largely of prismatic stereom. Narrow side plates are attached to the distal parts of the primary plates. They are elongate and usually form a narrow margin to the keel. The extension of the secondary plate along the keel is termed the carinal appendage. This may form an almost flat and clearly defined margin (text-fig. 1D; Pl. 98, fig. 5) or may be highly curved and almost totally obliterated by prismatic stereom (text-fig. 1E; Pl. 98, fig. 4). Individual prisms become larger adaxially and at the adaxial edge there is sometimes a thin crust of dense stereom. The supposed pygasteroid tooth is quite evidently unrelated to such keeled teeth.

In structure, pygasteroid teeth come closer to the teeth described from cassiduloids and clypeasteroids (see Märkel, 1970*b*; 1978) and the teeth of *Eodiadema* (see Smith 1981). In *Eodiadema*, cassiduloids, and the more primitive clypeasteroids the prism zone is small and central and the lateral plates overlap along the mid-line and form a broad triangular process. The lateral plates are folded adorally, though folding is usually not quite so developed as it is in pygasteroid teeth. The adaxial splitting of the free end of lateral plates is a feature found only in irregular echinoid teeth and comparable elements were illustrated in fibulariids by Märkel (1978, fig. 10*a*).

Märkel (1978) first pointed out the differences between 'regular type' teeth (i.e. keeled and grooved teeth) and 'clypeasteroid type' teeth (i.e. diamond-shaped or wedge-shaped teeth of irregulars). He distinguished these types on fundamental differences of tooth-element shape. The reconstruction of a pygasteroid tooth element based on the cross-section (text-fig. 1B, C) shows that it undoubtedly belongs to the 'clypeasteroid type'. The adorally folded lateral plate element, the restriction of the prism zone to a small, central region, and the overlap of lateral plate elements along the mid-line are all important features. However, the primary plates are rather larger than in most irregular echinoid teeth, hence the broad abaxial crossbar to the tooth. In this respect the primary tooth elements have some similarity to less elongate primary tooth elements of regular echinoids.

The differences between the supposed pygasteroid tooth on the one hand and teeth of *Eodiadema*, cassiduloids, and primitive clypeasteroids on the other are simply due to size. The pygasteroid tooth probably passed through a diamond-shaped stage in its growth. The structure of pygasteroid teeth represents modification and expansion of the simple tooth elements of irregular echinoids.

PHYLOGENETIC IMPLICATIONS

The tooth of pygasteroids is very similar in shape to the tooth of the holectypoid *Holectypus* (see Kier 1974, text-fig. 54; Smith 1981, text-fig. 6). Pygasteroid teeth are constructed like the teeth of other irregular echinoids and the teeth of *Eodiadema*. The minor differences seen simply reflect the large size attained by these teeth and are modifications through growth of the simpler tooth plan seen in *Eodiadema* and cassiduloids. The fact that the holectypoid *Camerogalerus*, which has relatively small teeth, possesses diamond-shaped teeth indistinguishable from the teeth of *Eodiadema* and cassiduloids (Smith 1981) supports the view that the larger tooth of *Holectypus* is a diamond-shaped tooth modified by growth.

The discovery that tooth elements of pygasteroids belong to the irregular type supports the view that all irregular echinoids belong to a monophyletic group as argued previously (Smith 1981). It is also in keeping with the suggestion that pygasteroids and holectypoids are sister groups and should be classified together.

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