

DENTITION AND RELATIONSHIPS OF THE
ECHINOID GENUS *Pygaster* J. L. R. AGASSIZ,
1836

by R. V. MELVILLE

ABSTRACT. Fragments of the lantern in a specimen of *Pygaster trigeri* Cotteau, from the Bathonian of France, show that previous hypotheses of the relationships of *Pygaster* need to be reconsidered. The action of Durham and Melville (1957) in establishing a separate order for the Pygasteridae is held to be justified.

THE echinoid genus *Pygaster* J. L. R. Agassiz, 1836, was regarded until recently as a member of the order Holoctypoida, and the implication of direct relationship with *Holoctypus* Desor, 1842, was expressly accepted by, among others, Lambert (1900, p. 46 and folding tables), Lambert and Thiéry (1914, p. 277), and Hawkins (1920, p. 453, text-fig. 2; 1943, p. lxix). In 1948 Mortensen (pp. 14-15) thought that the two genera (and the families based on them) were of different origins, although he still retained both in the Holoctypoida. Finally, in 1957, Durham and Melville (p. 246) accepted Mortensen's view and its implications and (p. 251) established a distinct order Pygasteroida for the single family Pygasteridae. This action rested partly on the assumption that *Pygaster* must have had grooved (aulodont) teeth, whereas those of *Holoctypus* are known to be keeled (stirodont).

In studying the echinoids in the Cotteau Collection at the École nationale supérieure des Mines de Paris in April 1956, I noticed a specimen of *Pygaster trigeri* Cotteau, from the Bathonian of Villey-St. Étienne (Meurthe et Moselle), France, bearing a number of adherent radioles and with parts of the jaw-apparatus within the peristome. By kind permission of the authorities of the École des Mines I was allowed to borrow this specimen for study, and I am glad to acknowledge their generosity. I am also grateful to Dr. Porter M. Kier (U.S. National Museum, Washington) and to Dr. W. H. C. Ramsbottom for taking the photographs that illustrate this paper, and to Dr. R. Casey for the drawings reproduced as Pl. 29, figs. 4 and 5. The expenses of the work were met by an allocation from the Government grant in aid of Scientific Investigations administered by the Royal Society, and thanks are expressed for this help. This paper is published with the permission of the Director, Geological Survey and Museum.

LANTERN FRAGMENTS

The specimen referred to is preserved in a buff marly limestone packed with rounded and ovoid oolites and pellets. The marly parts of the matrix are soft and easily removed, but there are patches of denser material and of crystalline calcite which are harder than the fossil. When first studied, the peristome contained two rotulae and parts of three pyramids, two of which proved to contain teeth. The rotulae show no remarkable features and are not further considered. Two general views and an enlarged adoral view

[Palaeontology, Vol. 4, Part 2, 1961, pp. 243-6, pls. 28-29.]

(Pl. 28, figs. 1, 2, 4) show the appearance of the specimen and the disposition of the lantern fragments in the peristome before preparation.

Two of the pyramids were dissected out of the matrix and further cleaning of each was attempted. Owing to their fragility and small size, both were somewhat damaged in this process; moreover, the fragment that contained part of a tooth was embedded in crystalline calcite, so that the structure of the tooth could not be satisfactorily displayed. The third pyramid was left in place, but its tooth could only be exposed by working from above, and the specimen was sawn into two pieces for this purpose. The pyramids are not remarkable in structure (Pl. 28, figs. 5, 6). The depth of the foramen magnum is not clearly shown, but it seems to have extended for about half the height of the pyramid and to have been fairly wide. Viewed from the oesophageal side (Pl. 29, fig. 1), the pyramid tapers rapidly adorally to a point about midway along its length and has a slightly expanded, spatulate termination (Pl. 29, fig. 3). The top surface (Pl. 29, fig. 2) appears to be smooth. The interpyramidal muscle-scars are regular, strongly marked and gently sinuate; there are between twenty-five and thirty grooves on the interpyramidal face (Pl. 28, fig. 6). The peripheral side of each demipyramid (Pl. 28, fig. 5) bears a strong sulcus, deepening and narrowing adorally, on the interpyramidal side. This sulcus defines a rounded keel on the side towards the suture joining the demipyramids of a pair.

The greatest interest of the specimen lies in the structure of the teeth (Pl. 29, figs. 3, 4, 5). Each tooth is a stout, nearly straight beam of calcite, triangular in cross-section. Although no internal boundaries exist between the parts of the tooth, its form can be simply explained in terms of a nearly flat back, or base, upon which rests a pair of stout longitudinal buttresses, separated by deeply impressed longitudinal grooves from the base beneath and from the rounded crest of the tooth above. The adoral end of the tooth is not known, but was presumably of the bluntly pointed, triangular shape with chisel-edged sides generally seen in regular echinoids. This structure is unlike any described previously in echinoids. As is well known, echinoid teeth are of two types. The aulodont type, regarded as the more primitive, has a grooved or trough-like blade, and the stirodont type consists of a base supporting a longitudinal keel. In both types the back of the tooth is gently rounded transversely to the length, with a weak median ridge, and the sides project laterally a little beyond the edges of a broad longitudinal strap, which has the appearance of reinforcing the tooth. Furthermore, in both types the cutting part

EXPLANATION OF PLATE 28

Figs. 1-7. *Pygaster trigeri* Cotteau, Bathonian, Villey-St. Étienne (Meurthe et Moselle), France. 1, Adapical view, $\times 1$. 2, Adoral view, $\times 1$. 3, Part of adapical view enlarged $\times 1\frac{1}{2}$ showing radioles. 4, Part of adoral view enlarged $\times 1\frac{1}{2}$ showing two demipyramids and part of a rotula. 5, The same, external view of a demipyramid, $\times 10$. 6, The same, interpyramidal view of same demipyramid, $\times 10$. 7, The same, rotula, $\times 10$.

EXPLANATION OF PLATE 29

Figs. 1-6. *Pygaster trigeri* Cotteau, same specimen as in Plate 28. 1, Broken demipyramid with part of tooth in oesophageal view, $\times 10$. 2, The same, adapical view of same demipyramid, $\times 10$. 3, The same, oblique view of tooth lying slightly askew in its demipyramid; note also part of perignathic girdle, $\times 10$. 4, The same, drawing of structures seen in fig. 3, approx. $\times 12$; *a*, *b*, auricles of perignathic girdle; *c*, spatulate end of demipyramid; *d*, crest of tooth. 5, The same, drawing of cross-section of tooth seen in fig. 3, $\times 45$. 6, Enlarged view of part of Plate 28, fig. 3, to show radioles, $\times 7$.

of the tooth is a bluntly pointed triangle, the sides of which cut by shearing against the corresponding edges of adjacent teeth, and the keel of the stirodont type stops short of this part of the tooth. That is, the keel has nothing to do with the cutting function. The whole structure is light, yet strong, very different from the massive construction seen in *Pygaster*.

RADIOLES

Although no complete radiole is known, it appears (Pl. 28, fig. 3) that they were comparatively short, not more than one-quarter to one-third of the diameter of the test. The smooth base flares gently out to the collar and the stem is strongly striated. The axis is solid.

These radioles are of the same sort as those occasionally found adhering to tests of *Plesiechinus ornatus* (J. Buckman) from the Inferior Oolite (Pea Grit) of the Cotswolds, which also have a solid axis. The late Dr. Mortensen, when he was shown such specimens, was reluctant to accept the radioles as certainly of *Plesiechinus*, since none was in its original relationship to a tubercle, and many other species of echinoids occur in the Pea Grit. The abundance of these radioles on the present specimen of *Pygaster trigeri*, however, and the fact that no other kind of radiole has been observed in either genus, shows that there is no reason to doubt their genuineness. The radioles of *Holectypus* (Mortensen 1948, text-fig. 10, p. 24) have a hollow axis, as do those of certain early Pseudodiadematidae which it is hoped to describe elsewhere.

RELATIONSHIPS OF *PYGASTER*

As mentioned in the Introduction, earlier theories of the direct relationship between *Pygaster* and *Holectypus* were discarded by Mortensen (loc. cit.). For him, the main distinguishing feature lay in the tubercles, which are smooth in *Pygaster* and crenulate in *Holectypus*, and he therefore derived the first from a Pedinid and the second from a Diadematid source. Durham and Melville (1957, p. 246) assumed that the teeth of *Pygaster* were grooved, on account of the hypothetical Pedinid origin of *Pygaster*. I think it unsound, and hope soon to explain my reasons elsewhere, to refer any genus older than the Upper Cretaceous *Palaeopedina* Pomel, 1887, to the Diadematidae, and consider that the origin of *Holectypus* is to be sought among the early Pseudodiadematidae. With regard to the Pedinidae, however, there is no doubt that in every feature except the periproct and the teeth, *Diademopsis* and '*Palaeopedina*' show the closest possible resemblance to Pygasteridae. The differences in the periproct are well known. The differences in the teeth, now made known for the first time, are striking; for while *Diademopsis* has typically aulodont grooved teeth, like those of all other Pedinidae whose teeth are known, those of *Pygaster* are not merely keeled, but seem to have gone a stage farther in developing the massive longitudinal buttresses described above. It thus appears desirable to postulate some unknown form, intermediate between Pedinidae and Pygasteridae, in which the teeth were of normal stirodont type. Such an echinoid, if it were endocyclic, would ordinarily be referred either to the Phymosomatidae or to the Stompneustidae, but neither of these families at present includes any genus that is both morphologically and stratigraphically suitable as a possible ancestor for *Pygaster*. If, on the other hand, the periproct in such a form were not enclosed within the apical system, then it would be a *Plesiechinus*. Thus the assumed progression from a Pedinid ancestor

to *Pygaster* would have involved evolutionary changes not only in the position of the periproct, but also in the structure of the teeth—in the latter case to a stage beyond any hitherto known. This suggestion does no violence to the assumption (Durham and Melville 1957, p. 247) that all the irregular echinoids except the Pygasteridae descended from stirodont regular ancestors, for there is no *a priori* reason why the teeth in an irregular echinoid with fully functional jaws in the adult should have remained always in the condition obtaining in the regular ancestor, nor why they should not themselves evolve along lines either parallel to or divergent from those followed by regular forms. In particular, the evidence of the teeth emphasizes the distinctness of *Pygaster* from the true Holoctypoids, and justifies the establishment of the order Pygasteroida Durham and Melville, 1957. The Pygasteridae may, perhaps, be regarded as an abortive attempt by one stock of regular echinoids to evolve into the Holoctypoid condition.

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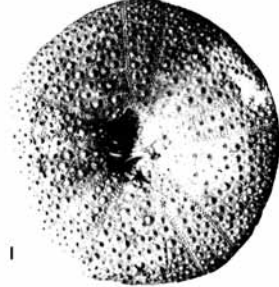
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R. V. MELVILLE
Geological Survey and Museum,
London, S.W. 7.

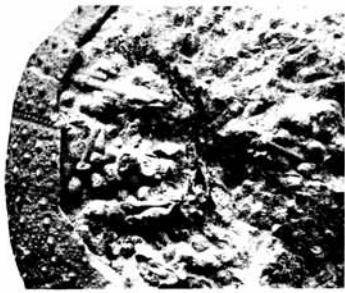
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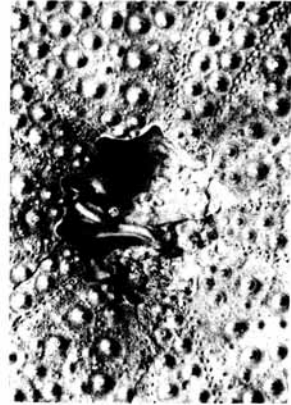
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2 × 1



3 × c.1½



4
× c.1½



5 × 10



7 × 10



6
× 10

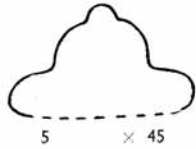
MELVILLE, *Pygaster*



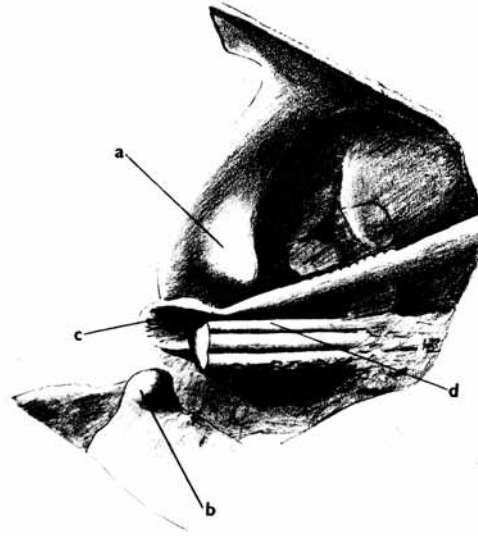
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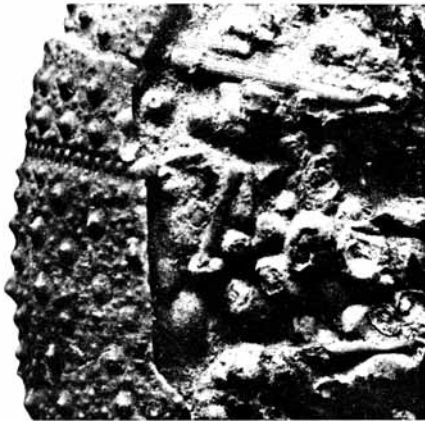
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5 × 45



4 × 12



6 × 7



3 × 10

MELVILLE, *Pygaster*