CORONATE ECHINODERMS FROM THE LOWER PALAEOZOIC OF BRITAIN

by STEPHEN K. DONOVAN *and* CHRISTOPHER R. C. PAUL

ABSTRACT. Coronates are pelmatozoan echinoderms with a functional stem, a bud-shaped theca, and erect, biserial, pinnate arms. They evolved early in the Middle Ordovician, probably from the 'eocrinoid' *Bockia*, and gave rise to the blastoids *sensu stricto*. The subclass Coronata contains six genera. *Mespilocystites* (early Caradoc–Ashgill) had geniculate radial furrows, while all later genera had planar or gently convex radii. Of these *Stephanoblastus* (Caradoc–Wenlock) had a very narrow stem and triradiate keels at the base of the theca. All other genera had triangular thecal bases. *Tormoblastus* (Ashgill) had a conical theca with a protruding base bearing three flanges, *Paracystis* (Caradoc) had a bowl-shaped theca with a sunken base, *Stephanocrinus* (Ashgill–Ludlow) a tall, steeply conical theca, and *Cupulocorona* gen. nov. (Ashgill–Wenlock) a conical to cup-shaped theca with a protruding base. The British coronate fauna includes five new species: *S. ramsbottomi* (Hirnantian) characterized by a large, angular conical theca with low coronal processes, *C. salopiae* (early Wenlock) characterized by a pyriform theca with low coronal processes and low ridges at the plate sutures, *C. rugosa* (Cautleyan–Rawtheyan) with a conical theca bearing very coarse ornament, *C. digitalis* (Cautleyan–Rawtheyan) with a conical theca and very long coronal processes, and *Stephanocrinus sensu lato* sp. (Cautleyan) which is poorly known but had very fine ribbing.

CORONATES are a small but distinctive group of Lower Palaeozoic pelmatozoans with a functional stem, a small theca with five interradial coronal processes ventrally and a fixed arrangement of thecal plates very similar to that of blastoids, and erect, biserial, pinnate arms. Opinions as to their affinities have varied in the past, but we believe they were most closely related to the blastoids. Although thecae of coronate echinoderms are not uncommon in the Ordovician and Silurian of Britain (no columns or arms have yet been discovered), the only previous references to their occurrence are in Bather (1900, pp. 96, 145), who mentioned that *Stephanocrinus* was found in the Silurian of Britain, and King and Wilcockson (1934, p. 17), in which Bather recognized a calyx from the Upper Ordovician at Hunterstye as *Stephanocrinus*. The latter is described below as *S. ramsbottomi* sp. nov. In 1952 W. H. C. Ramsbottom prepared an unpublished manuscript on some coronates including a proposed new species, *S. salopiae*, which is probably the species referred to by Bather (1900) and is redescribed here as *Cupulocorona salopiae*. Otherwise British coronates have been ignored or referred to as 'new cystidean' (Reed 1907, p. 537). Following the recent reassessment of *Stephanocrinus* (Brett *et al.* 1983), which elevated the Coronata to class status, it is timely to describe British representatives of the group.

GENERAL MORPHOLOGY OF THE CORONATES

Stem. Apparently homeomorphic, composed of small circular columnals with convex latera, narrow ($\frac{1}{8}$–$\frac{1}{10}$ thecal diameter) or extremely narrow ($\frac{1}{25}$ thecal diameter), circular in section and with a circular lumen as far as is known. Brett *et al.* (1983, fig. 1*k*) illustrated a discoidal holdfast which they associated with *S. angulatus*.

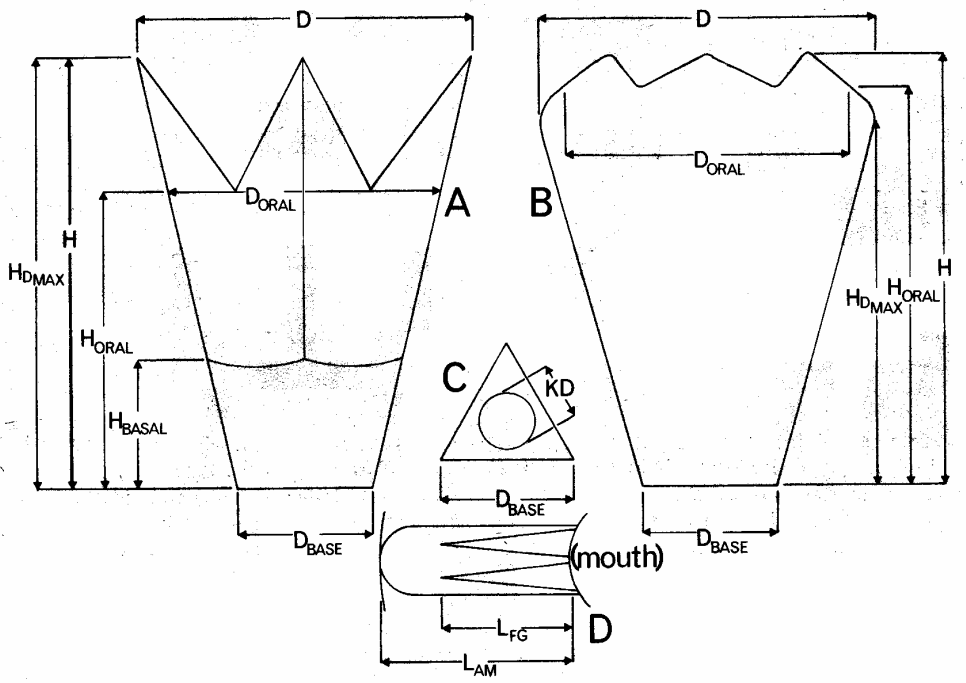
Theca. Elongate-conical through conical to cup- or bowl-shaped, base triangular or triradiate, top with five distinct coronal processes. Constant plate arrangement (text-fig. 5A) consisting of three basals of which the azygous basal occupies the AB interray; five radials all with cleft upper margins, the two 'wings' each forming half of the aboral side of a coronal process; six deltoids, a sub- and super-deltoid in the CD (posterior) interray adoral to the anus and one deltoid in each of the other

[Palaeontology, Vol. 28, Part 3, 1985, pp. 527–543, pls. 62–63.]

four interrays, deltoids triangular and raised to form the adoral portions of the coronal processes; five primary ambulacral plates at the tip of each ambulacrum and in the radial furrows between the coronal processes; five oral cover plates over the central mouth, the posterior of which is very slightly the largest; ten elongate ambulacral cover plates, one pair per ambulacrum. The basals and radials are usually ornamented with fine ridges or rows of granules which form rhombic patterns. In some genera there are also major ridges on the theca diverging upwards from the basals and forming a V W pattern, the base of the V being centred on the azygous basal.

Three orifices all in the oral surface (text-fig. 5B). A central, nearly circular mouth. An anus, almost as large as the mouth, situated at the base of the CD coronal process on the adoral side, and covered with an anal pyramid of three or four cover plates. Just adoral to the anus on the common suture of the sub- and super-deltoid a small tubercle with a transverse slit is sometimes found. This has been interpreted as a possible hydropore (Brett *et al.* 1983, p. 632). Both suture and orifice are frequently cryptic.

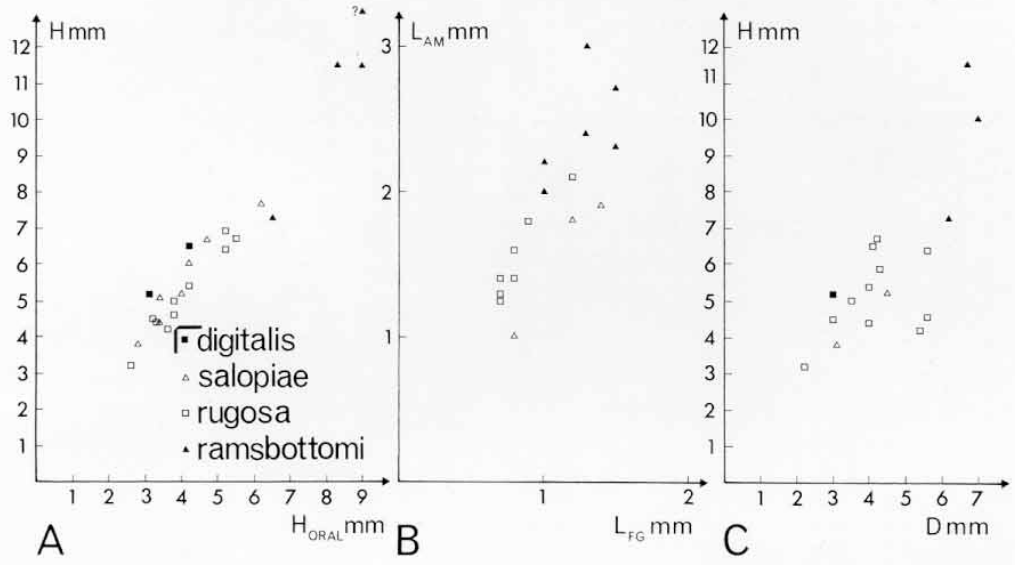
Subvective system. The ambulacra commence as five broad main grooves in the radial furrows between the coronal processes. In the floor of each main groove are two narrow food grooves which may unite near the mouth, but in some species remain separate along the entire length of the main groove. The main grooves terminate in a primary ambulacral plate, which bears two rounded facets of which the left (as viewed from the mouth down the ambulacrum) is always the smaller. The free arms are biserial and give rise to biserial lateral branches (brachioles) alternately. The arms are strongly



TEXT-FIG. 1. Standard measurements of coronate thecae. A, B, lateral views of thecae. C, base of theca. D, ambulacrum. H, height of theca, H_{DMAX}, height of theca at maximum diameter, H_{ORAL}, height of oral surface, H_{BASAL}, height of basal circlet, D, maximum diameter of theca, D_{ORAL}, diameter of oral surface, D_{BASE}, diameter of base of theca, KD, diameter of columnal facet, L_{AM}, length of ambulacrum, L_{FG}, length of food groove.

coiled when at rest (like the proboscis of a butterfly) and must have been considerably longer than the coronal processes when extended for feeding.

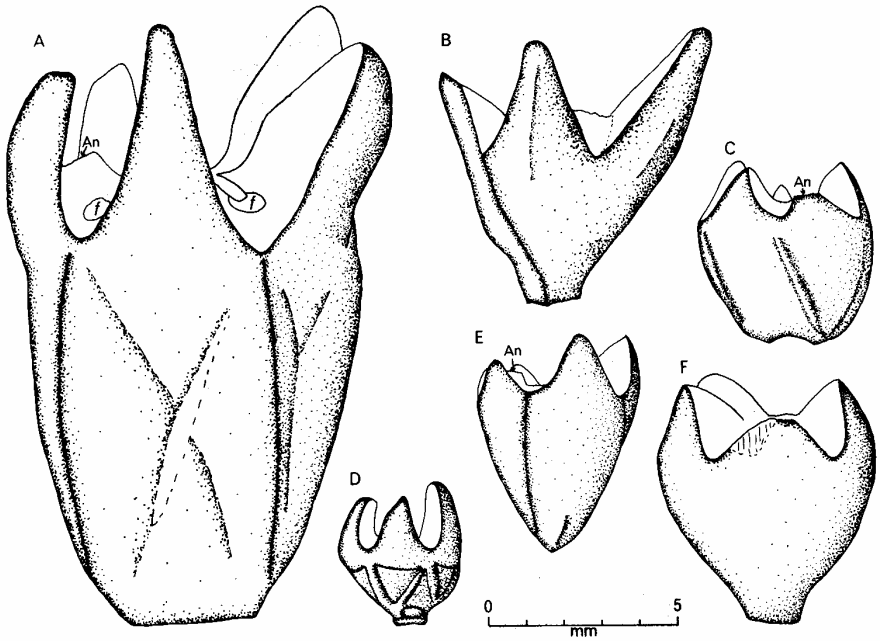
Measurements taken from specimens are explained in text-fig. 1 and summarized in Table 1. Although many parameters can be defined, it is not easy to differentiate between species graphically (text-fig. 2) due to the extreme similarity of thecae. Three bivariate plots are given; thecal height against height of the oral surface (2A), ambulacral length against length of radial furrows (2B), and thecal height against thecal diameter (2C). The best separation is given by text-fig. 2B, although the graphs suffer from a lack of data as most of the available specimens are not sufficiently well preserved to allow many measurements to be taken.



TEXT-FIG. 2. Bivariate plots of some of the measurements shown in text-fig. 1. A, height against height of oral surface. B, length of ambulacrum against length of food groove. C, height against diameter.

CHARACTERS OF THE INCLUDED GENERA

Brett *et al.* (1983) provided a very detailed and accurate description of *S. angulatus* Conrad, 1842, the first coronate to be described. They thus settled the basic characters of the type species of the type genus of the only family recognized within the Coronata. However, the status and detailed morphology of the other genera remain uncertain, as do the phylogenetic relationships of the group as a whole. North American coronates, including *S. angulatus*, are exclusively Silurian, whereas in Europe Ordovician representatives are definitely known in Britain (King and Wilcockson 1934, and herein), Bohemia (Barrande 1887), France (Chauvel and Le Menn 1973), Spain (Chauvel and Le Menn 1979), and Sweden (Regnèll 1945) and probably occur in Portugal as well (Delgado 1908). Coronates form a small but very distinctive group of pelmatozoan echinoderms. As far as is known all species and genera share an identical arrangement of thecal plates. Features which vary are general thecal shape, relative proportions of the coronal processes, surface ornament, and relative size of the stem (text-fig. 3), none of which is usually considered the type of character on which genera should be defined. Indeed it is not difficult to argue the case for assigning all known species to one genus, for which *Stephanocrinus* Conrad, 1842, is the oldest available name.



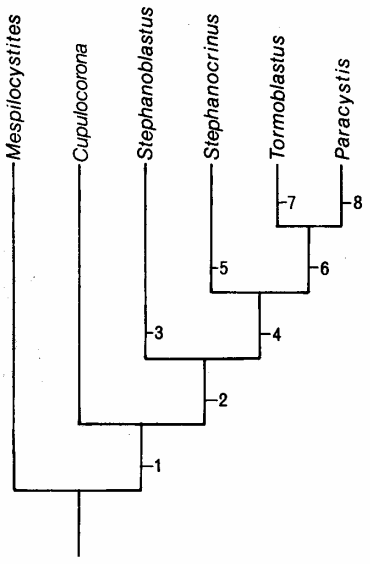
TEXT-FIG. 3. Thecal profiles in coronate genera. A, *Stephanocrinus*. B, *Mespilocystites*. C, *Paracystis*. D, *Tormoblastus*. E, *Stephanoblastus*. F, *Cupulocorona* gen. nov. All based on the type species of the genera. An, anus, *f*, primary ambulacral plate.

Nevertheless, some of the variations within the Coronata seem to be of phylogenetic significance. *Mespilocystites bohemicus* Barrande, 1887 (text-fig. 3B) from the Lower Caradoc of Trubsko, Czechoslovakia, is the oldest known species and a suitable starting point for comparisons (see Paul 1985, for a full description). It is characterized by a relatively low, broadly conical cup with very prominent coronal processes reaching half the total height which flare outwards so that their tips mark the widest part of the theca. All later forms have coronal processes that curve inwards towards their tips and in most the widest part of the theca is level with the oral surface. *M. bohemicus* also has strongly geniculate radial furrows between the coronal processes. The ambulacral grooves radiate horizontally from the mouth and terminate in facets for the arms which lie about half-way from the mouth to the periphery of the oral surface. Beyond the arm facets the radial furrows slope steeply downwards at an angle of about 40°. All other species, except *M. tregarvanicus* Le Menn from the Ashgill of Brittany, have planar or gently convex radial furrows, although the position of the arm facet varies from species to species. The base of the theca in *M. bohemicus* protrudes slightly and is triangular in cross-section. Within the triangle is a narrow, circular stem facet about one-tenth the diameter of the oral surface. The ornament of the main cup plates consists of obvious fine ridges which form rhombic patterns across plate sutures.

Several changes to this basic morphology had already occurred in the Caradoc, from which two Swedish species are known. *Paracystis ostrogothicus* Sjöberg, 1915 (text-fig. 3C), differs in having planar radial furrows, much lower coronal processes, and a stem facet which is impressed into the base of the theca. The corners of the basal triangle hang down slightly over the stem and the profile of the cup is a regular bowl shape. The surface ornament is composed of much coarser ridges than those of *M. bohemicus* and there are even more prominent ridges which form a V W pattern

around the theca, with the base of the V centred on the azygous basal, i.e. in the AB interray. The other Swedish Caradoc species, although discovered by F. A. Bather in 1907, has yet to be described. It has a slightly angular, bud-shaped theca with a minute stem facet about one-twenty-fifth of the diameter of the oral surface. From this facet three sharp ridges radiate to the points of the V and W angles on the lateral surface of the theca, so that the base of the theca is triradiate, not triangular. Otherwise cup plates are almost completely smooth and show only faint traces of concentric growth lines. *Stephanoblastus mirus* (Barrande 1887), from the Wenlock of Czechoslovakia is the only other described species with a triradiate base (text-fig. 3E) and is similar to the Swedish species, but it is more elongate and has very fine rhombic ridges on cup plates. *S. mirus* was made type species of *Stephanoblastus* by Jaekel (1918, p. 110) and it seems that this line became established in the Caradoc.

Tormoblastus bodae Jaekel, 1927 (text-fig. 3D), is known from a unique type specimen which has a conical theca with prominent V W ridges and a protruding triangular base which bears three horizontal flanges. Each flange is formed by two adjacent basals. Most of the remaining species fall into two distinct genera, *Stephanocrinus* and a new genus. *S. angulatus* Conrad, 1842 (text-fig. 3A), type species of *Stephanocrinus*, has a tall, steeply conical theca with tall coronal processes and a thecal profile that is slightly concave at the level of the basal : radial sutures. It also has prominent ridges in a V W pattern as well as finer ridges in rhombs. The second genus has a low, conical to cup-shaped theca with a triangular basal prominence, no V W ridges but finer ridges in rhombic sets, and generally low coronal processes (text-fig. 3F). It resembles *M. bohemicus* except that the coronal processes do not flare, the radial furrows are usually planar, and the theca is generally cup-shaped rather than conical. This genus lacks a suitable name and we propose *Cupulocorona* for it (see below). Both *Stephanocrinus* and *Cupulocorona* were already present in the Ashgill. *S. ramsbottomi* occurs in the Hirnantian of northern England, south-west Wales, and in the Boda Limestone (Ashgill) at Osmundsberget and Skålberget, Dalarna, Sweden, while a species of *Cupulocorona* also occurs in the Boda Limestone at Boda and Osmundsberget, and three new species from the Ashgill of Britain are described below. Our view of the evolutionary relationships of these genera is shown in text-fig. 4.

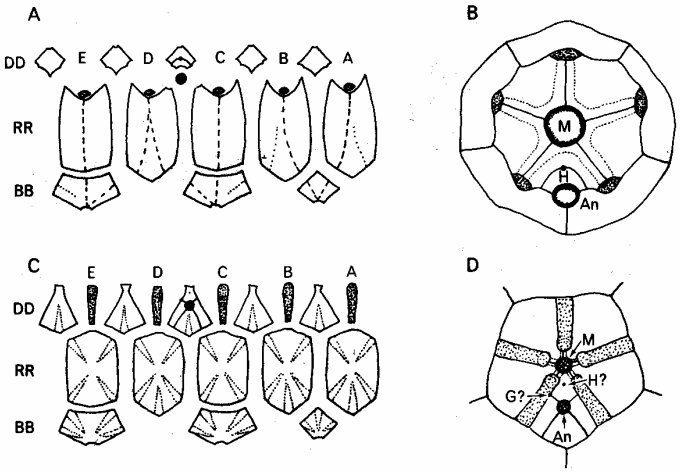


TEXT-FIG. 4. Cladogram showing inferred relationships between coronate genera. Synapomorphies (1–8) as follows: 1, loss of geniculate radial furrows; 2, development of V W pattern of ridges or angles; 3, very narrow stem and triradiate base to theca; 4, development of two additional ridges between V and W ridges; 5, tall conical theca with concave lateral surfaces; 6, ornament of coarse ridges only; 7, basal flanges; 8, bowl-shaped theca.

PHYLOGENETIC RELATIONSHIPS

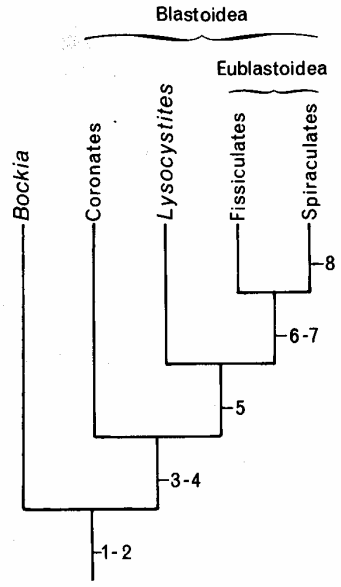
The systematic position of coronates has given rise to considerable debate. Coronates have been variously assigned to the crinoids (e.g. Wachsmuth and Springer 1886, p. 283; Bather 1900, p. 145; Fay 1962, p. 209; 1978, p. T575) or the blastoids (e.g. Etheridge and Carpenter 1886; Jaekel 1918, p. 109). Sprinkle (1980) considered them to be ancestral to the blastoids, while Brett *et al.* (1983) erected a new class, the Coronoidea, for them. Coronates share common features with blastoids and the enigmatic Silurian genus *Lysocystites*, most recently described by Sprinkle (1973, p. 139). Blastoids, coronates, and *Lysocystites* all have very similar arrangements of cup plates, including the following: three basals with the azygous basal in the AB interray, five radials, four single deltoids and two or more anal deltoids in the CD interray, and five radially positioned plates at the bases of the ambulacra. This combination of characters is not found in any other group of pelmatozoans.

The radially positioned plates at the bases of the ambulacra demonstrate most clearly the close affinities of blastoids, coronates, and *Lysocystites*. Blastoids differ from all other pelmatozoans in having hydrospires and lancet plates beneath the ambulacra. Hydrospires are an autapomorphy of the Blastoidea, being without homologue in other echinoderms; the lancet plate is not. Coronates have a single plate at the base of each arm which lies between the radial and two adjacent deltoids (text-fig. 5B). An erect arm with alternate biserial branches (brachioles) arises from this plate. As Sprinkle (1980) pointed out, to derive a blastoid ambulacrum from a coronate arm requires extension of the primary ambulacral plate to become the lancet and the development of a recumbent ambulacrum on top of it. *Lysocystites* (text-fig. 5C, D) has five elongate, radially positioned plates between the deltoids at the adoral ends of which are facets for erect ambulacra of unknown structure.



TEXT-FIG. 5. Plate diagrams in coronates and *Lysocystites*. A, B, Coronates. A, lateral view (broken lines indicate V and W ridges, dotted lines additional ridges found in *Stephanocrinus*, *Tormoblastus*, and *Paracystis*); B, oral surface. C, D, *Lysocystites*. C, lateral view (dotted lines indicate outlines of triradiate thecal pore structures); D, oral surface. A–E, Carpenter radii; An, anus; BB, basal plates; DD, deltoid plates; G, gonopore; H, hydropore; M, mouth; RR, radial plates; supposed homologues of blastoid lancet plates stippled. Note that these plates bear the facets for erect arms and always lie in a radial position between a radial plate and two deltoids. Note also that the mouth frame is composed of five deltoids even in *Lysocystites* where they are elongate.

These plates lie between two deltoids and are in contact with a radial. In our view they, too, are homologues of the lancet plate in blastoids. Coronates, blastoids, and *Lysocystites* differ in their pore structures. *Lysocystites* has unique pore structures running to the corners of the basals, radials, and deltoids. Coronates have n-shaped canals within the coronal processes (see Brett *et al.* 1983, for a thorough description), while blastoids have hydrospires. Brett *et al.* (1983) have argued that the differences between the ambulacra and pore structures in the Blastoidea and Coronata warrant the recognition of a separate class for the latter. Whether one accepts this new class or not, *Lysocystites* has the same taxonomic status as coronates and blastoids. Since it is clearly possible to infer relationships between blastoids, coronates, and *Lysocystites* (text-fig. 6), an alternative course of action is to unite the three within an enlarged class Blastoidea. With the exception of the inclusion of *Lysocystites* and the omission of the parablastoids, this is essentially the classification advanced by Jaekel (1918, p. 107 *et seq.*).



TEXT-FIG. 6. Cladogram showing inferred relationships between the 'eocrinoid' *Bockia*, the coronates, and blastoids. Synapomorphies (1–8) as follows: 1, three basal plates; 2, erect, biserial, pinnate arms; 3, cup formed by BB, RR, and DD only; 4, ambulacra on distinct base-plate (= lancet in eublastoids); 5, elongate ambulacral base-plate; 6, recumbent ambulacra; 7, hydrospires; 8, spiracles.

There remains the question of the ancestry of the Blastoidea, as modified and enlarged here. The most likely candidate is the 'eocrinoid' *Bockia*, even though at first sight it differs dramatically from blastoids. *Bockia* shares the following characters with blastoids *sensu lato*: a narrow circular stem, a cup with three basal plates (unfortunately the position of the smallest basal with respect to the Carpenter ambulacra remains unknown), and erect, biserial arms with alternating biserial lateral branches (brachioles) which arise from an oral prominence that had four normal deltoids and three posterior deltoids in the CD interray. The ambulacral structure is similar to that found in coronates, although not absolutely identical (see Bockelie 1981, for a more complete description of *Bockia*). To transform *Bockia* into a coronate requires cessation of plate addition early in growth, but after the basals, radials, and deltoids had formed, development of coronal processes, and the incorporation of the primary ambulacral plates into the theca. These last plates may have been derived from the small plates in the oral prominence of *Bockia* or alternatively they may be enlarged ambulacral plates. Regrettably the details of this part of the cup in *Bockia* are insufficiently known to

settle this point. The blastoid lineage was relatively successful, but ultimately became extinct in the Permian.

SYSTEMATIC PALAEONTOLOGY

Subphylum BLASTOZOA Sprinkle, 1973
Class BLASTOIDEA Say, 1825
Subclass CORONATA Jaekel, 1918
Family STEPHANOCRINIDAE Wachsmuth and Springer, 1886

Definition. Pelmatozoans with a slender homeomorphic stem; theca formed of three basals (the azygous in the AB interray), five radials, six deltoids (a sub- and super-deltoid in the CD interray and one each in the other four interrays), five primary ambulacral plates each bearing two ambulacral facets, five interradial oral cover plates of which the one in the CD interray is slightly the largest, ten long, thin ambulacral cover plates (a pair in each ambulacrum); deltoids and radials produced into erect coronal processes containing n-shaped canals; oral surface with three orifices, a large central mouth, a moderately large anus in the CD coronal process and covered by a pyramid of three or four anal cover plates, and a small slit-like hydropore on the sub-superdeltoid suture between the anus and the mouth; primary ambulacral plates bearing erect, biserial, pinnate arms with biserial lateral branches (brachioles), the two facets of the primary ambulacral plate bearing the main arm trunk and the first lateral branch.

Genus STEPHANOCRINUS Conrad, 1842

Type species. By monotypy, *Stephanocrinus angulatus* Conrad, 1842, from the Middle Silurian, Rochester Shale, of New York State.

Diagnosis. Narrow stem, large, elongate, conical theca with a triangular base, often with concave sides and with low or high coronal processes, planar radial furrows, and ornament of very strong V W ridges as well as finer ridges in rhombic sets.

Stephanocrinus ramsbottomi sp. nov.

Plate 62, figs. 1, 5, 6, 8; Plate 63, fig. 6; text-figs. 7A, 8B

v1907 New cystidean; Reed, p. 537.
v1934 *Stephanocrinus* sp.; Bather in King and Wilcockson, p. 17.

Derivation of species name. In honour of Dr. W. H. C. Ramsbottom.

EXPLANATION OF PLATE 62

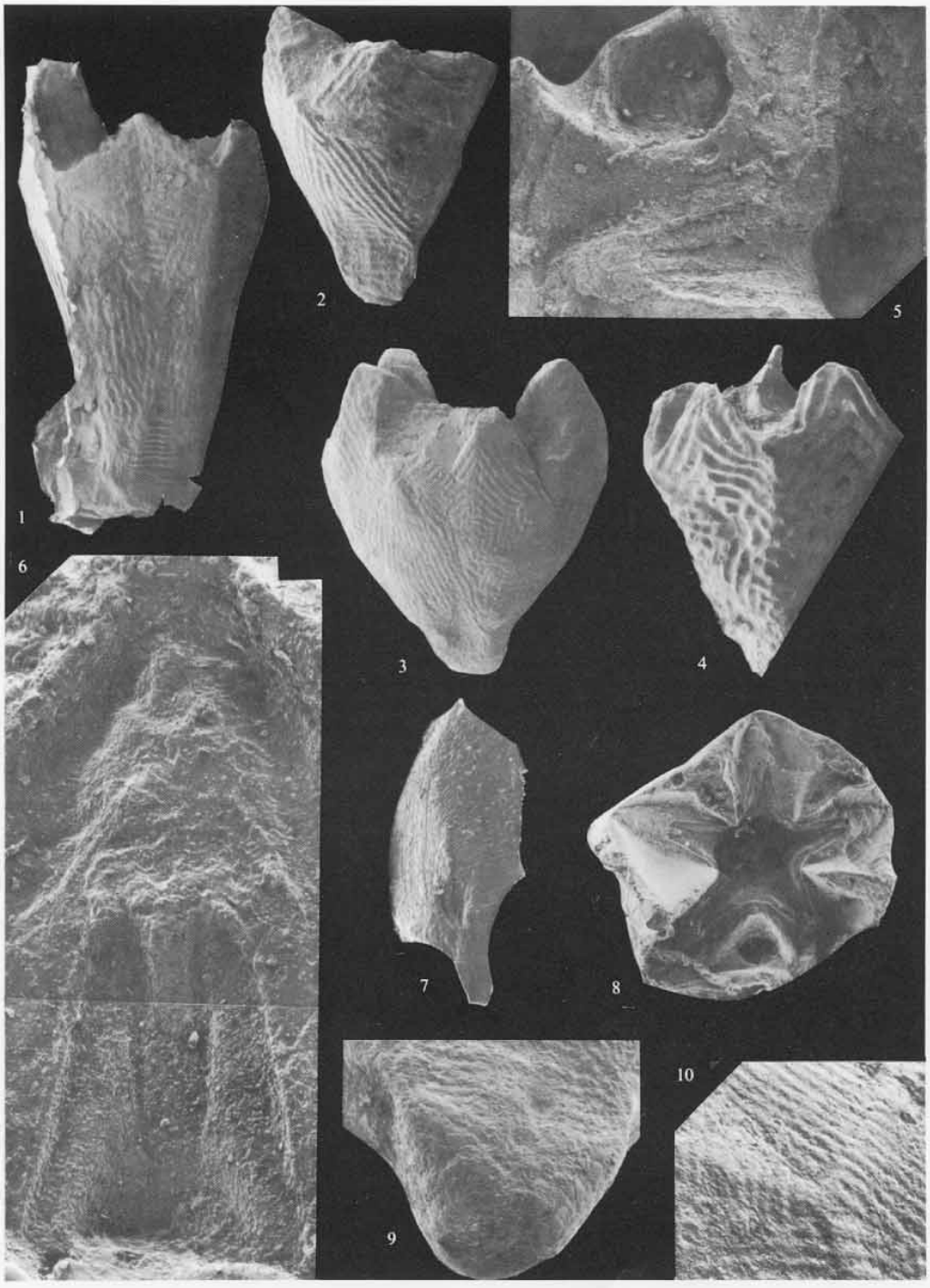
Figs. 1, 5, 6, 8. *Stephanocrinus ramsbottomi* sp. nov. 1, 8, holotype, BMNH E25427. 1, lateral view of theca, × 8. 8, oral surface, × 8·3. 5, BMNH E25428. Anus, two ambulacra, and part of the mouth, × 22. 6, BMNH E25426. Ambulacrum showing paired food grooves (mouth below), × 50.

Figs. 2, 3, 9, 10. *Cupulocorona salopiae* gen. et sp. nov. 2, BMNH E45531. Lateral view of the theca, × 15. 3, BMNH E45532. Lateral view of theca, × 11. 9, BMNH E6393. Oblique view of the triangular base of theca. The stem articulated on the depressed, circular facet, × 28. 10, BMNH E45530. Sutures between two radials (left) and a basal, preserved in positive relief, × 24.

Fig. 4. *Cupulocorona rugosa* gen. et sp. nov. SM A31002a. Lateral view of theca, × 12.

Fig. 7. ?*Stephanocrinus s. l.* sp. BMNH E69218. Lateral view of theca (orientation unknown), × 13.

All scanning electron micrographs of latex casts from natural moulds, except figs. 2, 3, 9, 10.



DONOVAN and PAUL, coronate echinoderms

Diagnosis. Low, triangular coronal processes, with ambulacral facets about half-way from the mouth to the periphery of the oral surface, and with a prominent convex ridge aboral to the facets.

Types. Holotype, British Museum, Natural History, (BMNH) E25427 from the Hirnantian at Hunterstye, north-west Yorkshire. Eighteen paratypes in BMNH and Sedgwick Museum, Cambridge (SM).

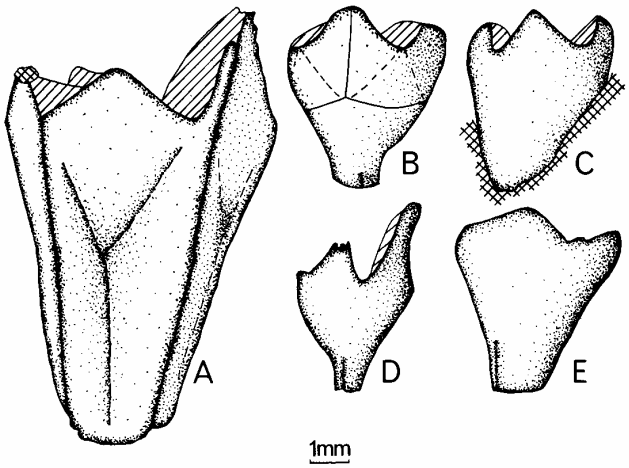
Other material. Twenty-one thecae, all of which are external moulds unless otherwise stated. BMNH E25426, E25427*a*, *b*, E25428*a–d* (*a* = internal mould); SM A31830, 1, 2*a*, *b*, 3*a*, *b*, 4–7 (internal moulds), A32077, A39061, 2*a*, *b*, A41084*a–d* (*a* = internal mould), A109797/8 (part and counterpart), X.772–X.774.

Horizons and localities. This species is known from three British localities, two of which indicate a definite Hirnantian age.

1. Ashgill Shales, old quarry on Hunterstye, Upper Crummackdale, Austwick district, north-west Yorkshire, NGR SD 780716. King and Wilcockson (1934, p. 17) also identified *Phacops* cf. *mucronata*, *Meristina crassa*, and *Rafinesquina* cf. *Strophomena hirnantensis* from this locality. Williams *et al.* (1972) regard the Ashgill Shales in this area to be of Hirnantian age, based on assessment of the brachiopod fauna by Wright (1968, table 3).
2. St. Martin's Cemetery Beds, roadside 110 m west of St. Martin's Cemetery, Haverfordwest, Dyfed, South Wales (Reed 1907, Cantrill 1907). Hirnantian (Williams *et al.* 1972, fig. 5).
3. North side of the bend in the lane from Keisley Hamlet to the west quarry, Keisley, Westmorland, NGR NY 712238. The precise horizon is unknown, but may be Lower Llandovery in age (Wright 1982).

In addition, specimens from the Boda Limestone (Ashgill) at Osmundsberget and Skålberget, Dalarna, Sweden, appear to belong to this species.

Description. Theca angular, elongate conical, with a pentagonal oral surface (Pl. 62, fig. 8; text-fig. 8B) and triangular base. The five angles of the oral surface joined to the three at the base by prominent ridges which form a V (Pl. 63, fig. 6) with its base in the AB interray, and a W with the tops in the C, D, and E rays. Faces of the theca slightly concave (Pl. 62, fig. 1; Pl. 63, fig. 6; text-fig. 7A). Stem facet round, usually more than half the diameter of the triangular base. Coronal processes triangular, varying from low with straight sides (Pl. 63, fig. 6) to high with incurved sides (Pl. 62, fig. 1). Ornament of low ridges arranged in rhombic patterns (Pl. 62, fig. 1; Pl. 63, fig. 6). Ambulacral grooves extend about half-way along the radial furrows (Pl. 62, fig. 5). Ambulacral, oral, and anal



TEXT-FIG. 7. Thecal profiles in British coronates. A, *Stephanocrinus ramsbottomi*, holotype, BMNH E25427. B, *Cupulocorona salopiae*, holotype, BMNH E6390. C, E, *C. rugosa*. C, paratype, SM A31002*a*. E, paratype, SM A31261*b*. D, *C. digitalis*, holotype, SM A40229.

cover plates unknown. Mouth central, circular. Anus circular, about half the diameter of the mouth (Pl. 62, figs. 6, 8; text-fig. 8B). Oral surface slopes slightly away from the mouth.

Discussion. S. ramsbottomi is the largest British coronate and is also the earliest member of the genus *Stephanocrinus* as we understand it. The earliest American species are from the Upper Llandovery (C_5), Hopkington Formation (Brett *et al.* 1983, p. 632). The present species differs from *S. angulatus* in having a plate ornament of ridges rather than rows of tubercles, lower coronal processes, the ambulacral facets nearer the mouth, and a more angular theca. It differs from other British coronates in not having a cup-like outline (text-fig. 7).

?*Stephanocrinus sensu lato* sp.

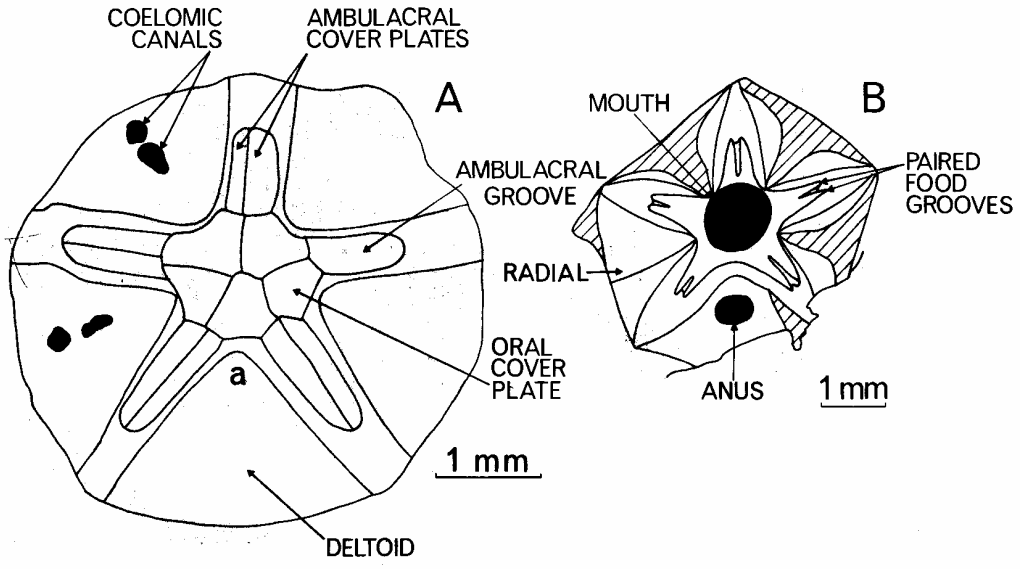
Plate 62, fig. 7; Plate 63, fig. 1

Material. A single, incomplete external mould, BMNH E69218, collected by C.R.C.P.

Horizon and locality. Sholeshook Limestone (Cautleyan; Price 1973, 1980), Sholeshook railway cutting, near Haverfordwest, Dyfed, South Wales, NGR SM 968171.

Description. The specimen is an external mould, without counterpart, of part of a theca (Pl. 62, fig. 7). Neither oral surface nor base of the cup visible. Part of two sides of theca apparent, the junction between them angular, suggesting a species of *Stephanocrinus*. Theca probably pentagonal in cross-section. On one side an ornament of fine striae is preserved (Pl. 63, fig. 1) which fan out and lie between 40° and 80° to the angle between the sides of the theca. On the second side the striae are subparallel to this ridge. The specimen is 3·2 mm wide by 7·6 mm long, individual striae about 0·07 mm wide.

Discussion. This specimen has a much finer ornament than other specimens from the Sholeshook Limestone (i.e. *Cupulocorona rugosa* gen. et sp. nov.). The theca is more angular and, apparently, proportionately more conical. The incomplete preservation precludes a more detailed description. The specimen seems to represent a stephanocrinid with an angular theca, but without better material a definite generic assignment cannot be made.



TEXT-FIG. 8. Oral surfaces of British coronates. A, *Cupulocorona salopiae*, holotype, BMNH E6390, a, approximate position of anus. B, *Stephanocrinus ramsbottomi*, holotype, BMNH E25427.

Genus CUPULOCORONA gen. nov.

Type species. Cupulocorona salopiae sp. nov.

Derivation of generic name. From the Latin *cupula* = a small cask, *corona* = a crown.

Diagnosis. Narrow stem, conical to cup-shaped theca with protruding triangular base and generally low coronal processes, planar or gently convex radial furrows, ornament of fine to coarse ridges in rhombic sets, but no prominent V W ridges.

Cupulocorona salopiae sp. nov.

Plate 62, figs. 2, 3, 9, 10; Plate 63, figs. 2, 3; text-figs. 7B, 8A

v1952 *Stephanocrinus salopiae*; Ramsbottom ms.

Derivation of species name. From the adjective Salopian = of Shropshire.

Diagnosis. Blunt coronal processes, pyriform theca with plate suture emphasized by low ridges.

Types. Holotype, BMNH E6390, paratypes, BMNH E6392–6394, E45530–45532.

Other material. Seven complete thecae, five of which are distorted.

Horizon and locality. The specimen labels state: 'Silurian. Lower Wenlock Shales, Buildwas Beds. E. bank of River Severn, a short distance above Buildwas Bridge, Shropshire.' Vine (1882, table, p. 48) records calyces of echinoderms from Maw's samples 36 and 37 in the Buildwas Beds, and the records probably refer to this species. The Buildwas Beds are of early Wenlock age, from mid-*centrifugus* zone to mid-*riccartonensis* zone (Cocks *et al.* 1971). It is not known if Maw's samples came from a single horizon or were gathered from throughout the outcrop. The specimen labels seem to refer to locality 132 of Dean (1968).

Description. Theca pear-shaped (Pl. 62, figs. 2 and 3). Base triangular with rounded corners (Pl. 62, fig. 9), stem cicatrix circular and depressed. Thecal cross-section changes from triangular to rounded pentagonal just above the base. Coronal processes large and triangular, with blunt angles (text-fig. 7B). Sutures between adjacent plates bear broad ridges (Pl. 62, fig. 10). Aboral surface of theca ornamented with fine ridges in rhombic patterns. Ambulacra bear paired food grooves, which slope gently away from the mouth and extend about 65% of the way to the periphery of the oral surface (Pl. 63, figs. 2 and 3; text-fig. 8A). Food grooves concealed by paired ambulacral cover plates. Five oral cover plates lie interradially over the mouth. The anus has not been identified with certainty, although the approximate position can be predicted (text-fig. 8A). The hydropore has not been seen. Two broken coronal processes, in the DE and EA interrays of the holotype, expose paired coelomic canals within. Measurements are given in table 1.

Cupulocorona rugosa sp. nov.

Plate 62, fig. 4; Plate 63, figs. 4, 7–9; text-fig. 7C, E

Derivation of species name. From the Latin *rugosa* = rough, corrugated.

EXPLANATION OF PLATE 63

Fig. 1. ?*Stephanocrinus s. l.* sp. BMNH E69218. Detail of ornament, × 55.

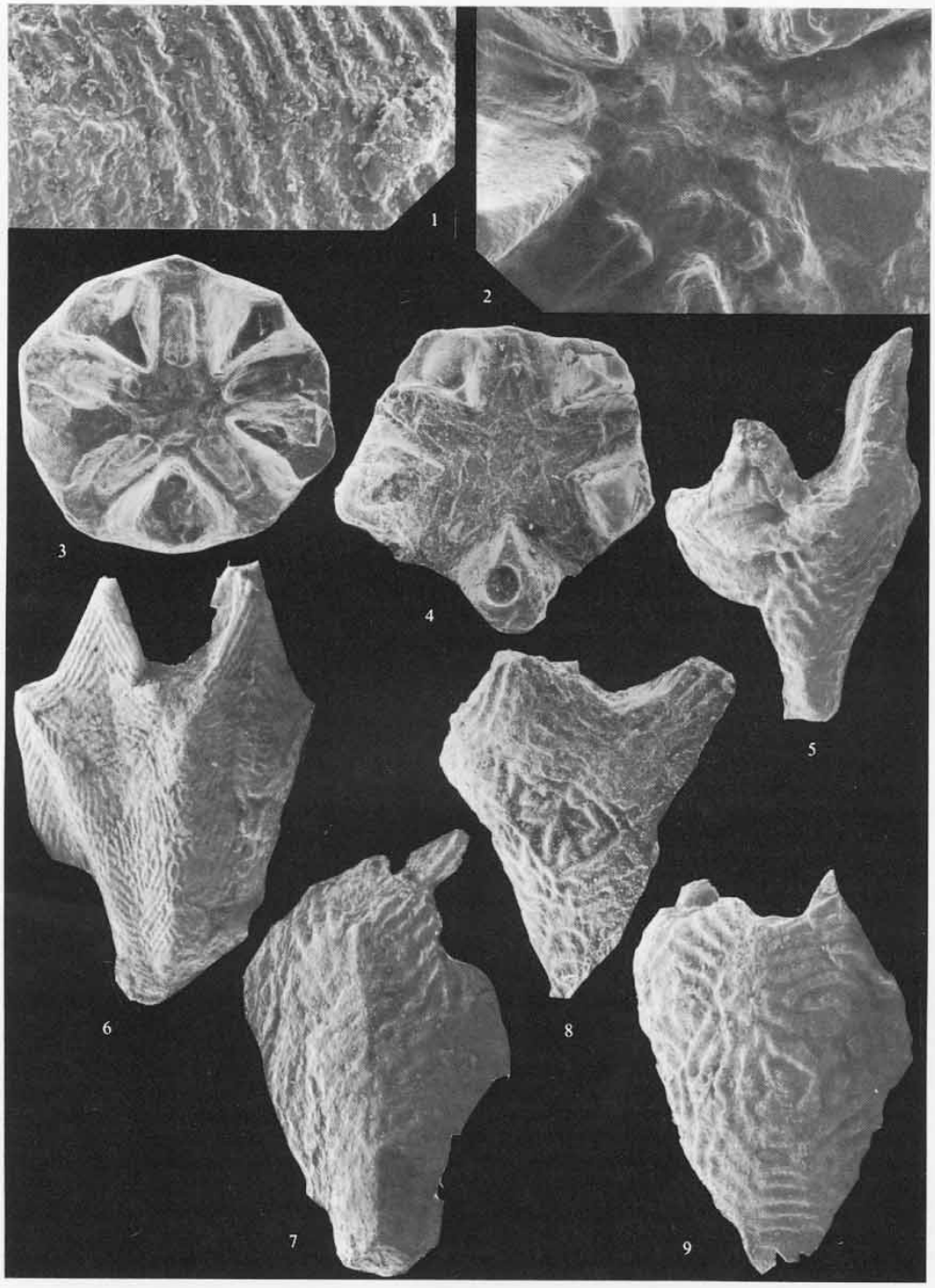
Figs. 2, 3. *Cupulocorona salopiae* gen. et sp. nov. Holotype, BMNH E6390. 2, oral cover plates (centre) and five pairs of ambulacral cover plates (A ray above), × 30. 3, oral surface (anus below), × 12·3.

Figs. 4, 7–9. *Cupulocorona rugosa* gen. et sp. nov. 4, SM A31813. Oral surface (anus below), × 12·3. 7, SM A40187. Lateral view showing base of theca, × 21. 8, holotype, SM A31004*b*. Lateral view, × 15·5. 9, SM A53930*a*. Lateral view, × 13.

Fig. 5. *Cupulocorona digitalis* gen. et. sp. nov. Holotype, SM A40229, × 15.

Fig. 6. *Stephanocrinus ramsbottomi* sp. nov. SM A109798. Lateral view of crushed theca, × 8.

All scanning electron micrographs of latex casts from natural moulds, except figs. 2, 3.



DONOVAN and PAUL, coronate echinoderms

TABLE 1. Measurements in mm of British coronate echinoderms

Spec. No.	D	D_{BASE}	D_{ORAL}	H	H_{DMAX}	H_{ORAL}	H_{BASAL}	KD	L_{FG}	L_{AM}
Stephanocrinus ramsbottomi										
BM E25426	6·8	?	6·7	?	?	?	?	?	1·0	2·2
BM E25427	6·7	2·0	6·3	11·5	= H	9·0	?	0·7	1·3	2·4
BM E25428	7·0	?	7·0	10·0	= H?	7·7?	?	?	1·5	2·3
BM E30485	Internal mould									
SM A31830	Poorly preserved base of a theca									
SM A31831	6·0	1·1	6·0	?	= H?	6·0	?	1·1	?	?
SM A31832	8·0	1·8	= D	12·0	9·2	9·2	?	1·3	0·7	2·4
SM A31833	8·1+	2·0?		13·0?	= H	9·0?	?	?	1·3	3·0
SM A31834–7	All internal moulds									
SM A32077	Deformed oral surface only									
SM A39061	7·3+	?	7·3	?	?	?	?	?	1·5	2·7
SM A39062	6·2	1·0	5·7?	7·3	= H	6·5	?	0·8	1·0	2·0
SM A40184	Poorly preserved									
SM A109797/8	?	?	?	11·5	= H?	8·3	?	?	?	?
Cupulocorona salopiae										
BM E6390	4·5	1·2	4·4	5·2	= H	4·0	2·0	0·6	1·2	1·8
BM E6392	?	1·6	?	6·7	= H	4·7	?	0·6	?	?
BM E6393	?	1·4	?	6·0	= H	4·2	3·2?	0·8	?	?
BM E6394	?	1·1	= D	4·4	= H	3·4	?	0·5	?	?
BM E45530	?	1·6	?	7·7	6·2	6·2	4·0	0·8	1·4	1·9
BM E45531	3·1	1·2	3·1	3·8	3·4	2·8	1·6?	0·65	0·8	1·0
BM E45532	?	1·2	?	5·1	3·8	3·4	2·4	0·6	?	?
Cupulocorona digitalus										
BM E30484	?	1·0	4·1	6·5	?	4·2	?	?	?	?
SM A40229	3·0	0·6	= D	5·2	= H	3·1	?	?	?	?
Cupulocorona rugosus										
SM A31001	5·6	?	5·4	4·6	= H	3·8	?	?	1·2	2·1
SM A31002	4·0	?	4·0	4·4	3·3	3·3	?	?	0·8	1·6
SM A31003	4·0?	?	3·8	5·4	4·2	4·2	?	?	?	1·7
SM A31004	4·2+	?	4·2	?	?	?	?	?	0·8	1·4
SM A31259	5·6	?	5·6	6·4+	5·2+	5·2+	?	?	0·9	1·8
SM A31260	4·2+	0·7?	4·0+	6·7+	= H	5·5+	?	0·7	?	?
SM A31261	4·3?	0·9	4·1	5·9	= H	5·2	?	0·6	0·7?	1·7
SM A31813	4·3	?	4·0	?	= H	?	?	?	0·7	1·4
SM A40185	Preserves part of the cup ornament only									
SM A40186	3·0+	0·8	= D	4·5	= H	3·2	?	0·6	?	?
SM A40187	2·2	0·6	= D	3·2	= H	2·6	?	0·5	?	?
SM A40188	3·5	0·9	= D	5·0	= H	3·8	?	0·6	0·7	1·4
SM A40189	3·2?	?	3·2	?	?	?	?	?	0·7	1·25
SM A53929	5·4	1·6	5·0	4·2	= H	3·6	?	?	?	?
SM A53930	Poorly preserved									

Diagnosis. Coarse-ribbed ornament and coronal processes which are lower than wide.

Types. Holotype, SM A31004, from the Upper Ordovician, Redhill Beds, at Prendergast Place near Haverfordwest, Dyfed, South Wales, plus fourteen paratypes (SM).

Other material. Fifteen specimens in the Sedgwick Museum collections (all external moulds unless otherwise indicated). A31001*a*, *b* (part and counterpart), A31002*a*, *b* (part and counterpart), A31003, 4*a*, *b* (*a* = internal

mould), A31259*a*, *b* (part and counterpart), A31260, 1*a*, *b* (part and counterpart), A31813, A40185–40187, 8*a*, *b* (part and counterpart), 9*a*, *b* (*a* = internal mould), A53929*a*, *b* (*b* = artificial cast), A53930*a*, *b* (*b* = artificial cast).

Horizons and localities. This species is known from five localities and horizons, all of which are Ashgill in age.

1, 2. The Sholeshook Limestone, both in the railway cutting (NGR SM 968171) and at Prendergast Place (NGR SM 957166), near Haverfordwest, Dyfed, South Wales. Most of the Sholeshook Limestone is Cautleyan in age, but the youngest rocks at Prendergast Place are Rawtheyan, Zone 5, according to Price (1980).

3. The Redhill Beds at Prendergast Place which Price (1980, p. 486, table 1) considered to be confined to the Rawtheyan, Zone 5.

4. The Lower Phillipsinella Beds at locality 1 of King (1923, p. 494, fig. 2), Aber Marchnant, SW Berwyn Hills, Powys (NGR SJ 039194). These beds contain *Kloucekia robertsi* (Reed 1904) which Ingham (1977, p. 118) regarded as an important index fossil for Rawtheyan, Zone 5.

5. The Dolhir Beds (mid-Cautleyan to Rawtheyan; Hiller 1981) at two localities in the Glyn Ceiriog district, Clwyd. (*a*) 'Tram cutting ENE of Coed-y-Glyn-isaf' (specimen label) and (*b*) on the road close to, and north of, Gelli (NGR SJ 184367; Groom and Lake 1908).

Description. Thecal cross-section round (Pl. 63, fig. 8) to pentagonal (Pl. 62, fig. 4), with circular to pentagonal oral surface (Pl. 63, fig. 4) and triangular base (Pl. 63, fig. 7). Stem facet round. Coronal processes triangular, lower than wide. Ornament of coarse ridges in rhombic patterns (Pl. 62, fig. 4; Pl. 63, figs. 7–9). Ambulacral, oral, and anal cover plates unknown. Ambulacral grooves about 50% of the length of the radial furrows, with paired food grooves at their distal ends. Mouth circular to weakly pentagonal; anus circular.

Cupulocorona digitalis sp. nov.

Plate 63, fig. 5; text-fig. 7D

Derivation of species name. From the Latin *digitus* = finger.

Diagnosis. Long finger-like coronal processes, ornament of coarse ridges, conical thecal profile, and constricted base.

Types. Holotype, SM A40229, from the Ashgill, Phillipsinella Beds at Aber Marchnant, SW Berwyn Hills. Paratype, BMNH E30484.

Other material. Two thecae, the holotype being an external mould with a counterpart.

Horizons and localities. 1, type locality (see *C. rugosa*) and 2, 5 m above the Pusgillian Pen-y-Garnedd black shales at Powys Arms Quarry, Pen-y-Garnedd, south-east of Llanfyllin, Powys, possibly Cautleyan (P. J. Brenchley, pers. comm.).

Description. Theca low, conical, with a nipple-like triangular base. Stem facet not seen. Coronal processes finger-like or triangular with curved sides (neither specimen shows both sides of the theca so the precise nature of the coronal processes is not established). Ornament of coarse rhombic ridges. Oral surface not seen.

Acknowledgements. We thank Dr. D. Price, Sedgwick Museum, Cambridge, and Dr. A. B. Smith and Mr. D. N. Lewis, British Museum, Natural History, for the loan of specimens. Dr. W. H. C. Ramsbottom kindly gave us a copy of his unpublished manuscript on British and Swedish coronates. Scanning electron micrographs were produced by Mr. C. J. Veltkamp of the Botany Department, Liverpool University, and Table 1 was typed by Ms. Grainne Moloney. Some of the photomicrographs were printed by Mr. D. J. McCabe. Finally, part of this work was undertaken during the tenure of NERC research grant GR3/4732, which is gratefully acknowledged.

REFERENCES

BARRANDE, J. 1887. *Systême Silurien du centre de la Bohême. 1e partie: Recherches paléontologiques. v. 7. Classe des Échinodermes. Ordre des Cystidés*, xix + 233 pp., 39 pls. Leipzig and Prague.

BATHER, F. A. 1900. The Echinoderma. *In* LANKESTER, E. R. (ed.), *A Treatise on Zoology*, vol. 3, 344 pp. London.

BOCKELIE, J. F. 1981. The Middle Ordovician of the Oslo Region, Norway. 30. The eocrinoid genera *Cryptocrinites, Rhipidocystis* and *Bockia*. *Norsk geol. Tidskr.* **61,** 123–147.

BRETT, C. E., FREST, T. J., SPRINKLE, J. and CLEMENT, C. R. 1983. Coronoidea: a new class of blastozoan echinoderms based on taxonomic reevaluation of *Stephanocrinus*. *J. Paleont.* **57,** 627–651.

CANTRILL, T. C. 1907. Stratigraphical note. *Geol. Mag.* **44,** 537–538.

CHAUVEL, J. and LE MENN, J. 1973. Échinodermes de l'Ordovicien Supérieur de Coat-Carrec, Argol (Finistère). *Bull Soc. géol. miner. Bretagne* Ser. c, **4,** 39–61, pls. 1–3.

——— 1979. Sur quelques échinodermes (Cystoïdes et Crinoïdes) de l'Ashgill d'Aragon (Espagne). *Géobios,* **12,** 549–587, 3 pls.

COCKS, L. R. M., HOLLAND, C. H., RICKARDS, R. B. and STRACHAN, I. 1971. A correlation of Silurian rocks in the British Isles. *Quart. Jl geol. Soc. Lond.* **127,** 103–136.

CONRAD, T. A. 1842. Observations on the Silurian and Devonian systems in the United States, with descriptions of new organic remains. *J. Acad. nat. Sci. Philad.* **8,** 228–280, pls. 12–17.

DEAN, W. T. 1968. Geological itineraries in south Shropshire. *Geol. Ass. Guide,* **27,** 48 pp.

DELGADO, J. F. N. 1908. *Systême Silurian du Portugal Étude de Stratigraphie Paléontologique,* 247 pp., 4 pls. Lisbon.

ETHERIDGE, R. JN. and CARPENTER, P. H. 1886. *Catalogue of the Blastoidea in the Geological Department of the British Museum (Natural History),* xv + 322 pp., 20 pls. London.

FAY, R. O. 1962. Ventral structures of *Stephanocrinus angulatus* Conrad. *J. Paleont.* **36,** 206–210, pl. 35.

—— 1978. Order Coronata Jaekel, 1918. *In* MOORE, R. C. and TEICHERT, C. (eds.). *Treatise on Invertebrate Paleontology. Part T. Echinodermata 2,* pp. T574–T578. Geol. Soc. Am. and Univ. Kansas Press.

GROOM, T. and LAKE, P. 1908. The Bala and Llandovery rocks of Glyn Ceiriog (North Wales). *Quart. Jl geol. Soc. Lond.* **64,** 546–595.

HILLER, N. 1981. The Ashgill rocks of the Glyn Ceiriog district, North Wales. *Geol. J.* **16,** 181–200.

INGHAM, J. K. 1977. The Upper Ordovician trilobites from the Cautley and Dent districts of Westmorland and Yorkshire. *Palaeontogr. Soc.* [*Monogr.*], **3,** 89–121, pls. 19–27.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. *Paläont. Z.* **3,** 1–128.

—— 1927. Über *Tormoblastus* n.g., eine coronate Blastoidee, aus dem Ordovicium Schwedens. *Ark. Zool.* **19A** (4), 6 pp., 1 pl.

KING, W. B. R. 1923. The Upper Ordovician rocks of the southwestern Berwyn Hills. *Quart. Jl geol. Soc. Lond.* **79,** 487–507, pl. 26.

—— and WILCOCKSON, H. W. 1934. The Lower Palaeozoic rocks of Austwick and Horton-in-Ribblesdale, Yorkshire. Ibid. **90,** 7–31.

PAUL, C. R. C. 1985. Ordovician and Silurian coronates from Czechoslovakia. *Geol. J.* **20,** 21–29.

PRICE, D. 1973. The age and stratigraphy of the Sholeshook Limestone of southwest Wales. Ibid. **8,** 225–246.

—— 1980. A revised age for the topmost Sholeshook Limestone Formation (Ashgill) of South Wales. *Geol. Mag.* **117,** 485–489.

REED, F. R. C. 1904. New fossils from the Haverfordwest district. Ibid. **41,** 106–109, pl. 5.

—— 1907. The base of the Silurian near Haverfordwest. Ibid. **44,** 535–537.

REGNÈLL, G. 1945. Non-crinoid Pelmatozoa from the Palaeozoic of Sweden: a taxonomic study. *Meddn Lunds geol-miner. Instn,* **108,** 255 pp., 15 pls.

SAY, T. 1825. On two genera and several species of Crinoidea. *J. Acad. nat. Sci. Philad.* **4,** 289–296.

SJÖBERG, S. 1915. *Paracystis ostrogothicus* g. et sp. n., en egendomlig Pelmatozo från Östergötlands Chasmopskalk. *Geol. For. Stockholm Forhandl.* **37,** 171–178, pls. 2–3.

SPRINKLE, J. 1973. Morphology and evolution of blastozoan echinoderms. *Spec. Publ. Mus. comp. Zool. Harv.* 284 pp., 43 pls. Cambridge, Mass.

—— 1980. Origin of blastoids: new look at an old problem. *Geol. Soc. Am. Abstr. Progr.* **12,** 528.

VINE, G. R. 1882. Notes on the Polyzoa of the Wenlock Shales, Wenlock Limestone, and Shales over Wenlock Limestone. From material supplied by G. Maw, Esq., F.L.S., F.G.S. *Quart. Jl geol. Soc. Lond.* **38,** 44–68.

WACHSMUTH, C. and SPRINGER, F. 1886. Revision of the palaeocrinidae, pt. 3, sect. 2. Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions. *Proc. Acad. nat. Sci. Philad.* (1885), 225–364, pls. 4–9.

WILLIAMS, A., STRACHAN, I., BASSETT, D. A., DEAN, W. T., INGHAM, J. K., WRIGHT, A. D. and WHITTINGTON, H. B. 1972. A correlation of Ordovician rocks in the British Isles. *Spec. Rep. geol. Soc. Lond.* **3,** 74 pp.

WRIGHT, A. D. 1968. A westward extension of the Upper Ashgillian *Hirnantia* fauna. *Lethaia,* **1,** 352–367.

—— 1982. The Ordovician–Silurian boundary at Keisley, northern England. *In* BRUTON, D. L. and WILLIAMS, S. H. (eds.). Abstracts for meetings 20, 21 and 23 August 1982, IVth International Symposium on the Ordovician System. *Palaeont. Contr. Oslo Univ.* **280,** 60.

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Typescript received 1 June 1984
Revised typescript received 29 November 1984