ABNORMAL GROWTHS IN SOME DEVONIAN GONIATITES

by MICHAEL R. HOUSE

ABSTRACT. Specimens of *Sobolewia* from the Givetian of Cornwall and Algeria are described which show a regular pitting on the internal moulds. The same phenomenon is noted on an Algerian Eifelian goniatite and also on German specimens of *Sellanarcestes* from the Emsian and Eifelian and on an Eifelian *Anarcestes*. The pits, which are commonly arranged in sub-radial rows, are interpreted as formed in life as mound-like growths on the inside of the anterior part of the body chamber shell, but not along the apertural margin. Several hypotheses on their origin are discussed.

THE curious pitting seen on the internal moulds of some Devonian goniatites which is here described was first observed on specimens of *Sobolewia* from the locality described by Fox (1894, p. 637) at Pentonwarra Point, Trevone, north Cornwall. The fauna here was recently shown to belong to the Terebratum Zone of the Middle Devonian Maenioceras Stufe and not to the Upper Devonian as had hitherto been supposed (House 1956). The goniatite genera now known from this locality include *Tornoceras*, *Aulatornoceras*, *Protornoceras*, *Maenioceras*, *Sobolewia*, *Agoniatites*, *Wedekindella*, and *Werneroceras*, but only certain specimens of *Sobolewia* show the pitting.

During April 1957 a period was spent in Paris examining the superb collections of Devonian ammonoids from North Africa at the Sorbonne. Discussion with Madame Germaine Petter of the Centre de Recherches Sahariennes revealed that many Saouran specimens of *Sobolewia* show the pitting as does one Eifelian specimen. In August 1958, whilst studying the ammonoid collections in the Geologisch-Paläontologisches Institut at Göttingen, one Emsian goniatite was noted showing pits. Later, at the Geol.-Pal. Institut at Marburg, Dr. O. H. Walliser was able to show the writer several Middle Devonian specimens which also showed pitting.

Special thanks are due to Madame Petter for discussion in Paris and for reading and commenting on the typescript and to Professor Pierre Pruvost for providing facilities for study at the Sorbonne. Dr. Herman Schmidt and Dr. Otto H. Walliser are also to be thanked for discussion and for making specimens available for study. In an unsuccessful attempt to discover whether such pits occurred on the moulds of ammonoids of other periods the matter was discussed, in person or by correspondence, with most leading specialists. Acknowledgement is due especially to Mr. W. S. Bisat and to the late Dr. W. J. Arkell. Also appreciated are the comments of Dr. Otto Haas, Professor F. Hodson, and Dr. G. A. L. Johnson. The Durham Colleges in the University of Durham have given grants to facilitate travel in Europe in the course of monographic work on the English Devonian ammonoids. Mr. C. Chaplin of the Durham Colleges, Dr. Walliser of Marburg, and Mr. Jack Scott of the U.S. National Museum in Washington have given help in the preparation of the accompanying photographs.

DESCRIPTION

Cornish specimens. The specimens of *Sobolewia* from Trevone are preserved as internal moulds of iron pyrites with occasional pyritic casts of the original shell. Pitting has been

[Palaeontology, Vol. 3, Part 2, 1960, pp. 129–136, pl. 24.]

seen on specimens between 8 mm. and 21 mm. diameter and it occurs on septate portions of the moulds and on at least the posterior portions of the body chamber. Not all specimens of *Sobolewia* show the pitting and some show only occasional development of pits.

The pits range between 0·3 mm. and 0·9 mm. in diameter and their sides slope convexly inward to form a sub-conical depression which may reach 0·5 mm. in depth. Where observed the pit bottom is rounded. The outer margin of the pits grade evenly

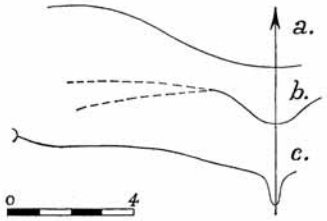


FIG. 1

FIG. 2

TEXT-FIG. 1. *Sobolewia* aff. *nuciformis* (Whidborne). *a*, Course of growth lines. *b*, Approximate course of pit rows (variable over the umbilico-lateral areas). *c*, Suture. Scale in millimetres. All based on SM. H7422 collected by the author from the Terebratum Zone, Givetian, at Pentonwarra Point, Trevone, North Cornwall.

TEXT-FIG. 2. *Sellanarcestes* cf. *wenkenbachi* (Kayser). Diagram showing one suture and the distribution of pitting on a specimen in the Göttingen Geologisch-Paläontologisches Institut from the Emsian Mandelner Schichten at Mandeln, Germany. The dotted line shows a hypothetical arrangement of the pits into rows. Each scale division represents approximately 5 millimetres.

into the internal mould of the shell. The relation of the pits to the shell has been elucidated in one instance by the dissection of an undisturbed pyritic cast of the shell from above a pit. The outer surface of the shell showed no evidence of disturbance. Pits formed on the moulds of mural areas of the septa show no difference from those found elsewhere. Occasionally two or more pits may partly coalesce.

In some specimens the pits occur rarely and it is not possible to distinguish any regular arrangement of them. In several specimens, however, the pits are seen to be arranged in rows which pass out from the umbilicus, cross the lateral areas either radially or with a slight forward projection, and on the ventro-lateral slopes pass back to form a shallow and narrow sinus on the venter (text-fig. 1*b*). In some specimens there are five to eight of these rows in a half whorl with about five pits between the umbilicus and the venter. There is approximately an equal development of pits on either side, but the pits are not symmetrically placed. The pit arrangement between successive rows does not show precise agreement. The distance between the rows agrees in general with the distance between the septa. The rows do not agree with the course of the growth lines (text-fig. 1*a*, *b*, Pl. 24, fig. 5) at the same diameter, nor do they correspond with the course of growth lines for one whorl orad of the pit rows.

North African specimens. Specimens of *Sobolewia* in the Sorbonne from the Givetian of the Redjel Imrad collected by J. Fallot show pitting on the internal moulds exactly

comparable with that described for Cornish specimens. In no specimen is there any trace of the original shell. Other genera from the same locality show no pitting.

A single specimen from the southern border of the Erg el Djemel (Ougarta) from the Eifelian 'niveau à *Pinacites jugleri*' shows the pitting in a remarkable way (Pl. 24, fig. 6). This specimen is unfortunately not generically determinable since it is crushed laterally and the sutures cannot be seen. The specimen is 20·4 mm. in diameter and at least the last whorl represents the body chamber. Pitting can be observed on the right side of the specimen, but that side is poorly preserved. The figured left side shows no orderly arrangement of pits in the apicad portion of the body chamber, but in the subsequent whorl they become almost invariably arranged into forwardly projecting slightly concave rows with some suggestion of a backward deflexion over the venter. There is a noticeable absence of pits on the umbilical shoulder: between the shoulder and the venter there are usually between eight and ten pits. Ventro-laterally the pit arrangement is disturbed and although there is some indication of a backward deflexion to form a sinus there are many pits which do not follow this regular course. Except in a few cases there is not complete agreement in the position of pits in successive rows. Whilst the pits are usually of the same size they occasionally coalesce and there are some smaller pits. The small particles seen within many of the larger pits are pyritic concretionary structures. Growth-lines are not well shown on the specimen but in the early portion of the last whorl there is evidence that they sweep very slightly back from the umbilicus to form a very shallow sinus on the outer flanks: their course over the venter cannot be discerned.

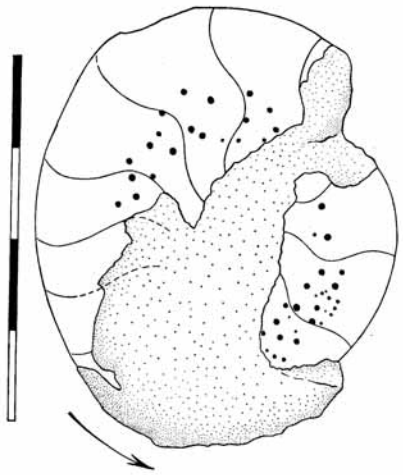
German specimens. One specimen of *Anarcestes sp.* in the Clausthal Museum (No. L 62) from the Upper Eifelian Goslaren Schiefer (Pl. 24, fig. 7) shows a pattern of pitting which is closely comparable to that seen on the Cornish and Algerian specimens. Again the pits are apparently arranged into sub-radial rows with some evidence of a ventral sinus. The separation between the rows in this case does not agree with the septal separation at the same diameter, but it may agree with the septal separation at earlier diameters which cannot be seen. The pit arrangement is not laterally symmetrical.

There is a specimen in the Geol.-Pal. Museum at Berlin (No. c104) from the Eifelian Ballersbacher Kalk at Blauer Bruch near Wildungen which Dr. O. H. Walliser has determined as *Sellanarcestes* cf. *wenkenbachi* (Kayser) (Pl. 24, figs. 8, 9) which shows pitting with a different arrangement to that so far described. Although there is a radial pattern there are fewer pits and these appear to be spirally arranged and single prominent pits lie in a constant ventro-lateral position throughout the last whorl.

A specimen from the Upper Coblencian (Emsian) of Mandeln which Schmidt (1926, p. 293) figured and referred to '*Anarcestes wenkenbachi*' shows evidence of pitting (text-fig. 2). This specimen is in the Geol. Pal. Institut at Göttingen. In this example the pits are not frequent and are completely without symmetry in their arrangement, but they can be interpreted as arranged into a row which has a salient on the outer flanks and a concavity on the venter.

The most remarkable pitting is exhibited by a single specimen of *Anarcestes* (*A.*) *sp.* in the Clausthal Geol.-Pal. Institut from the Eifelian Wissenbacher Schiefer (text-fig. 3). In this case the pitting is restricted to a broad band low on the flanks. There is no evidence to suggest any radial arrangement of the pits at all. Further, the pits are not

of uniform size, and very small pits occur among pits of similar size to those found in the forms already described.



TEXT-FIG. 3. *Anarcestes* (*Anarcestes*) *sp.* Lateral view of a specimen in the Clausthal Museum labelled '*Anarcestes vittatus*' from the Eifelian Wissenbacher Schiefer showing pits on the internal mould. The arrow shows the direction towards the aperture. Each scale division represents 5 millimetres. Based on drawings and a photograph and checked against the original specimen by Dr. O. H. Walliser of Marburg.

INTERPRETATION

The possibility that the pits are post-fossilization features is clearly ruled out in the case of *Sobolewia* by their relation to the shell and mural portions of the septa: these show that the pits were formed during life. In the other cases it is difficult to conceive how such regular pitting could have arisen accidentally. There is therefore no comparison with the pitting which has been described, for example, on the surface of the holotype of *Perisphinctes* (? *P.*) *listeri* (de Haan) from the Jurassic Corallian Beds of Nunnington, Yorkshire, which Dr. Vernon Wilson has suggested may be due to the subsequent action of rootlets and humic acid (*in* Arkell 1950, p. 265). The Cornish specimens described here have been extracted from freshly exposed and unweathered intractable slate.

From the preceding description and observations the following inferences on the origin of the pits may be made.

1. The pits are moulds of mounds which were developed during life on the inner surface of the shell.

2. The mounds were probably solid since mural portions of the septa reflect their shape and iron pyrites subsequently formed around them.

3. The mounds were formed in the body chamber and near to the aperture, but were not formed along the shell-growth margin. Where there is a regular arrangement of the pits into rows the course of the rows does not agree with that of the growth lines.

4. At least in specimens other than the *Anarcestes* (*A.*) *sp.* from the Wissenbacher Schiefer, the arrangement of the pits into rows which agree approximately in their separation with the septal distance suggests that the mounds were formed periodically after each forward movement of the visceral mass associated with septal formation.

The several possible causes of the mounds will, for convenience, be discussed under three heads.

(1) *Functional mounds.* There are at least three known ammonoid structures with which the mounds may have been functionally associated: *a*, small muscle attachment; *b*, incipient false constrictions; *c*, modified conellae.

The evidence appears to tell against the mounds representing the site of small muscles. Were this the case it might be expected that the pit arrangement would be laterally symmetrical and that there would be nearly precise agreement between the position of the pits in successive rows. Further, it might be expected that all specimens of affected genera preserved as internal moulds would show the pitting, but this is not the case. However, a pitting on the interior of the posterior parts of the nautiloid body chamber has been illustrated in *Phragmoceras* by Foerste (1929) and Sweet (1959) has illustrated similar structures in the genera *Parryoceras*, *Beloitoceras*, *Oncoceras*, and *Diestoceras*. But in these cases the pitting is regular and restricted to a band immediately orad of the last septum. The pit rows in the Devonian goniatites are not comparable with the course of the annulus for Crick (1898) has shown that when this structure is shown on ammonoids it is still in the posterior part of the body chamber as in the living *Nautilus*.

The pits show little analogy with constrictions except that the course of the pit rows shows agreement with false constrictions in failing to accord with the growth lines, in being structures on the inside of the body chamber, and in their formation being near the aperture. The frequency of constrictions rarely, if ever, agrees with the septal frequency. No constrictions have been recorded in the Devonian genera affected by the pitting. Pit-like depressions on the lateral areas of the internal moulds of some ammonoids with constrictions do occur, however, and they are shown on *Dunbarites rectilateralis* (Miller) (see Miller and Furnish 1940, p. 532, pl. 63, figs. 1, 4), but there are never rows of pits as shown in some Devonian goniatites.

The mounds are not directly comparable with the conellae described within the shell of certain Jurassic ammonites (Hölder 1952; 1952*a*) for although these structures are conical their apices are directed outwards, whereas the apices of the mounds in the Devonian goniatites are directed inwards. Further, the relative size of conellae is much smaller than the mounds. Also conellae are usually interpreted as formed by diagenic dissolution of the shell, whereas the Devonian structures were clearly formed in life.

(2) *Alien organic growths.* Internal discrete alien organic growths might be expected to leave trace of a distinct boundary on the internal moulds. This is not seen on the Devonian specimens and in all cases the pits are in smooth continuity with the surrounding areas. The pits on the body chamber of *Manticoceras oxy* Clarke, refigured by Miller (1938, Pl. 16), were formed by orbiculoideans growing on the internal surface of the

body chamber and these show the distinct boundary to be expected from organic growths.

Borings through the shell from the outside are common among recent Mollusca and may give rise to internal mounds. Professor F. Hodson informs the writer that borings are not uncommon on the shells of Carboniferous goniatites and they are well shown on the holotype of *Hibernicoceras posthibernicum* Hodson and Moore (1958, pl. 4, fig. 1). Structures have also been figured by Schindewolf (1934, pl. 2, fig. 7*a*, *b*) as borings in the shell of a specimen of *Cymaclymenia striata* (Münster) from the Upper Devonian of Hönnetal, Germany. The pits in *Sobolewia* can hardly be due to borings since the shell above the pits is undisturbed. Whilst no trace of the shell is visible in the affected North African Eifelian specimen (SM. H 7423) the arrangement of the pits into periodic rows could only be explained as due to borings if some soft part structure extended fully one whorl beyond the aperture of the body chamber which is itself at least one whorl in length: it seems unlikely that this could be the case.

(3) *Localized shell thickenings*. The continuity between the pits and adjacent areas suggests that the mounds were tumerous concretions of actual shell material which formed after each advance of the body mass. Such tumerous growths might be due either to organic infection or inorganic irritation which led to the precipitation of actual shell material. In either case the resulting structures could be termed pathological (Moodie 1923, p. 29). Were organic infection the cause it is surprising that the pits are usually so regular for, at times, the infection might be expected to disrupt the soft parts considerably. The possibility that the mounds might be caused by the irritation of permanent cysts or similar structures within the visceral mass is considered unlikely because of the lack of agreement in the position of the pits in successive rows.

An inorganically or organically caused irritation not primarily related to the shell or the soft parts seems a more likely solution. Small particles could conceivably enter between the shell and the visceral mass and lead to structures comparable with the pearl mounds of present-day lamellibranchs. The precise origin of natural pearls has been so disputed that attempts to deduce it for Devonian goniatites are unlikely to be profitable. Magraw (1956) has recently suggested that foreign particles may explain abnormal apertural developments in *Gastrioceras*. If a similar type of interpretation is correct for *Sobolewia* then the rows of mounds must be caused by some structure in the soft parts

---

EXPLANATION OF PLATE 24

Figs. 1–5. *Sobolewia* aff. *nuciformis* (Whidborne). 1, SM. H7421 collected by the author from the Givetian Terebratum Zone at Pentonwarra Point, Trevone, north Cornwall. ×4. 2–5, SM. H7422 collected by the author from the same locality and horizon. 2, 3×4, 4×12, 5×11.

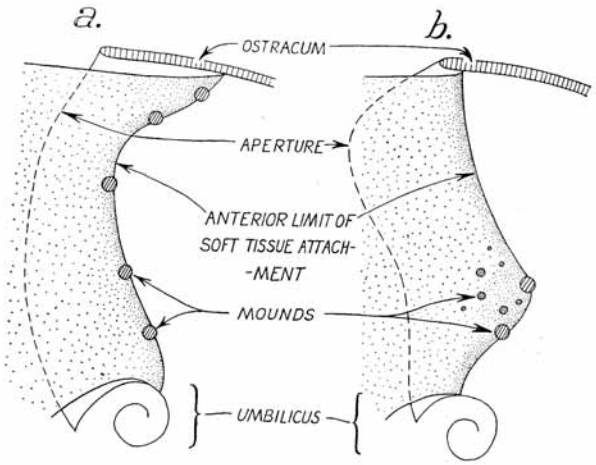
Fig. 6. Goniatite indet. SM. H7423 from the Eifelian 'niveau à *Pinacites jugleri*', Erg el Djemel (Ougarta), North Africa. ×3.

Fig. 7. *Anarcestes sp*. Clausthal Museum No. L.62 from the Upper Eifelian Goslaren Schiefer. ×4.

Figs. 8, 9. *Sellanarcestes* cf. *wenkenbachi* (Kayser). Berlin Museum No. c104 from the Middle Couvinian (Eifelian) at Blauer Bruch near Wildungen. ×2.

All the specimens are of natural internal moulds, but SM. H7422 retains a portion of the original shell preserved as a pyritic cast. The specimens were lightly coated with a sublimate of ammonium chloride before being photographed. The prefix SM. refers to the Sedgwick Museum collections where some of the figured specimens have been deposited.

which limited the backward passage of foreign particles. Perhaps this structure might be the anterior limit of soft part attachment, comparable with the pallial line of the lamellibranch. The restriction of the mounds to a band on the flanks could be explained by a lateral sinus along the 'pallial line' (text-fig. 4). This line, in other forms, might be the site of the precipitation of false constrictions. The wrinkle layer on Devonian goniatites commonly reaches near to the aperture and the striae of it do not follow the course of the growth lines. There is, unfortunately, insufficient evidence on the course of the wrinkle layer in the affected Devonian goniatites to tell whether the pit rows follow the same course.



TEXT-FIG. 4. Diagram showing a hypothetical relation between mounds and soft parts in *a*, *Sobolewia* and *b*, *Anarcestes*. Based on specimens described in the text.

CONCLUSIONS

The evidence at present available is not conclusive as to the origin of the pits seen on some Devonian goniatites, but appears to favour an hypothesis that the pitting is due to pearl-like mounds which were formed in life on the inside of the body chamber and probably caused by the irritation of foreign particles which entered between the body and the shell: the particles were apparently restricted in their passage backward by some unknown structure in the soft parts, possibly the anterior limit of soft part attachment. Periodic forward movement of the visceral mass associated with septal formation during growth then explains the arrangement of the pits into periodic rows the separation of which generally agrees with the septal distance. A sinus formed along the limit of soft part attachment could explain the restriction of the pits into a lateral band in some cases.

The genera in which this phenomenon has been observed are all members of the

Devonian family Anarcestidae with the possible exception of *Sobolewia* which is commonly placed in the Prolobitidae. Affected specimens occur in the Emsian, Eifelian, and Givetian. Occurrences are known in North Africa, Germany, and England.

REFERENCES

ARKELL, W. J. 1950. Two early-named valid species of English Upper Jurassic ammonites. *Geol. Mag.* **87,** 265–6, pl. 13.

CRICK, G. C. 1898. On the muscular attachment of the animal to its shell in some fossil Cephalopoda (Ammonoidea). *Trans. Linn. Soc. London. (Zool.),* **7,** 71–113, pl. 17–20.

FOERSTE, A. F. 1929. Three studies of Cephalopoda. *Denison Univ. Bull. Journ. Sci. Lab.* **24,** 265–381.

FOX, H. 1894. On some fossils from the coast sections in the parishes of Padstow and St. Merryn. *Trans. R. geol. Soc. Cornwall,* **11,** 634–44.

HODSON, F. and MOORE, E. W. J. 1958. Goniatites from the Upper Viséan shales of County Leitrim, Eire. *Liv. and Manch. Geol. J.* **2,** 86–105, pl. 3–10.

HÖLDER, H. 1952. Über Gehäusebau, insbesondere Hohlkiel, jurassischer Ammoniten. *Palaeontographica,* **102**A, 18–48, pl. 3–7.

—— 1952*a*. Der hohlkiel der Ammoniten und seine Entdeckung durch F. A. Quenstedt. *Jahreshefte Ver. vaterl. Naturkunde Würtemberg,* 1952, 37–50.

HOUSE, M. R. 1956. Devonian goniatites from North Cornwall. *Geol. Mag.* **93,** 257–62.

MAGRAW, D. 1956. Abnormalities of growth in specimens of *Gastrioceras* from the Lower Coal Measures. *Liv. and Manch. Geol. J.* **1,** 394–9, pl. 33.

MILLER, A. K. 1938. Devonian ammonoids of America. *Spec. Pap. geol. Soc. Amer.* **14,** i–xiii, 1–202, pl. 1–39.

MILLER, A. K., and FURNISH, W. M. 1940. Studies in Carboniferous ammonoids: Parts 1–7. *J. Paleont.* **14,** 356–77, 521–43, pl. 45–49, 62–65.

MOODIE, R. L. 1923. *Palaeopathology. An introduction to the study of ancient evidences of disease.* Univ. of Illinois Press, Urbana.

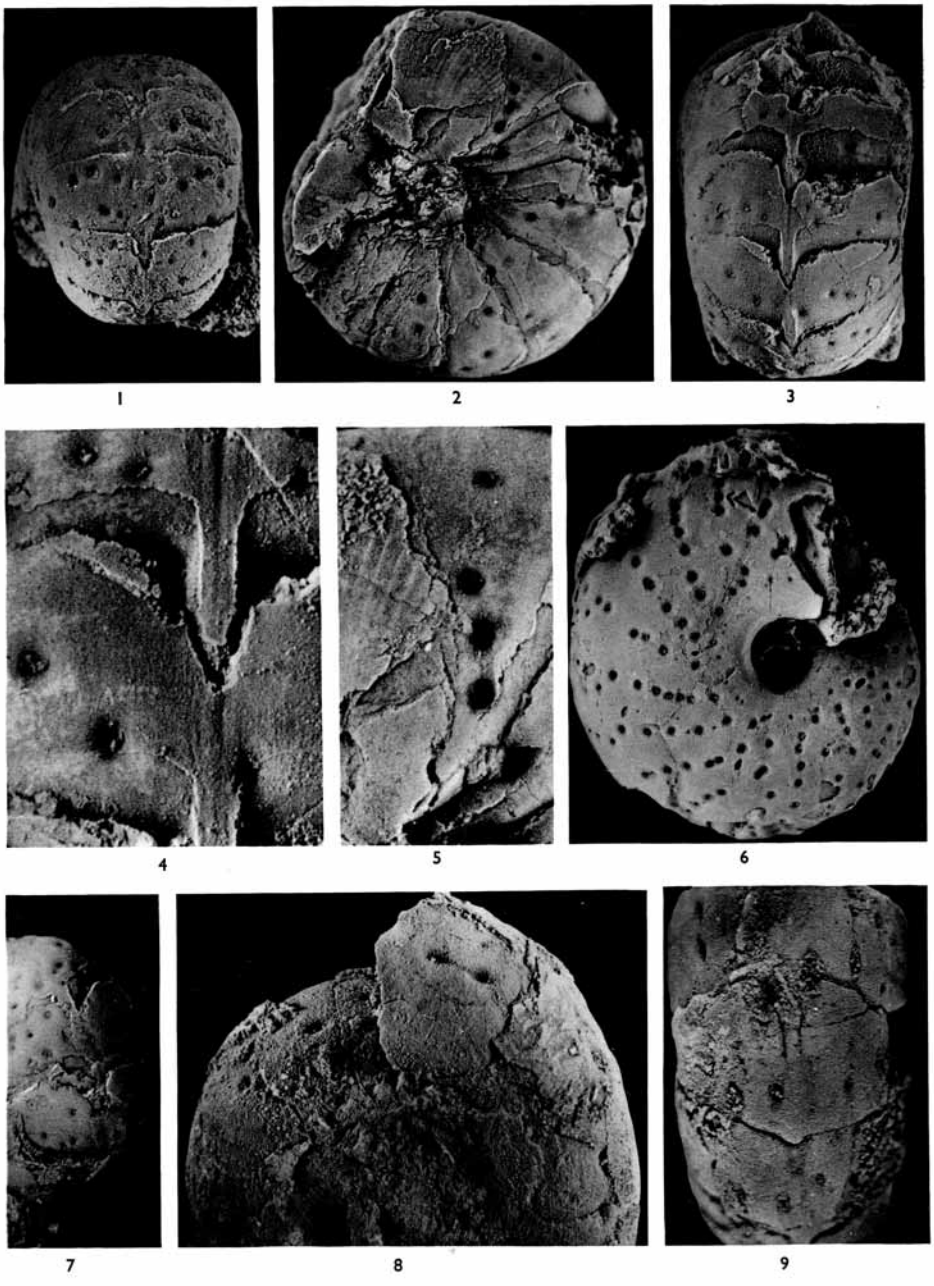
SCHINDEWOLF, O. H. 1934. Über Epöken auf Cephalopoden-Gehäusen. *Pal. Zeit.* **16,** 15–31, pl. 2.

SCHMIDT, H. 1926. Beobachtungen über mitteldevonische Zonen-Goniatiten. *Senckenbergiana,* **8,** 291–5.

SWEET, W. C. 1959. Muscle-attachment impressions in some Paleozoic nautiloid cephalopods. *J. Paleont.* **33,** 293–304.

MICHAEL R. HOUSE
Department of Geology,
The Durham Colleges,
Durham City

Manuscript received 30 April 1959



HOUSE, Abnormal growths in Devonian goniatites