THE DEVONIAN BLASTOID *BELOCRINUS* FROM FRANCE

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ABSTRACT. The nature and validity of the Lower Devonian blastoid genus *Belocrinus* Munier-Chalmas from north-western France has been in doubt since its original description. A complete specimen of the type species, *B. cottaldi* (Munier-Chalmas) is described and illustrated. The genus *Belocrinus* is redefined; it is similar to, but not synonymous with, the genus *Cordyloblastus* Fay. The number of anal deltoids and hydrospires in *Belocrinus* could not be determined. The ontogenetic development of the plates of the calyx is also described.

IN 1876, Munier-Chalmas briefly described a peculiar fossil from the Lower Devonian of north-western France which he named *Belemnocrinus cottaldi.* He believed that it was a crinoid, composed of five longitudinal pieces. Finding his generic name to be preoccupied, he proposed the name *Belocrinus* for it in 1881. The description was repeated by Oehlert (1882) and specimens were illustrated for the first time; in his plate legend (p. 363) he described the calyx as being composed of three pieces. Etheridge and Carpenter (1883) were the first workers to attribute this fossil to the Blastoidea. They called attention to Oehlert's figures and stated that they appeared to represent the elongated basal cup of a *Troosticrinus* or *Pentremitidea* (p. 245). Munier-Chalmas furnished them with a specimen which they described and illustrated in 1886; they diagnosed the material as the large basal plates of a *Metablastus.* No additional material other than the basals was known until Phillipot (1957) described a complete specimen which was in the H. de Keravel collection at the Université de Rennes. His description furnished the first detailed information about the radials, deltoids, and ambulacra. Unfortunately, the summit was obscured by matrix. On the basis of the available evidence, he continued Etheridge and Carpenter's assignment of the species to *Metablastus.*

Recent developments in preparatory techniques have made it possible to expose hitherto obscured structures. A. Phillipot and M. Y. Milon kindly allowed the writer to further develop the specimen described by Phillipot with an air abrasive machine. By this means, it has been possible to determine that it has four spiracles and an anispiracle, thus separating it from *Metablastus*, which has paired spiracles. It appears to represent a valid genus, for which the name *Belocrinus* has priority. The writer studied the basal plate in the British Museum (Natural History) which was figured by Etheridge and Carpenter (E166). It is an isolated basal plate of the same type as is illustrated in Plate 39, fig. 7, and as are found in the complete specimen. These are all from Bois-Roux in France and belong to the same species. No type specimen was ever designated for this species; the complete specimen described and figured herein is designated the hypotype for nomenclatural purposes. It is described below and the ontogenetic development of the principal plates determined.

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SYSTEMATIC DESCRIPTION

Class BLASTOIDEA
Order SPIRACULATA
Genus BELOCRINUS Munier-Chalmas 1881

Type species. Belemnocrinus cottaldi Munier-Chalmas.

1876 *Belemnocrinus* Munier-Chalmas, p. 105 (junior synonym of White 1862).
1881 *Belocrinus* Munier-Chalmas, p. 503.
1938 *Belocrinus* Munier-Chalmas; Bassler, p. 52.
1943 *Belocrinus* Munier-Chalmas; Bassler and Moodey, p. 212.

Generic diagnosis. Spiraculate blastoids with five spiracles, one of which is an anispiracle located between an epideltoid (?) and hypodeltoid (?), all deltoids quite visible in side view, a single pore occurring between adjacent side plates along radial and deltoid margins, lancet covered by side plates, calyx elongate club-shaped; large, massive basals; ten hydrospire groups; number in each unknown.

Age. Lower Devonian, north-west France.

Remarks. The generic characters of this form are similar to those of the genus *Cordyloblastus* (see Fay 1964, p. 86) but present information indicates that they are separate genera. They each have five spiracles; the number of anal deltoids in *Belocrinus* is not clear, however, and they could be the same as in *Cordyloblastus*. The deltoids of these two forms apparently differ, there being an extensive external aboral growth sector in the former (see later). There also appear to be ambulacral pores along both the radials and deltoids of *Belocrinus*; Fay (1961, p. 54) described these as being absent along the deltoids in *Cordyloblastus* (see Pl. 39, figs. 9, 10). The basals of the former are also unusually pronounced, giving the calyx an extremely elongate appearance. In view of the uncertainty as to the configuration of the anal deltoids, however, it is recommended that the generic name *Belocrinus* should not be extended beyond *B. cottaldi* until the nature of the anal deltoids can be determined.

Belocrinus cottaldi (Munier-Chalmas)

Plate 39, figs. 1–8, 11

1876 *Belemnocrinus cottaldi* Munier-Chalmas, p. 105.
1877 *Belemnocrinus cottaldi* Munier-Chalmas; Delage, p. 81 (*non vide*).
1881 *Belocrinus cottaldi* (Munier-Chalmas); Munier-Chalmas, p. 503.
1882 *Belocrinus cottaldi*, (Munier-Chalmas); Oehlert, p. 362, pl. 9, figs. 3*a–e*.
1883 *Troosticrinus cottaldi*? (Munier-Chalmas); Etheridge and Carpenter, p. 245.
1883 *Pentremitidea cottaldi*? (Munier-Chalmas); Etheridge and Carpenter, p. 245.
1886 *Metablastus cottaldi* (Munier-Chalmas); Etheridge and Carpenter, pp. 201–3, pl. 5, fig. 22.
1899 *Metablastus cottaldi* (Munier-Chalmas); Bather, pp. 18, 19.

1938 *Belocrinus cottaldi* (Munier-Chalmas); Bassler, p. 52.
1943 *Belocrinus cottaldi* (Munier-Chalmas); Bassler and Moodey, p. 212.
1957 *Metablastus cottaldi* (Munier-Chalmas); Phillipot, pp. 64–68, text-figs. 1–5.

Description. Calyx elongate club-shaped in side view, pentagonal in oral view. Length 44·0 mm.; width 14·5 mm. Pelvis extremely long for a blastoid, massive, conical, flaring out gradually beneath ambulacra. Vault parabolic. Vault 13·7 mm., pelvis 30·3 mm.; pelvic angle 30°. Greatest width at ambulacral tips; cross-section pentagonal with slightly concave interambulacral areas.

Basalia three, azygous basal in AB interambulacral area (for terminology see Fay 1961), extremely massive, narrow, elongate. Azygous basal quadrate, slightly asymmetric; lower edges very narrow V shape, distal edges broader V; length 24·2 mm., width 5·7 mm. Point of origin located very near proximal tip. Growth has occurred on both distal and lateral edges. Plate has grown 20·3 mm. distally, 2·2 mm. laterally. When BR (distal) growth axis of azygous basal (see Pl. 39, fig. 8) reached 5·0 mm. from origin, interbasal (BB) 0·8 mm.; at 11·2 mm., BB 1·4 mm. If BR+BB = 100% total growth at a given increment, then BR at 5·0 = 86% total growth, at 11·2 = 88%, at 20·3 = 90%; thus BR accelerating relative to BB during ontogeny. Well-developed interbasal growth axis; sharp, elevated sides to azygous basal which become reduced distally. Upper surface very slightly convex. Fine growth-lines parallel to plate edges; 9 per mm. on BR axis.

Larger basals hexagonal; distal edges double V shape; lateral edges very narrow V shape. Sides sharply elevated due to interbasal growth axis. Upper surface very slightly convex. Length (to centre) 22·0 mm.; to one of points 24·3 mm.; width 9·3 mm.; distal (BR) growth axis 21·4 mm., growth front 5·1 mm. Fine growth-lines parallel sutures.

Three basalia together have a trigonal rounded cross section, slightly concave along sutures (Pl. 39, fig. 2). They taper abruptly proximally near base to form a small round facet for attachment of column (now chipped); attachment area 1·0 mm. in diameter; no crenellar facets preserved. Each large basal has a crack extending proximally from

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EXPLANATION OF PLATE 39

Figs. 1, 2. Oral and basal views of only complete specimen of *Belocrinus cottaldi* Munier-Chalmas; anispiracle at 6 o'clock. Figs. 3–6, 8, and 11 of same specimen. ×2.

Fig. 3. Inclined oral view of *B. cottaldi* at BC interambulacral area, showing reflected radiodeltoid suture and internal septum dividing spiracles. ×8.

Fig. 4. Lateral A ambulacral view of *B. cottaldi.* ×2.

Fig. 5. Enlarged oral view of *B. cottaldi* showing the four spiracles and the anispiracle (latter at 6 o'clock). Peristome in centre. ×8.

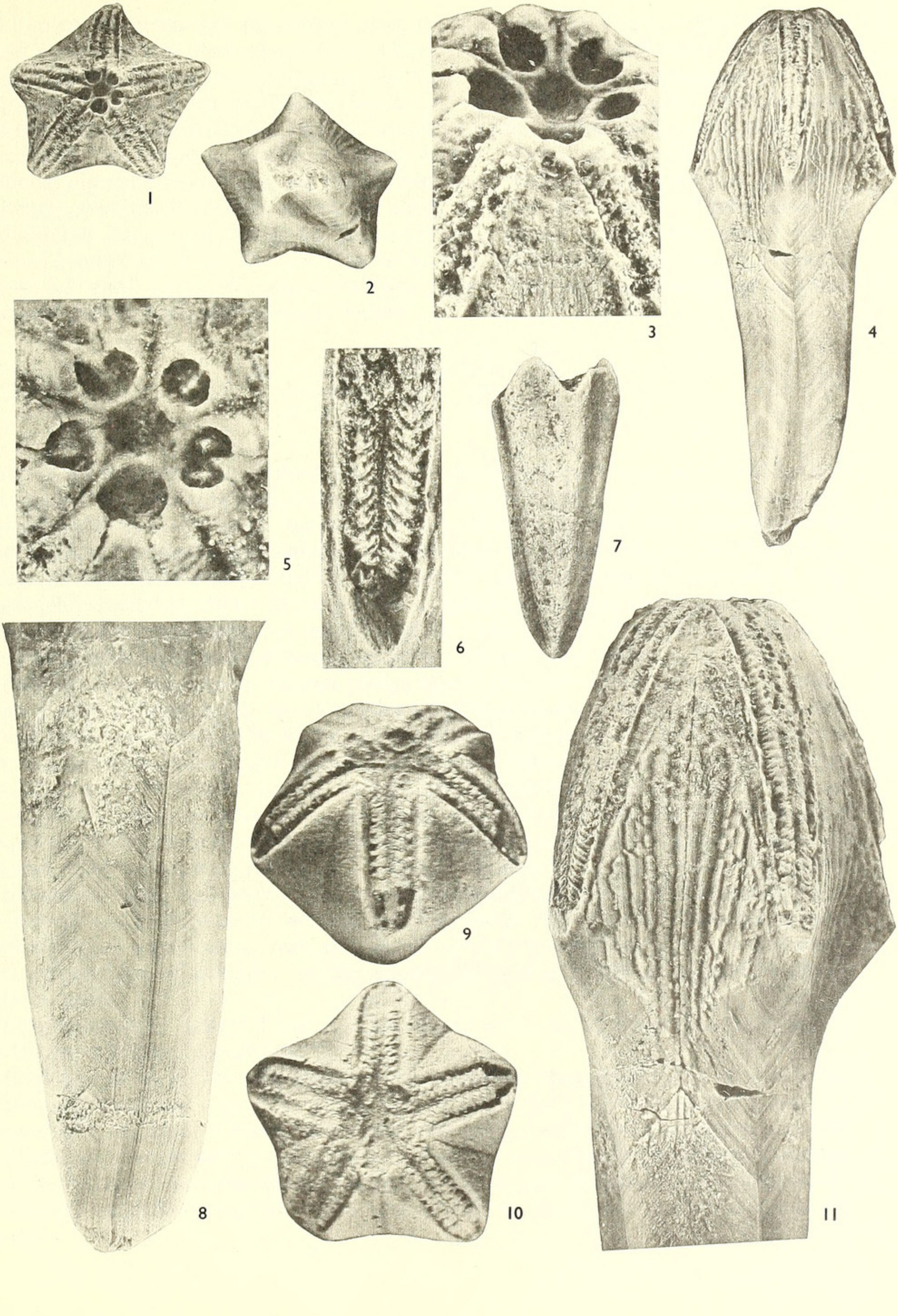
Fig. 6. Aboral end of B ambulacrum, showing brachiolar facets, pore furrows, side and main food grooves, and cover plate lobes and furrows. ×8.

Fig. 7. Isolated basal plate of *B. cottaldi*, UMMP 51144. ×2.

Fig. 8. Enlarged view of basal plates of *B. cottaldi*, showing growth lines of interbasal (BB—vertical) and basal-radial (BR—inclined) sectors. Origins at lower corners of figure. ×4.

Figs. 9, 10. Inclined B ambulacral and oral views of *Cordyloblastus eifelensis* (Roemer), USNM S5086, showing four spiracles and anispiracle (at 6 o'clock in fig. 10). Note presence of pores only along radials and presence of small deltoid body aboral to spiracles. ×8.

Fig. 11. AB interambulacral view of *B. cottaldi*, showing growth-lines of radiodeltoid (RD—upper inclined), inter-radial (RR—vertical), and radial-basal (RB—lower inclined) sectors of radials. ×4.



MACURDA, Devonian blastoid *Belocrinus*

the top centre. Each dies out before reaching origin of plate; growth-lines appear to cross without interruption. Apparently not a primary suture; significance unknown.

Radials five, narrow, elongate (aboral portion V shaped; lateral sides almost parallel), with deep narrow V for ambulacra (see Pl. 39, fig. 4). Height 3·1 mm.; width at base 5·3 mm., at ambulacral tip 6·5 mm., at deltoids 4·9 mm. Radial grew outwards in three directions from origin at aboral tip of ambulacrum (Pl. 39, fig. 11); 12·3 mm. towards radiodeltoid suture (RD axis), RD front (area along which calcite added) = 1·5 mm.; 5·3 mm. towards interradial suture (RR axis), RR front 17·1 mm.; 8·9 mm. towards radial-basal suture (RB axis), RB front 5·0 mm. Earlier ontogenetic stages: when RR = 3·7 mm., RD = 8·2 mm. and RB = 5·1 mm. respectively; when RR = 2·0 mm., RD = 3·5 mm., RB = 2·7 mm. If RD+RR+RB = 100% of total growth at a given instance then following percentages found:

	RD	RR	RB
RR = 2·0 mm.	43%	24%	33%
= 3·7 mm.	48%	22%	30%
= 5·3 mm.	46%	20%	34%

Only RR shows a continuous trend, apparently slowing down; rate of growth of RD and RB appears to increase. Fine growth-lines parallel interradial and radial-basal sutures; those parallel to radiodeltoid not as evident. Interradial growth area ornamented by low, slightly irregular ridges parallel to interradial suture (Pl. 39, fig. 11). Calcite of plates an endoskeleton, secreted by mesoderm. Layer of tissue between radial and basal plates secreted calcite on both edges simultaneously; rate of secretion by tissue between radials and basals 2·3 times faster on basal BR axis than on radial RB axis. Rate of growth of BR axis 3·8 times that of RR, 1·7 times that of RD.

Deltoids four, surround peristome (four regular plus anal deltoids). Length 3·8 mm. Adoral edge 0·7 mm. wide, forms border of peristome. Large single spiracle divides adoral portion from body (Pl. 39, fig. 5). Spiracle ovoid, diameter 1·1 mm. Septum arises 0·5 mm. below adoral edge of spiracle, divides it internally, and connects adoral and aboral portions of deltoid. Adoral edge of spiracle formed by adoral edge of deltoid, adoral lateral edges by adjacent lancet plates, aboral lateral edges by side plates, and aboral edge by adoral edge of aboral portion of deltoid. Latter part of plate is triangular, 3·0 mm. long; greatest aboral width at radiodeltoid suture 2·5 mm.; width just aboral to spiracle 0·5 mm. Radiodeltoid suture peculiar shape (Pl. 39, fig. 3). Portion adjacent to interradial suture junction straight; half-way along radiodeltoid suture sharp bend adorally. Each leg 0·8 mm.; base of triangle 1·5 mm. Significance of shape unknown.

Ornamentation of deltoids obscure; apparently faint growth lines parallel to radiodeltoid suture.

Entire growth of deltoid 3·8 mm.; rate of growth of BR 5·3 times this, and RD 3·2, RR 1·4, RB 2·3 times respectively.

Anal spiracle an anispiracle, length 1·4 mm., width 1·3 mm. Number of anal deltoids uncertain, apparently an epi- and hypodeltoid (see below). Epideltoid forms part of edge of spiracle, width 1·0 mm. Internally, two prongs can be seen extending aborally to divide anal hydrospire areas from anus but aboral ends obscured by matrix. Junction with aboral part of anal deltoids not visible. Portion of anal deltoids aboral to anispiracle presumably a hypodeltoid. Borders of anispiracle as for spiracles, except epideltoid adoral edge, hypodeltoid aboral edge. Latter 0·9 mm. wide here (greater width than other deltoids to accommodate anus); greatest width at radiodeltoid suture 3·5 mm. Configuration of hyporadial suture as for regular radiodeltoid suture; inner leg of suture 1·2 mm., outer 0·5 mm.; length of base of triangle 1·6 mm. Length of hypodeltoid 3·7 mm. Full length of anal deltoids 4·7 mm. Ornamentation of hypodeltoid apparently as for regular deltoids.

Ambulacra five, linear, narrow, tapering gradually; slightly convex lengthwise. Length 13·7 mm., greatest width 2·2 mm. Lancet does not reach peristome except in one ambulacrum (weathering); normally begin 0·3 mm. from peristome. Lancet exposed only at most adoral end of ambulacrum. Two side plates per mm., 27 on one side of an ambulacrum. Side plates elongate, obliquely disposed to centre of ambulacrum (Pl. 39, fig. 6). Outer edge embayed by an elongate outer side plate which reaches outer edge of ambulacrum, and a pore which is formed by a notch on the adoral edge of the outer side plate and aboral edge of the side plate. Abmedial edge of pore formed by radial or deltoid. Cross-section of ambulacrum from main food groove to abmedial edge convex. Side plates slope upwards from food groove for one third of distance, then slope downwards remaining two-thirds. Abmedial edge about three times lower in cross-section than main food groove. Brachioles were attached to large, elongate, elliptical brachiolar facet, which was on the downward sloping outer edge of the side plates; axis of facet inclined adorally, upper edge being closer to oral area. Brachiolar facet located on side and outer side plates. Brachiolar food groove descended to ambulacrum at high point on cross-section of side plate, becoming a short side food groove which joins the main food groove. Latter ascended adorally. Cover plate lobes and furrows can be seen along main food groove; suggestion of presence along side food grooves as well. A long, narrow, adorally directed arcuate pore furrow originates near main food groove (but separate from it) admedially to crest of side plate, descends to the pore via a depression between adjacent high points where the brachiolar food groove meets the side food groove (Pl. 39, fig. 6). After passing through the depression it rests on the suture between the side plate and outer side plate. Judging from the brachiolar facet, brachioles were relatively large and elongate in cross-section but no trace now preserved.

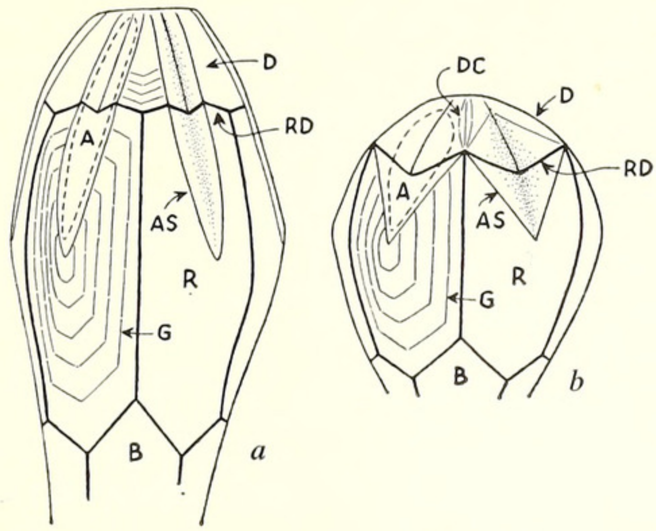
Spiracles four plus an anispiracle; apparently ten hydrospire groups, but number in each unknown.

Peristome pentagonal; width 1·5 mm.

Remarks. The above description is based on the only known complete specimen which is in the collections of the Institut de Géologie, Université de Rennes, Rennes (Ille-et-Vilaine), France. The only other known material are basal plates.

The growth lines preserved on the plates of blastoids render them ideally suited for ontogenetic study. Ontogenetic data are presented above for the principal plates but the data are biased as there is no reflection of specific variation. However, ontogenetic studies in the Mississippian blastoid *Orophocrinus* (Macurda 1966) appear to indicate that ontogenetic curves derived from an individual or a series of individuals generally reflect the ontogenetic development of the species under study. The growth of the principal plates of blastoids proceeds by small increments which are added to the lateral edges of the plate. If there are simultaneous additions on all plates, the number of growth lines along various growth axes should correspond with one another. This was analysed in this specimen but the results were inconclusive.

The size of the basal plates relative to the other plates is very unusual. Normally these are quite small, being confined to a relatively small area at the base of the calyx. It is also unusual for a measurable interbasal axis to be developed in blastoids.



TEXT-FIG. 1. Schematic diagrams of two blastoids showing differences in growth patterns in radials and deltoids in such genera as *Belocrinus* and *Orophocrinus* (fig. *a*) and *Phaenoblastus* and *Phaenoschisma* (fig. *b*). Ambulacral sinus (those parts of radials and deltoids which lie beneath ambulacra or slope steeply in toward them) indicated by AS. Ambulacra (A) proper have been removed; position indicated by dashed lines. Fig. *a* shows the configuration of growth-lines (G) in genera in which there is growth along the radiodeltoid suture external to the ambulacral sinus (RD). Note reflexed growth-lines by ambulacral sinus and presence on aboral portion of deltoid (D). Fig. *b* illustrates the case in which there is no growth external to the ambulacral sinus. Note lack of reflexed growth-lines by sinus and absence on aboral portion of deltoid, which is now a deltoid crest (DC). Basals indicated by B.

Belocrinus appears to be very similar to *Cordyloblastus*. In the latter genus, the deltoid is not exposed in side view (but there is a small edge of the deltoid body exposed aboral to the spiracle), while the deltoids of *Belocrinus cottaldi* are prominently developed in side view. The exposure or non-exposure of the deltoid is controlled by the developmental pattern of the plate; this is a reflection of the genetic make-up of the organism. In blastoid genera such as *Phaenoschisma* and *Phaenoblastus* (text-fig. 1), the aboral portion of the deltoid never grows outside the ambulacral sinus. Thus there are never any growth lines of the radiodeltoid front of the radial exposed outside the ambulacral sinus, growth occurring entirely within it. The growth-lines of the interradial front extend up to the sinus and are never reflected as they are in genera such as *Orophocrinus* (text-fig. 1), where the deltoid grows external to the ambulacral sinus. The growth-lines in the radiodeltoid sectors of the radials in the AB interambulacral area of *Belocrinus cottaldi* (Pl. 39, fig. 11) appear to indicate that the deltoid has grown outside the ambulacral sinus throughout most, if not all, of its ontogeny, resulting in its exposure in side view. The growth-lines in the radiodeltoid sectors are not as evident as those of the