

A PARABLASTOID FROM THE ARENIG OF SOUTH WALES

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ABSTRACT. *Blastoidocrinus antecessens*, from the early Arenig Bolahaul Member of the Ogof Hên Formation at Llangynog, South Wales, is the oldest known parablasteroid and the first recorded from the British Isles. It is characterized by almost smooth deltoids with weakly scalloped margins and a stellate thecal outline. A single deltoid is known from the Treiorwerth Formation (Upper Arenig) of Anglesey.

Currents in the respiratory cataspores of parablasteroids entered the aboral slits and exited through the adambulacral pores, contrary to Hudson's (1915) interpretation. Cataspore canals deepened during growth by internal resorption and external resecretion within the thecal cavity. This wasteful mode of enlargement may have limited the success of the Parablasteroidea.

ALL but one of the specimens described in this paper come from a small disused quarry near the village of Llangynog (some 8 km south-west of Carmarthen), South Wales, in which are exposed some 15 m of silty mudstones the lower 2.5 m of which have yielded an extraordinarily rich and diverse fauna. The basal beds of the quarry lie about 13 m above the highest exposed crags of a coarse conglomerate with clasts of vein quartz and rhyolite. The conglomerate is seen locally to overly Tremadoc rocks (Cope, Fortey and Owens 1978) and is identified with the Allt Cystanog Member of the Ogof Hên Formation described by Fortey and Owens (1978) to the east of Carmarthen. Overlying the Allt Cystanog Member is the Bolahaul Member (Fortey and Owens 1978, pp. 233–234) known from several places in the area to the south-west of Carmarthen (Cope 1979) and it is to this member of the Ogof Hên Formation that the beds in the quarry belong. Their early Arenig age is shown by the common occurrence of the trilobites *Merlinia murchisoniae* (Murchison) and *Neseuretus parvifrons* (M'Coy). In addition a single specimen of *Phyllograptus* aff. *angustifolius* Hall has been found (see Fortey and Owens, 1978, p. 288). At Llangynog the fauna also includes (in order of abundance) bivalves, brachiopods, nautiloids, gastropods, dendroids, hyolithids, conulariids, monoplacophorans, and a single rostroconch. Because of the importance of this fauna, which is seemingly confined to a single small quarry, precise details of the locality are not published here. Full details are, however, deposited with the parablasteroid specimens in the register of the National Museum of Wales.

Except for two isolated deltoid plates, the Llangynog parablasteroid specimens come from a single bed of bioturbated silty mudstone containing occasional vein quartz and rhyolite pebbles; the unit is 10–15 cm thick and lies some 1.5 m above the lowest horizon exposed in the quarry. This bed has yielded most elements of the fauna mentioned above, but fossils are not as abundant in it as in beds a little higher in the quarry. The other two deltoid plates come from an horizon approximately 1 m above the main parablasteroid-yielding bed. Altogether almost 1 tonne of the parablasteroid-yielding bed was collected and broken up in the laboratory to furnish the material on which this description is based. When all the available material was examined, it became clear that it belonged to the parablasteroid genus *Blastoidocrinus* Billings, previously known from the Lower and Middle Ordovician of North America. The Welsh specimens differ in some respects from all previously described American forms and so are here described as a new species, *B. antecessens*.

Re-examination of a small collection of echinoderm fragments from the Upper Arenig Treiorwerth Formation of Anglesey, sent to CRCP by Dr. D. E. Bates in 1975 revealed a further isolated parablasteroid deltoid (Pl. 51, fig. 9), which probably also belongs to *B. antecessens*.

Parablastoids, as the name implies, are primitive, stemmed echinoderms with a cup superficially similar to that of a blastoid, but which bears distinctive internal respiratory structures, called cataspire by Hudson (1915). Parablastoids have five recumbent ambulacra which extend down over the theca between five large deltoid plates. The deltoids support the cataspire internally. In *Blastoidocrinus* the base of the cup is composed of numerous rather small plates, while in *Meristoschisma* Sprinkle, there is a single circlet of radial plates, with minute basals within the hollow where the stem attaches to the theca. The base of the theca is poorly known in *Blastocystis* Jaekel, the third genus of parablastoids. The cataspire of parablastoids are similar to the hydrospires of true blastoids in being composed of internal canals, but they differ in being largely associated with a single plate, the deltoid. Each cataspire canal opens at one end in a small pore along the ambulacral margin of the deltoid and at the other in a slit along the aboral edge of the deltoid. In *Blastocystis* and *Blastoidocrinus* the aboral opening is a short slit, while in *Meristoschisma* it is a long slit, internally divided into a series of short slits by calcite ridges (see Sprinkle 1973, pls. 34–41). Sprinkle also pointed out that there is not necessarily a one to one relationship between the number of deltoid slits and adambulacral pores and hence that some cataspire canals must branch.

Hudson (1911, pp. 203 *et seq.*) deduced that sea water entered via the adambulacral pores and exited through the deltoid slits. He coined the term 'cataspire' (1915, p. 165) for these unique structures because he believed the flow was away from the mouth (i.e. aboral) in contrast to the adoral flow in true blastoid hydrospires (which Hudson termed anaspire).

Isolated deltoids, as well as the original internal mould, show that the new Welsh species possessed cataspire and is hence a parablastoid. One specimen shows the complex plating of the aboral theca while another reveals the ambulacral 'wing plates' (see below) which together characterize *Blastoidocrinus*.

SYSTEMATIC PALAEONTOLOGY

Class PARABLASTOIDEA Hudson 1907

Diagnosis. Stemmed blastozoan echinoderms with a blastoid-like cup, the oral surface of which is composed entirely of five recumbent ambulacra and five large deltoid plates. Each deltoid bears internal respiratory structures, called cataspire, which consist of a set of canals that open in pores along the ambulacral margins, and in slits along the aboral margin, of the deltoid.

Discussion. The cataspire system is unique to parablastoids and nothing quite like it is found in any other echinoderm group. Although cataspire canals are internal, thin, folded membranous structures like rhombiferan dichopores or blastoid hydrospires, unlike these structures they are largely associated with a single thecal plate, the deltoid. Both dichopores and hydrospires are almost equally developed in two adjacent plates.

Currently three genera are assigned to the class and they are most easily distinguished on their ambulacral and thecal structure. In *Meristoschisma*, the only genus of the family Meristoschismatidae, the ambulacra are relatively short and wide, taper rapidly away from the oral pole and the aboral portion of the theca is composed of five large radials and very small basals which lie entirely within the depression into which the stem inserts. In *Blastoidocrinus* the ambulacra are relatively long and narrow, scarcely taper at all so that their sides appear to be parallel, and each is surmounted by a blade-like structure composed of up to three 'wing plates' against which the brachioles rested in life. The aboral theca of *Blastoidocrinus* is complex and incorporates basals, radials, bibrachials, and interbrachials (see Hudson 1907, fig. 1, p. 99). The third genus, *Blastocystis*, is poorly known, but to judge from Schmidt's (1874) original figures, it has parallel-sided ambulacra without 'wing plates' and possibly large plates in the aboral theca. At present, *Blastoidocrinus* and *Blastocystis* are referred to the family Blastocystidae Jaekel, 1918. The two parablastoid families are most easily distinguished on the deltoids which have long slits (divided internally) for the cataspire canals in meristoschismatids, but a single short slit confined to the aboral margin of the

deltoid in blastocystids. Thus even isolated deltoids may be assigned to their respective families. The new Welsh species has deltoids with aboral slits only, ambulacra with 'wing plates', and an aboral theca which includes radials and bibrachials. It is therefore referred to the genus *Blastoidocrinus*.

Family BLASTOCYSTIDAE Jaekel, 1918

Diagnosis. Parablastoids with parallel-sided ambulacra and deltoids with cataspire slits along the aboral margin only.

Genus BLASTOIDOCRINUS Billings, 1859

Type species. *Blastoidocrinus carchariaedens* Billings, 1859, by monotypy.

Diagnosis. A genus of Blastocystidae with ambulacra-bearing wing plates and the aboral theca composed of a large number of different plates.

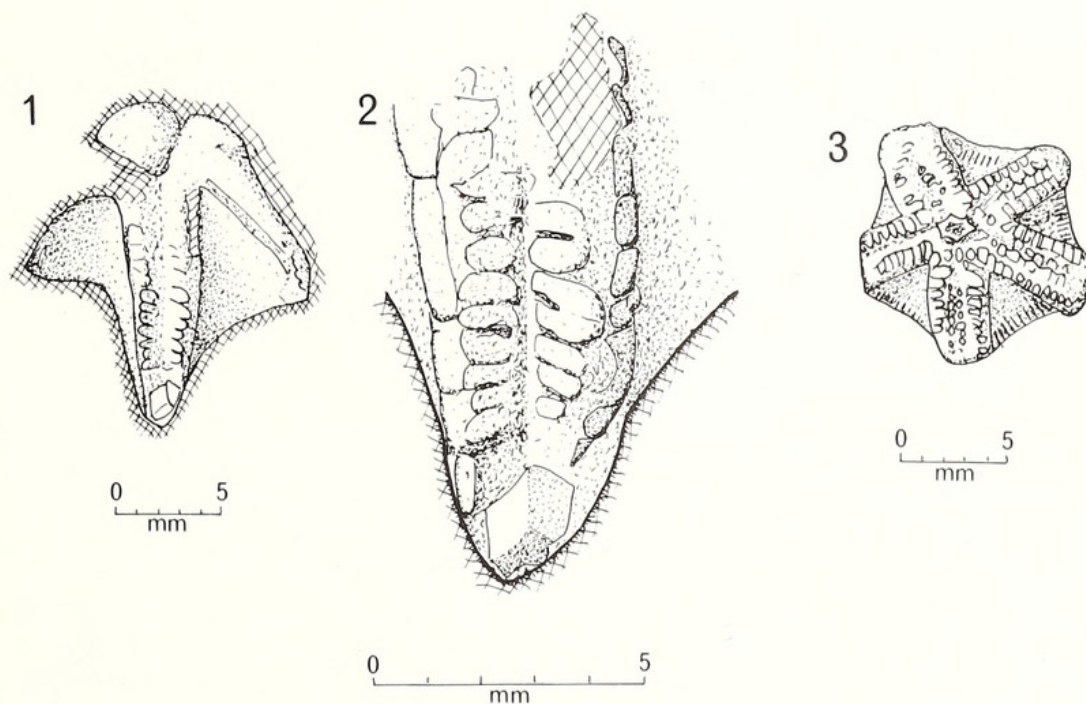
Blastoidocrinus antecedens sp. nov.

Plate 51; text-figs. 1-9

Diagnosis. A species of *Blastoidocrinus* with stellate thecal outline, almost smooth deltoids, and other thecal plates ornamented with only a few irregular ridges and grooves.

Types. Holotype (Pl. 51, fig. 2; text-fig. 3), National Museum of Wales, NMW 78. 8G. 1. Paratypes, National Museum of Wales, NMW 78. 8G. 2-34.

Material. Four partially complete or partially exposed thecae and thirty isolated deltoid plates.

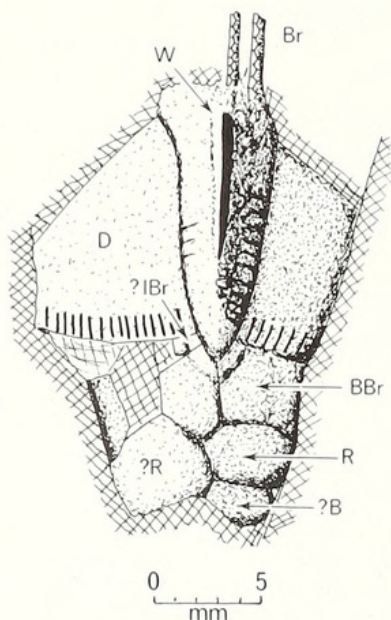


TEXT-FIGS. 1-3. Camera lucida drawings of *Blastoidocrinus antecedens* sp. nov. L. Arenig, Llangynog, South Wales. 1, paratype (NMW 78. 8G. 2) to show thecal outline and one ambulacrum which has lost the 'wing plates'. 2, detail of best preserved ambulacrum of the same specimen. 3, holotype (NMW 78. 8G. 1) to show stellate thecal outline. Matrix cross-hatched in figs. 1, 2.

Horizon and locality. Bolahaul member, Ogof Hên Formation (early Arenig), near Llangynog, South Wales, and Treiorwerth Formation (Bates, 1968) (Upper Arenig) Anglesey, North Wales.

Description. Stem (Pl. 51, fig. 1): associated with the specimens is a small fragment of stem, about 7.5 mm long by 3 mm maximum diameter and composed of 10 or 11 columnals. The columnals are circular in section, cylindrical, and smooth externally. Apparently they had a moderately large rounded lumen and the articulation surfaces lack radiating crenellae or any other ornament. It is by no means certain that this stem fragment belongs to *B. antecessens*, but its lack of external ornament suggests that it might originate from this species. The only other stem fragments appear to belong to a glyptocystitid cystoid.

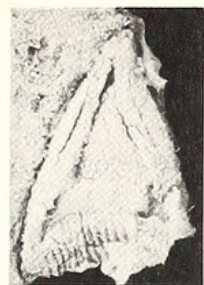
Theca: pentagonal to star-shaped in outline (Pl. 51, fig. 3; text-figs. 1, 3). The best-preserved example (the holotype) is about 12 mm across. The five deltoids are identical, triangular in outline, and, in the holotype, 6 mm tall by 4 mm across the aboral suture. Each bears traces of nine to eleven cataspire canals. Larger isolated deltoids reach 16 by 12 mm and have up to twenty-two cataspire canals. Thus if thecal proportions do not change with growth, the theca must have reached 30–35 mm in diameter. Aborally, the theca has a pair of bibrachials radially beneath the tip of each ambulacrum and (probably) five radials which form a closed circlet beneath the bibrachials. From their size, the bibrachials do not surround the theca completely and we infer that interbrachials also existed, one of which is possibly preserved on one paratype (text-fig. 4).



TEXT-FIG. 4. Paratype (NMW 78. 8G. 3) to show ambulacral 'wing' (w) and plates of the aboral theca. ?B, possible basal plate; BBr, bibrachial plates; Br, brachiole; D, deltoid; IBr, inter-brachial plates; ?R & R, possible radial plates. Matrix cross hatched.

EXPLANATION OF PLATE 51

Figs. 1–13. *Blastoidocrinus antecessens* sp. nov. L. Arenig, Llangynog, South Wales and Treiorwerth Formation, Anglesey, North Wales. 1, latex of external surface of large isolated deltoid. NMW 78. 8G. 8, $\times 3$. 2, latex of stellate plate that may represent the central plate of *B. antecessens*. NMW 78. 8G. 6, $\times 3$. 3, stereophotos of Holotype, NMW 78. 8G. 1, $\times 4$. 4, partial theca showing aboral surface of cup and one ambulacrum. NMW 78. 8G. 3, $\times 2.5$. 5, stereophotos of latex of specimen in fig. 4 to show cup plating and ambulacral 'wing' (above). NMW 78. 8G. 3, $\times 2.5$. 6, latex of internal surface of a small deltoid showing damaged cataspire folds. NMW 78. 8G. 7, $\times 3$. 7, latex of external surface of almost smooth deltoid. NMW 78. 8G. 10, $\times 3$. 8, stereophotos of internal surface of very large deltoid showing traces of cataspire folds. NMW 78. 8G. 5, $\times 3$. 9, stereophotos of isolated deltoid from the Treiorwerth Formation, Anglesey. NMW 81. 11G. 1, $\times 3$. 10, latex impression of stem fragment which possibly belongs to *B. antecessens*, NMW 78. 8G. 4, $\times 3$. 11, latex impression of external surface of very large deltoid (counterpart to fig. 8). Note the cataspire slits (below). NMW 78. 8G. 5, $\times 3$. 12, stereophotos of latex of partial theca showing one ambulacrum without 'wing plates'. NMW 78. 8G. 2, $\times 3$. 13, latex impression of internal surface of one small deltoid of NMW 78. 8G. 3, $\times 3$. All figures whitened with ammonium chloride sublimate.

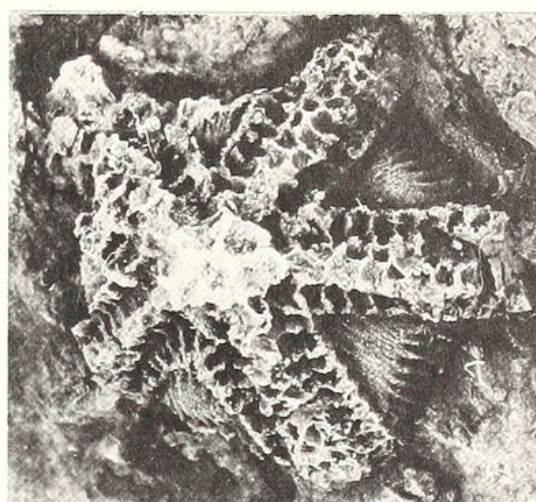
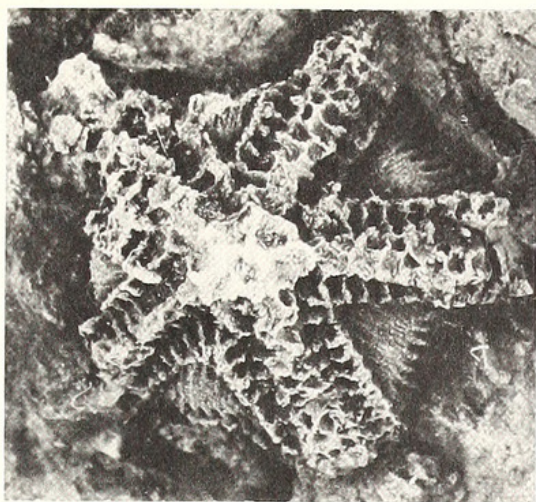


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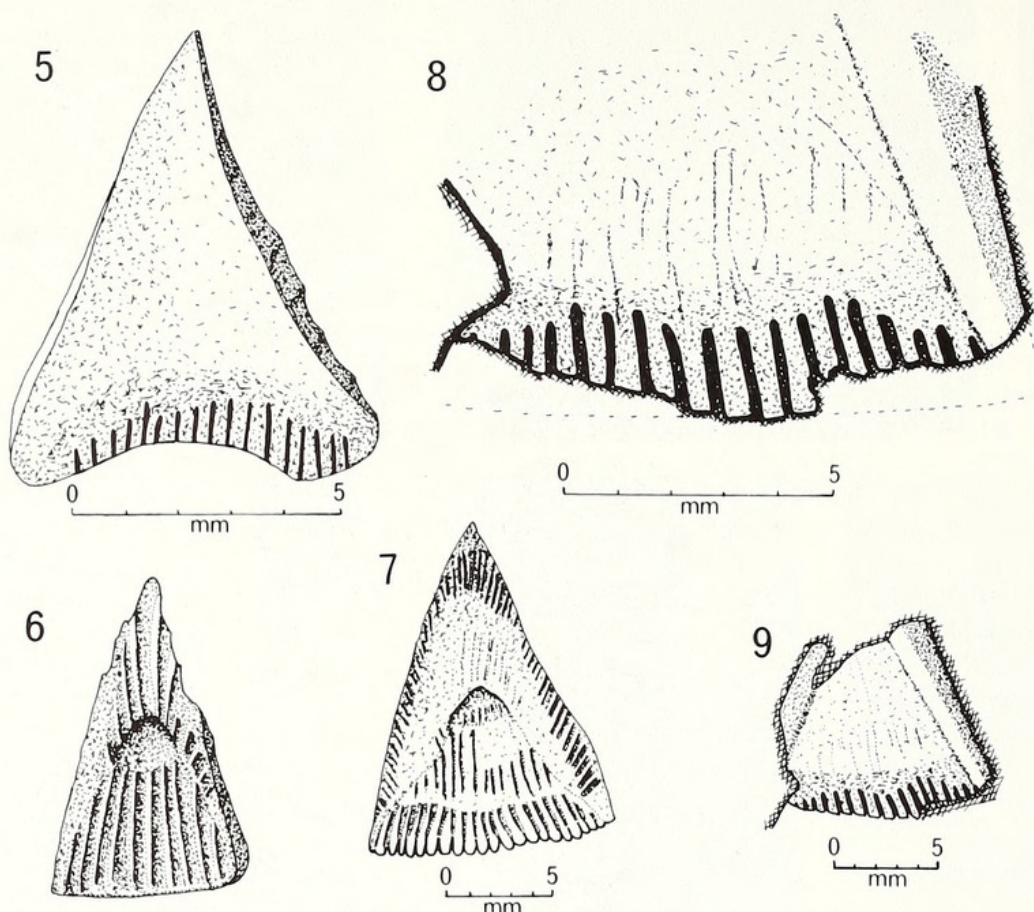
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TEXT-FIGS. 5-9. Camera lucida drawings of isolated deltoids of *Blastoidocrinus antecedens* sp. nov. L. Arenig, Llangynog, South Wales. 5, paratype, external, NMW 78. 8G. 10 showing aboral cataspire slits, smooth surface, and weakly scalloped margins. 6, paratype, internal, NMW 78. 8G. 7, to show traces of cataspire canals. 7, internal surface of paratype NMW 78. 8G. 5 a large radial with many cataspire canals. 8, 9, external of same paratype (NMW 78. 8G. 5) to show thickened adambulacral margin, aboral cataspire slits, and weak traces of ornament. Larger scales refer to figs. 5-6, 8; smaller to figs. 7, 9.

This paratype is crushed and retains no traces of basal plates, but one of the preserved radials is strongly folded so that it may be inferred that the theca had a deep aboral depression into which the stem inserted, as in *B. carchariaedens*, the only other species in which the complete theca is known. In *B. carchariaedens* the basals are very small and lie entirely within this basal depression. This was probably the case in *B. antecedens* too.

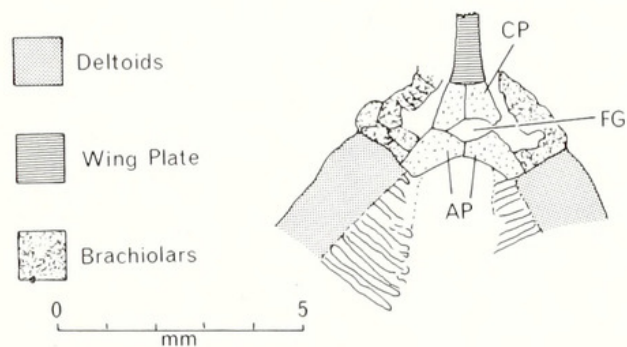
Isolated deltoids reveal an almost smooth external surface with short cataspire slits aborally (text-fig. 5) and occasionally very faint grooves parallel to the slits and a little above them (Pl. 51, fig. 11; text-figs. 8-9). The cataspire slits are short and narrow, perhaps reaching 2.0 mm long by 0.2 mm wide in the largest plates. The lateral edges of the deltoids are thickened and often scalloped to a greater or lesser degree where the ambulacral flooring plates fit against them. This scalloping is much less obvious than that on isolated deltoids of other species of *Blastoidocrinus* (see, for example, Sprinkle 1973, pls. 34, 36, 37). Internally, the deltoids preserve traces of the cataspire canals (text-figs. 6, 7) except in a small central area. In the adoral and lateral two-thirds of the deltoids cataspire canals converge, but in the aboral third they diverge slightly (text-fig. 6). Each canal must be bent, but it is virtually impossible to trace any one canal across these bends in the available plates.

Subjective system: there are five equal, parallel-sided ambulacra. In the holotype each bears two series of flooring plates, an outer series of rectangular plates, ten or eleven of which occur in each ambulacrum, and an inner series of smaller, pentagonal plates which meet at a zigzag suture and seem to bear a one to one

ratio to the outer flooring plates. Thus it would seem that the number of outer flooring plates per ambulacrum (and probably the number of brachioles) approximately equalled the number of cataspire folds per deltoid. This suggests that there was an opening for the cataspire folds at the base of each brachiole beside the outer flooring plate, as in *B. carchariaedens*. The numbers of flooring plates and cataspire folds need not correspond exactly, since each deltoid receives cataspire canals from half of each adjacent ambulacrum. One external mould (Paratype NWM 78. 8G. 2; text-fig. 2) apparently shows two sets of flooring plates, while another (NWM 78. 8G. 3; Pl. 51, fig. 5; text-fig. 4) shows the ambulacral 'wing', a blade-like structure lying above the ambulacral food groove and against which the brachioles folded in life. In the holotype the ambulacra are about 8 mm long and 3 mm wide proximally; in one of the paratypes one ambulacrum reaches 11 by 4 mm. Externally the outer flooring plates are narrow and the inner ones make up most of the width of the ambulacrum; internally the reverse is the case. The external mould that shows the flooring plates best (text-fig. 2) apparently preserves no trace of 'wing plates', but another example does preserve the 'wing' (Pl. 51, fig. 5; text-fig. 4). This ambulacral structure differs a little from that described by Hudson (1907, pp. 111 *et seq.*; fig. 2, p. 105). Hudson's section shows outer flooring plates (which he called adambulacrals) forming the entire width of the ambulacrum internally and external to them a pair of what are effectively cover plates which bear the 'wing plates' above (i.e. externally). Food from the brachioles must have passed over Hudson's adambulacrals to a central food groove beneath the cover plates and the wing plate (see text-fig. 10). In *B. antedens* it is difficult to make out the exact structure of the ambulacra, but clearly from the holotype (which is an internal mould), two series of plates *floored* the ambulacrum, not just the one shown in Hudson's section of *B. carchariaedens*.

Adorally, traces of a few brachioles are preserved on two paratypes. They are clearly biserial and very narrow. None is complete.

TEXT-FIG. 10. Cross-section through one ambulacrum of *Blastoidocrinus carchariaedens* Billings, type species of *Blastoidocrinus* (after Hudson, 1907, fig. 2, p. 105). AP, ambulacral plate; CP, cover plate; FG, food groove.



Discussion. This discovery extends the known stratigraphic and geographical ranges of the class Parablastoidea. *Blastocystis rossica* Jaekel comes from the Kunda Formation (Upper Arenig–Lower Llanvirn) of Pulkowa, Ingermanland, U.S.S.R., and was hitherto the oldest known parablastoid. All other parablastoids were known from North America; *Blastoidocrinus rossi* Sprinkle, *B. nevadensis* Sprinkle, and *B. ? elongatus* Sprinkle from the Llanvirn; *B. carchariaedens* Billings from the basal Llandeilo, while both species of *Meristoschisma* come from the Llandeilo–Caradoc boundary in the southern Appalachians. The new species comes from close to the base of the local Arenig section at Llangynog and is the oldest known form.

FUNCTIONING OF THE CATASPIRES

Hudson (1915) in a stimulating paper concluded that the respiratory structures of true blastoids and the parablastoids differed from all other types of internal (i.e. endothecal) respiratory structures in echinoderms because the currents of sea water that flowed through them were generated (partly or wholly) by the brachioles of the ambulacra. He believed that food was carried along the brachioles by cilia which induced water currents as well. Naturally, he assumed that the current in the respiratory structures entered at the ambulacral pores and exited at the other end of the canals. Thus he regarded the two types of pore-structures in true blastoids and parablastoids as being

fundamentally opposed in their current directions. In blastoids the currents entered the ambulacral pores and travelled towards the mouth to exit through the spiracles (at least in spiraculates), while in parablasteroids the currents travelled away from the mouth to exit through the deltoid slits. Hudson (1915) designated these structures anaspores and cataspores, respectively. Examination of isolated deltoids of *Meristoschisma hudsoni* Sprinkle from the Benbolt Formation of Tennessee gives cause to believe that the currents in cataspores also travelled towards the mouth, i.e. from the deltoid slits to the adambulacral pores, as Sprinkle (1973, p. 165) has already suggested.

The reasoning is two-fold. First, externally the deltoid slits in *M. hudsoni* seem to be simple and very long and thin. Internally, each slit is obviously divided into a series of short slits and the cataspore canals are much wider. Now no animal can control the composition of the surrounding sea water. There is always a danger of canals becoming clogged with suspended particles. This danger can be avoided if the entrance to any canal is the narrowest point, because any particle capable of entering the canal can pass right through. Particles trapped at the entrance can pass along the slit or be removed by a brief reversal of the current. On the other hand, if the exit is the narrowest point, particles of a critical diameter might pass through the canal but become lodged at the exit. To clear them would require reversing the currents to carry the particle all the way back along the canal. This is inefficient at best, always assuming such reversal of currents is possible. Thus the morphology of the cataspore slits in the deltoids of *M. hudsoni* suggests that they were entrances not exits.

The second point is that with any system of endothecal canals there is always a danger of recycling. Deoxygenated sea water might leave one canal and then enter another or be sucked back into the same one. Again this is inefficient. Recycling can be minimized by locating exits together and away from entrances, but also by inducing a strong excurrent which is carried away from the thecal surface to mix with normal sea water before there is any chance of re-entry. Since current velocity is inversely proportional to the cross-sectional area of the canals, constricting the exit boosts the excurrent. Note that the exit may have a smaller cross-sectional area but still be wider, than the entrance. The ideal canal would have a slit-like entrance and a circular exit, the total area of which was less than that of the entrance. Once again then, the narrow deltoid slit of *M. hudsoni* has the form of an entrance, while the more or less circular adambulacral pores have the morphology of exits.

The conclusion that cataspore currents flowed from the deltoid slits towards the adambulacral pores seems inescapable. The term 'cataspores' may be retained despite its misconceived origin, especially as the alternative term 'anaspores' has never been used since Hudson coined it. Furthermore, Hudson's supposition that the brachioles produced water currents is probably wrong. They merely transport boluses of mucus and food, so the exiting currents from the cataspores need not have worked against supposed feeding currents.

As Sprinkle (1973, p. 164) has pointed out, aborally the internal cataspore canals of *Meristoschisma* are just attached to the adoral edge of the radials, while their adoral ends are shared by a pair of ambulacral plates which surround the adambulacral pore. Nevertheless, the main bulk of the canals in all parablasteroids is attached to, and lies under, a deltoid plate and could only increase in length at the two margins of the deltoid. However, Hudson (1907, p. 106) noticed that cataspore canals were deepest in the central portions of the deltoids. The peculiar and unique arrangement whereby the bulk of these canals lies under the deltoids inevitably involves a more complex pattern of growth than in the respiratory structures of rhombiferans or blastoids. Existing cataspore canals could only increase in depth by resorption within the canal and resecretion outside it (i.e. within the thecal cavity). In blastoid hydrospires and in all cystoid rhombs the canals cross a plate suture and are more or less equally developed in two plates. As the plates grew, existing canals could be deepened at the suture. Thus once a portion of a canal was formed, there was no need to alter it in any way subsequently. The relatively complex and inefficient growth pattern in parablasteroids may partly account for their lack of success.

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