NEW ORDOVICIAN BOTHRIOCIDARIDAE FROM GIRVAN AND A REINTERPRETATION OF *BOTHRIOCIDARIS* EICHWALD

by C. R. C. PAUL

ABSTRACT. Five specimens of bothriocidarid sea urchins are described; one is the seventh known example of *B. globulus* Eichwald. The other four represent *Neobothriocidaris* gen. nov. characterized by having perforate plates arranged in rows and one pore of each pore-pair shared by two plates. *N. peculiaris* and *N. minor* spp. nov. are separated on the number and arrangement of spine mamela.

The holotype of *N. peculiaris* has parts of two radial water vessels preserved within the single columns of imperforate plates which have been regarded as inter-radial in *Bothriocidaris*. On the assumption that *Neobothriocidaris* and *Bothriocidaris* are closely related genetically, the single columns of imperforate plates in the latter are reinterpreted as being radial. The five apical plates become genitals with one modified as a madreporite. Growth of the corona is more readily explained and the entire columns of imperforate plates may represent oculars. Details of the peristome and jaw apparatus do not however fit the new interpretation very well.

A SINGLE specimen of a sea urchin related to but distinct from the earliest known genus, *Bothriocidaris*, was located in the Gray collection of echinoderms from Girvan now in the British Museum (Natural History). Subsequently, additional specimens were located among material collected by Mr. R. P. Tripp and sent to Professor G. Regnéll of Lund; among the Hunterian Museum collections and, after the manuscript was completed, among material loaned by Dr. A. Lamont to the late W. K. Spencer. These are referred to as the BMNH, the Lund, the Hunterian, and the Lamont specimens for convenience.

Quite independently of this Professor Regnéll had recognized and prepared a manuscript on a single example of *Bothriocidaris* ss. among the Tripp collection. With characteristic generosity he made the specimen and photographs available to the present author so that a complete record might be made. The author is also indebted to Dr. R. P. S. Jefferies and Mr. H. G. Owen, British Museum (Natural History) (BMNH), Dr. W. D. I. Rolfe, Hunterian Museum (HM), and Mr. R. P. Tripp for the loan of material. Dr. V. Jaanusson kindly loaned specimens of *Bothriocidaris pahleni*. Special thanks are due to Dr. Jefferies for a translation of Männil's paper on *Bothriocidaris*. Useful discussion and criticism have been received from Professor J. W. Durham, Dr. G. M. Philip, Dr. P. M. Kier, Dr. R. P. S. Jefferies, and Mr. A. G. Brighton. This work was completed during the tenure of a Science Research Council Research Scholarship which is gratefully acknowledged. Finally thanks are due to Professor O. M. B. Bulman for research facilities in the Sedgwick Museum, Cambridge.

DESCRIPTION OF SPECIMENS

A. The Tripp Specimen

Bothriocidaris globulus Eichwald

Plate 85, figs. 1–4

[Palaeontology, Vol. 10, Part 4, 1967, pp. 525–41, pls. 84–85.]

This specimen (Tripp Coll. 2464 a–b) consists of internal and external counterparts showing fifteen plates in three columns—two of perforate plates and a central column of imperforate plates.

External counterpart. The external counterpart (2464 a. Pl. 85, figs. 1–3) shows moulds of five imperforate plates in the central column and four and six perforate plates in the adjacent columns. The perforate plates are in definite columns and each pore-pair is entirely within a single plate. Part of the adoral half of the corona is preserved and the lowest imperforate plate is terminal in the column, the two adjacent perforate plates meeting below it. Unfortunately the 'primordial ambulacral' plates of these columns are missing.

The lowest imperforate plate is irregularly hexagonal, angular below, and 1–75 mm. wide by 2·0 mm. high. The second plate is irregularly heptagonal. Both bear a single subcentral, perforate spine mamelon about 0·3 mm. in diameter. The third plate is 2·75 × 2·05 mm., regularly hexagonal, and angular above. There are two small plates side by side above it (Pl. 85, fig. 1), and the column reaches a width of 3·65 mm. at this point. There are three perforate mamela 0·3 mm. in diameter on the third plate and one on the right-hand plate above. The left is obscured by some remaining coronal calcite.

The surface of the plates was strongly convex (concave in mould) and covered with fine asperities. The matrix has penetrated the original organic spaces in the test. The stereom network was of the usual three-dimensional arrangement of calcite rods approximately perpendicular and parallel to the plate surfaces.

In the right column there are six perforate plates all much broader than tall. The lowest is 2·0 × 0·85 mm. and the largest measurable (the fourth) 3·15 × 1·6 mm. Each has a pore-pair and peripodium medially near the lower margin of the plate. The peripodia are circular, 0·8 mm. in diameter internally and with a conspicuous rim, weaker below. The peripodium floor is weakly convex (concave in mould) with a peripheral channel connecting the two pores. A line joining the two pores of a pair meets the vertical at 28°. There are two pairs of mamela on the peripodium of each plate. Numbering the mamela clockwise from the lower left, one and two form one pair. A pair of mamela are 0·5 mm. apart, two and three are 0·6 mm., and one and four 1·0 mm., all measured centre to centre. In no plate are all four mamela perforate. When perforate they are 0·3 mm. in diameter but when imperforate only about 0·2 mm. Two plates (4th and 5th) have both perforate and imperforate mamela on their surfaces. The perforate plates are strongly convex and covered with asperities. The left column shows four plates of

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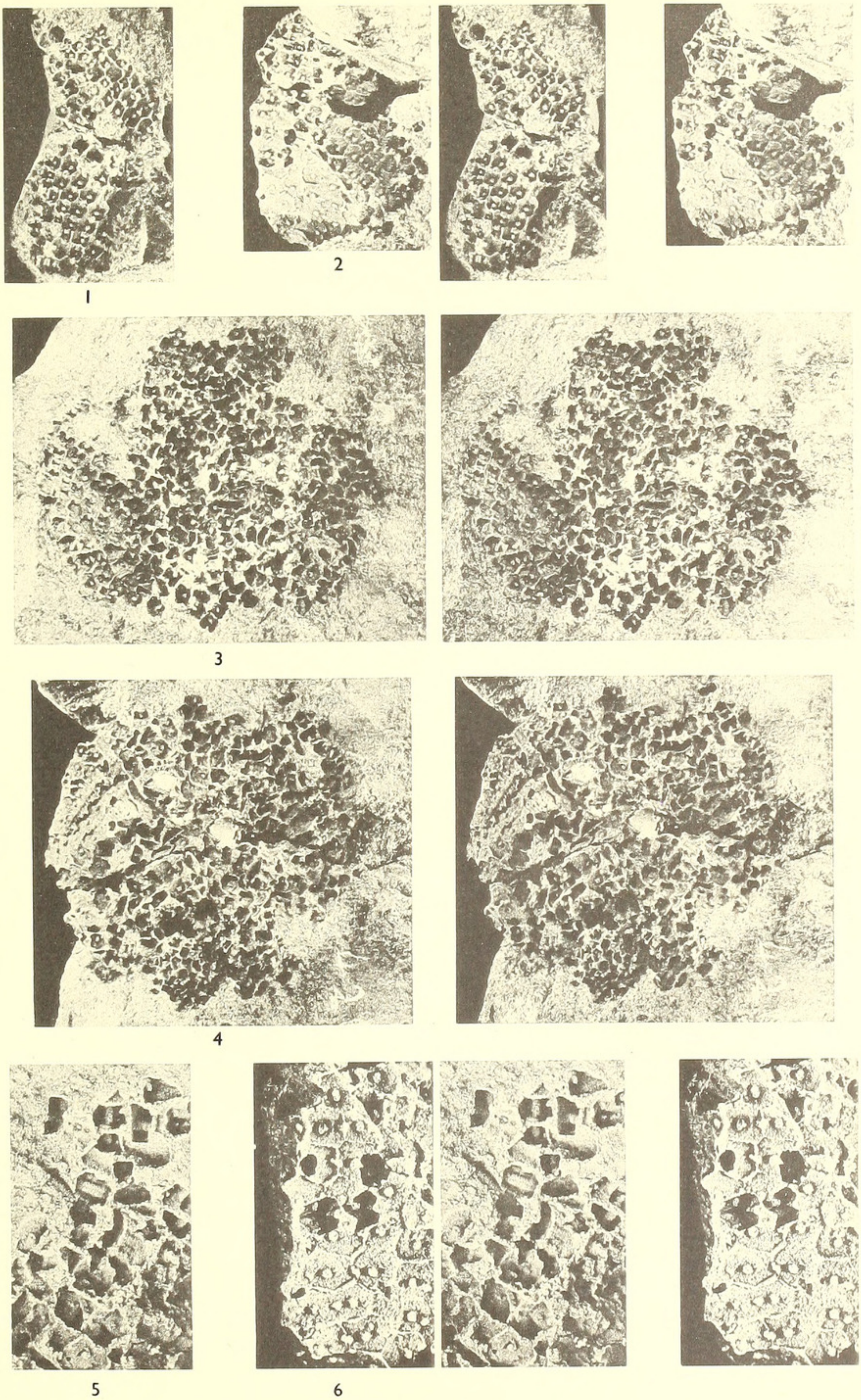
EXPLANATION OF PLATE 84

Stereo-photos of *Neobothriocidaris peculiaris* gen. et sp. nov. 1, BMNH E 42523 c. 2, BMNH E 42523 b internal counterpart of E 42523 c. 3, E 42523 a. 4, E 42523 b internal counterpart of E 42523 a. 5, Detail of several loose plates in E 42523 b showing entire casts of the central pores of the perforate plates and in one plate (top centre) the cast of the terminal portion of a lateral vessel connected to the cast of a sutural pore. 6, Detail of several articulated plates of E 42523 b and three inverted plates. The lower pair of inverted plates show casts of the terminal portions of the lateral vessels connected to the casts of the sutural pores and the lower left shows part of the cast of another lateral vessel. The upper plate shows casts of three lateral vessels (to the lower right) passing into the plate beside the cast of the sutural pore.

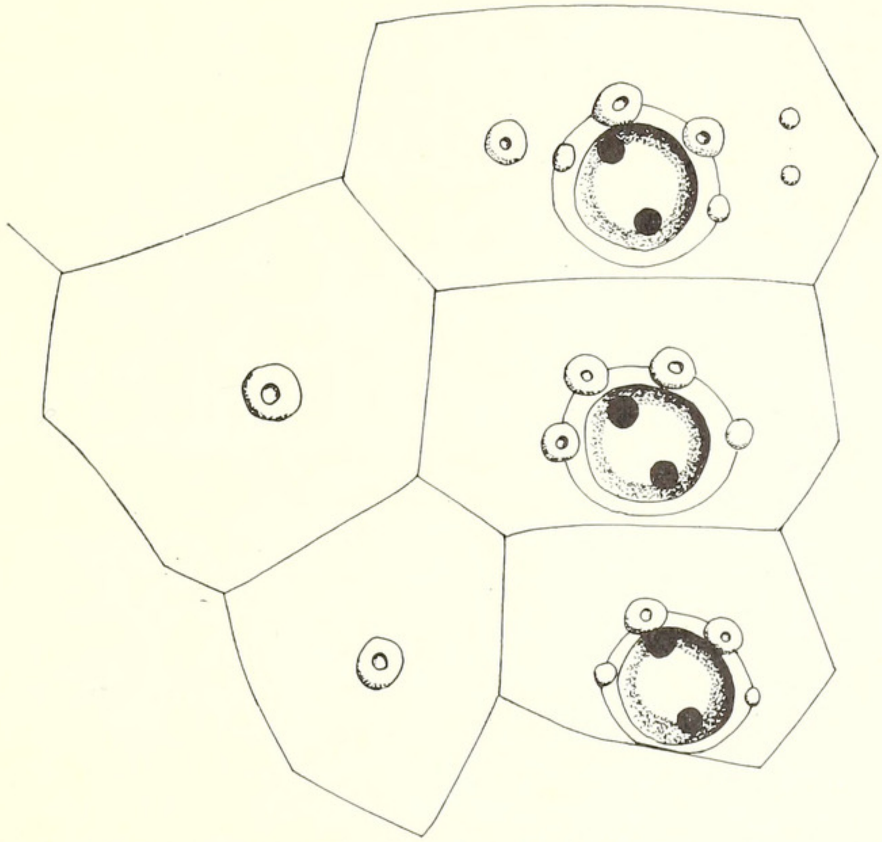
Figs. 1–4 × 2, figs. 5–6 × 5 and whitened with ammonium chloride sublimate.



PAUL, Bothriocidaridae from Girvan

which two have some calcite remaining. The stereom network was the same in both types of plates.

Internal counterpart. This (2464 b. Pl. 85, fig. 4) does not correspond exactly to the external. It shows moulds of plates 2 and 3 and the pair of small plates in the central column; none of the plates of the left column; plates 3–6 of the right column; and a seventh not present on the external mould. There are no indications of a radial water



TEXT-FIG. 1. A *camera lucida* drawing of some of the plates of *Bothriocidaris globulus* Eichwald from Girvan.

vessel within the plates or impressed on their internal surfaces. In the perforate plates the more central pore of each pair is larger (0·3 mm.) than the other (0·2 mm.) and has an internal rim. Both pores are within a single plate.

Comparison with other species of Bothriocidaris. Only *B. globulus* Eichwald has four spine mamela on each peripodium rim. The present specimen is compared with Männil's (1962) excellent account of *B. globulus.* Männil states that the ambulacral (perforate) plates reach 4·0 mm. wide by 3·0 mm. high but the lowest are 2·0 × 1·5 mm. The peripodia are 1·0 mm. in diameter internally and the line joining the pairs of pores meets the vertical at 24–28°. There are two pairs of mamela on the peripodium rim, reaching 0·5 mm. in diameter, and additional mamela on the plate surface. The mamela of a pair are separated by 0·5 mm., two and three by 1·0 mm., and one and four by 1·3 mm. Männil's figure (fig. 3*d*, p. 169) shows four perforate mamela on the peripodia which are in the same position on a plate as those of the present specimen. The plates are strongly convex and covered with asperities.

The imperforate plates reach 3 mm. wide by 2 mm. high and bear 1–4 subcentral mamela. These plates are convex and covered with asperities.

The present specimen agrees closely with Männil's description of *B. globulus*. It differs, however, in the the size of the peripodia and mamela and in not having all four mamela on the peripodium rim perforate. The similarities outweigh the differences, however, and this specimen is accepted as the seventh known example of *B. globulus*. Slight differences are to be expected in view of the widely separated localities and different stratigraphic horizon. The present specimen is from a small exposure beneath the kilns in the main quarry at Craighead, nr. Girvan (*fide* Anderson and Pringle, 1946). The Craighead Kiln Mudstones are of Uppermost Caradoc age according to Williams (1962). In Estonia, *B. globulus* occurs in the Vormsi horizon (f_{1b}) which Männil (1962) accepted as uppermost Caradoc but which Whittington and Williams (1964, p. 251) consider to be Lower Ashgill and equivalent to the Lower Drummock group of Girvan. Possibly *B. globulus* appeared earlier in Scotland than in Estonia.

B. The British Museum Specimen

These are three fragments of external mould and an internal mould of a largely disarticulated test which was probably globular and about 25 mm. in diameter (BMNH E 42523 a–d. Pl. 84, figs. 1–6, Pl. 85, figs. 9–11). A small articulated area shows rows of perforate plates and columns of imperforate plates.

E 42523 a. This counterpart shows the external mould of a small articulated area of the corona consisting of about 45 plates and measuring 15×7 mm. (Pl. 84, fig. 3, Pl. 85, fig. 10). There is also a large area of randomly orientated disarticulated plates. The imperforate plates in the articulated area are arranged in a column which apparently bends towards the bottom. (The portion of the test preserved shows neither pole. Throughout the terms 'top', 'base', etc., indicate the arbitrary orientation used for description.) The imperforate plates are hexagonal with two sides forming the top and base. The two upper sloping sides are excavated to bear part of one of a pair of pores in the adjacent perforate plates (fig. 3). The perforate plates and pore-pairs are arranged in rows at an oblique angle to the column of imperforate plates and form chevra whose axes coincide with the column of imperforate plates (fig. 2). Three relatively large plates in one row are replaced in the next, and subsequent rows, upwards by four small plates

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EXPLANATION OF PLATE 85

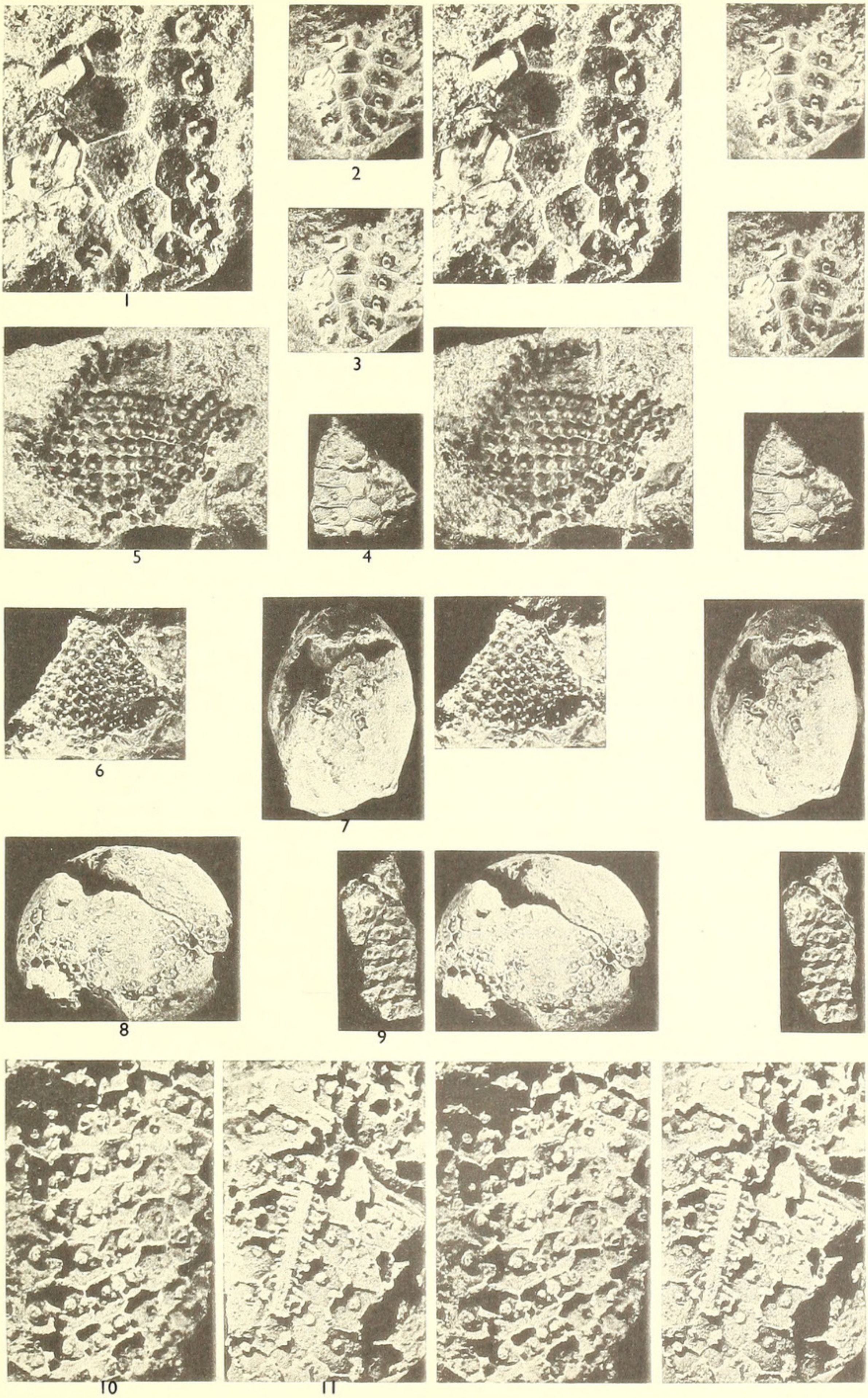
Figs. 1–4. Stereo-photos of *Bothriocidaris globulus* Eichwald from the Kiln Mudstones, Craighead, Girvan. 1, Detail of both types of coronal plates in 2464 a. 2, 2464 a. 3, A reversed pair of stereo-photos giving the illusion of reversed topography and showing the original convexity of the plates: 2464 a. 4, 2464 b internal counterpart.

Fig. 5. Stereo-photos of the holotype of *Neobothriocidaris minor* gen. et sp. nov. from the Starfish Bed, Threave Glen, Girvan.

Figs. 6–8. Stereo-photos of the paratype of *N. minor* from the Kiln Mudstones, Craighead, Girvan. 6, The external counterpart showing the arrangement of the plates. 7, 'Apical' view of the internal counterpart. 8, Lateral view of the internal counterpart.

Fig. 9–11. Stereo-photos of the holotype of *N. peculiaris*. 9, BMNH E 42523 d. 10, Detail of both types of plates in BMNH E 42523 a. 11, Detail of the internal counterpart of the portion of E 42523 a shown in Fig. 10, to show the casts of the radial and lateral vessels of the water vascular system. E 42523 b.

Figs. 2–9 ×2, figs. 1, 10–11 ×5. Figs. 4, 6–8, 10–11 whitened with ammonium chloride sublimate



PAUL, Bothriocidaridae from Girvan

of which the ones nearest the imperforate plates are smallest and apparently relatively newly formed. Spines were borne on both types of plate.

E 42523 b. The internal mould shows the exact counterpart of the area of articulated plates on E 42523 a and a triangular area, 14×13×12 mm., adjacent to it (Pl. 84, figs. 2, 4–6, Pl. 85, fig. 11). Each perforate plate was pierced subcentrally by a pore which passed right through the plate. A second pore was shared by two adjacent plates and passed up the suture between them. Along the column of imperforate plates is the cast of a tubular vessel which gives off paired lateral branches passing within the perforate plates (Pl. 85, fig. 11). There were apparently five lateral branches for each row of perforate plates. The main vessel is 0·4 mm. in diameter and traceable for 4·5–5 mm. The lateral vessels are 0·15 mm. in diameter. One lateral vessel could be traced right across a perforate plate and was completely enclosed within it in life. The casts of the sutural pores closest to the main vessel are connected to the casts of lateral vessels in some cases. It is difficult to interpret this structure as anything other than a radial vessel of the water vascular system giving off lateral braches to feed the pore-pairs and tube-feet. The number of lateral branches suggests there were five perforate plates in each row on either side of the columns of imperforate plates and therefore there were ten perforate plates between adjacent columns.

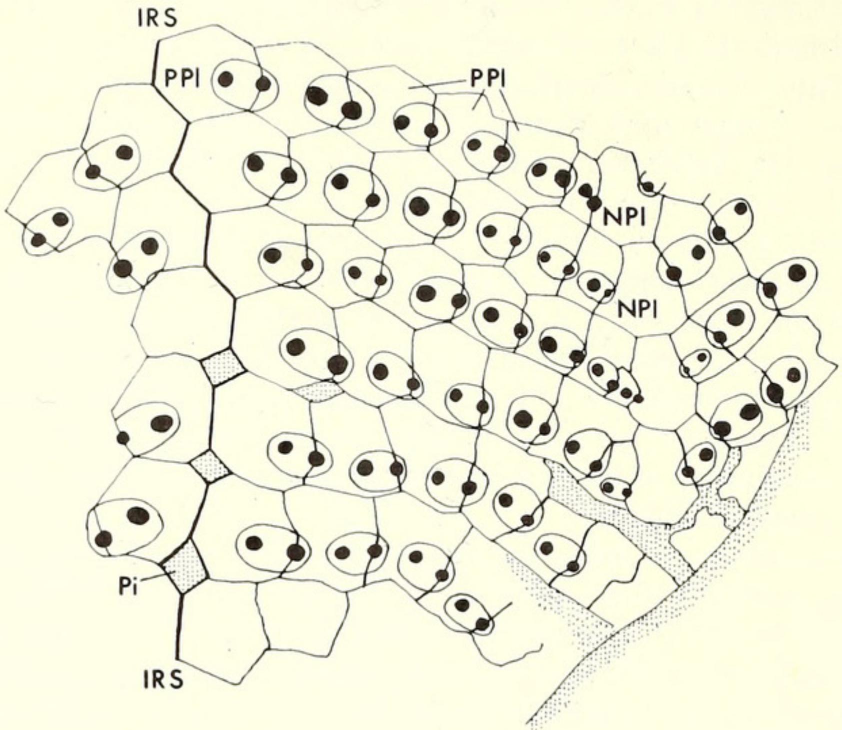
The triangular area is bounded on the right by five imperforate plates of another column showing another radial water vessel. The left margin is confluent with the area described above. Thus this counterpart shows an area between two radii of the test apparently somewhere near the ambitus as the two radii converge only slightly upwards. In this region there are nine perforate plates in the rows between the two radii. In one row there is a small accessory plate which bears no pores. Despite the odd number of plates in the rows between the radii there is no central inter-radial column of perforate plates which can be distinguished from the others. The two limbs of adjacent chevra alternate and there is a single suture, the inter-radial suture, running down the test which has no sutural pores (text-fig. 2). All other vertical sutures have sutural pores. The perforate plates adjacent to the inter-radial suture are noticeably larger than those adjacent to the columns of imperforate plates. There is a gradual increase in size in an ad-inter-radial direction.

The radial and lateral vessels of the second radius are the same size as those of the first. Each of the five imperforate plates is 1·2–1·3 mm. vertically.

A small portion of this mould has E 42523 c as external counterpart. The latter shows part of another column of imperforate plates but no corresponding radial water vessel is preserved on E 42523 b. Several of the perforate plates have complete casts of the central pores preserved. There was no connection between them and the lateral water vessels.

E 42523 c. This is an external mould of a small area of articulated plates corresponding to part of E 42523 b (Pl. 84, fig. 1). It shows the five plates of the right radius of E 42523 b, one of which is slightly out of line so there can be no doubt as to which plates correspond on the internal and external counterparts. In many moulds of perforate plates small portions of the casts of the lateral vessels can be seen attached to casts of the sutural pores. There is another column of imperforate plates which apparently terminates or is interrupted.

E 42523 d. This is an external mould of a very small area of articulated plates corresponding to part of E 42523 b (Pl. 85, fig. 9). It shows the plates adjacent to the inter-radial suture and the small accessory plate without pores which bore spines. There are marked pits at the junction of three sutures along the inter-radial suture.



TEXT-FIG. 2. A *camera lucida* drawing of part of the test of HM E 1247 to show the arrangement of poriferous plates (PPl) in rows and non-poriferous plates (NPl) in a column. IRS, inter-radial suture; Pi, pits.

The imperforate plates are basically hexagonal, approximately 1·4 mm. high and wide, and of unknown thickness. Each plate has two sides adjacent to imperforate plates above and below and is in contact with four perforate plates laterally (text-fig. 3). The two upper sloping sides bear half a sutural pore and the surface is slightly excavated to form part of the peripodium. The peripodium rim is less conspicuous in this area than at the opposite end. Centrally in each plate there is an elongate spindle-shaped elevation, 0·85 mm. long, consisting of a large central perforate mamelon 0·35 mm. in diameter, and two secondary mamela, one above and one below. The upper mamelon is generally larger, reaching 0·27 mm. and frequently perforate. The lower rarely exceeds 0·20 mm. and is imperforate.

The smallest perforate plate is 0·6×0·6 mm and is trapezoid with the shortest side adjacent to an imperforate plate. In the same row of perforate plates one plate near the inter-radial suture measures 1·5×1·5 mm. Not all the large plates are adjacent to the inter-radial suture, however. One plate adjacent to an imperforate plate measures 1·6×1·3 mm. but is replaced by two small plates in the next row.

Perforate plates adjacent to imperforate plates have their lower sloping sides excavated to bear the other half of the common sutural pore (text-fig. 3). Subcentrally there is another pore opening externally at the same level as the sutural pore and provided with a rim on the internal surface. The pores vary in diameter from 0·13 mm. in the smallest plates to 0·25 mm. in the largest. They reach 0·3 mm. internally. They are set at the base of an oval peripodium which varies from 0·66×0·4 mm. in the smallest plates to 0·8×0·6 mm. in the plates near the inter-radial suture. The increase in size of the pore-pairs is much less than that of the plates bearing them. The two pores are separated by a slight ridge (not developed in the smaller peripodia) on the peripodium floor. The peripodia have a continuous rim, more strongly developed near the single perforate mamelon. The smallest plates lack mamela as they are only 0·1 mm. larger than the peripodia. The largest plates have two additional mamela about 0·5 mm. apart. These can be distinguished as a larger, 0·25 mm. diameter, set 0·3 mm. from the primary mamelon which reaches 0·3 mm.; and a smaller below, 0·16 mm. diameter, set 0·43 mm. from the primary. There are also slight swellings on the peripodium rim either above or below the primary mamelon which may have been secondary mamela (E 42523 c).

On the far margin of the perforate plates there is another excavation for half a sutural pore and this arrangement continues to the inter-radial suture. Although the pore pairs are unequally shared by two plates, the peripodium forms a complete unit and strongly resembles those of *Bothriocidaris pahleni* Schmidt and *B. globulus* Eichwald, specimens of which were available for comparison.

C. The Hunterian Museum Specimen

Plate 85, fig. 5

This is an external mould, 18×15 mm., of part of a test (HM E1247). The major part is still articulated and shows one radius, considerable areas of adjacent 'inter-radii', and one inter-radial suture. The numbers of plates between the radius and inter-radial suture in five rows are 5, 6, 7, 6, 6 (text-fig. 2). In the second and third rows the plates adjacent to the radius are very small, 0·3×0·5 mm., and incompletely developed. The column of imperforate plates bends slightly towards one pole. The area beyond the termination is partly disarticulated. A short distance from the termination there are two plates without pores which may belong to the apical system. If so, the chevra were inverted in life. In this specimen perforate plates developed along the margins of the imperforate plates and there were two which were still forming when the animal died. The inter-radial suture shows some external pits and there were small depressions on the perforate plates adjacent to it. Several plates show casts of lateral water vessels.

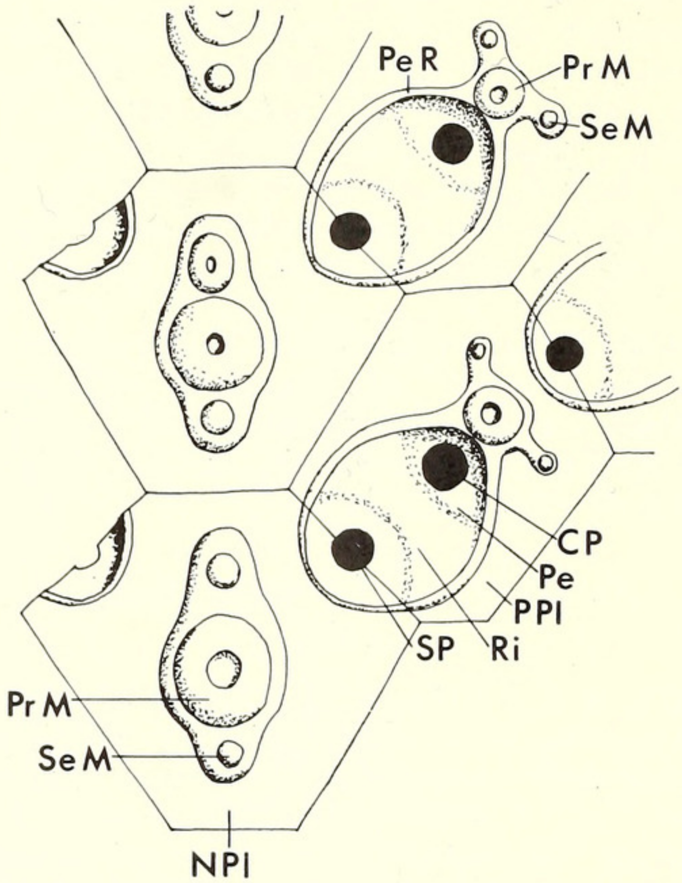
There are only two mamela on the imperforate plates: a large central perforate mamelon and a smaller imperforate one, corresponding to the larger of the two on the previous specimen (text-fig. 4). The peripodium rims are less distinct and occasionally impinge on a third plate. On the rim there is a large perforate mamelon and a single imperforate mamelon adjacent to it. Also adjacent to the primary mamelon is a small pit in the plate surface. Occasionally there is a single swelling on the rim below the primary mamelon (text-fig. 4).

The largest perforate plate is 1·25×1·25 mm. with mamela 0·35 and 0·23 mm. in diameter. The central pores reach 0·23 mm. The mamela of the imperforate plates are 0·33 and 0·27 mm. and the plates reach 1·05×1·25 mm.

D. The Lund Specimen

Plate 85, figs. 6–8

These are four fragments of external mould and an almost complete internal mould. All the fragments of external mould are coated with a dark brown deposit which obscures the finer detail. Only one fragment shows the plate arrangement clearly.

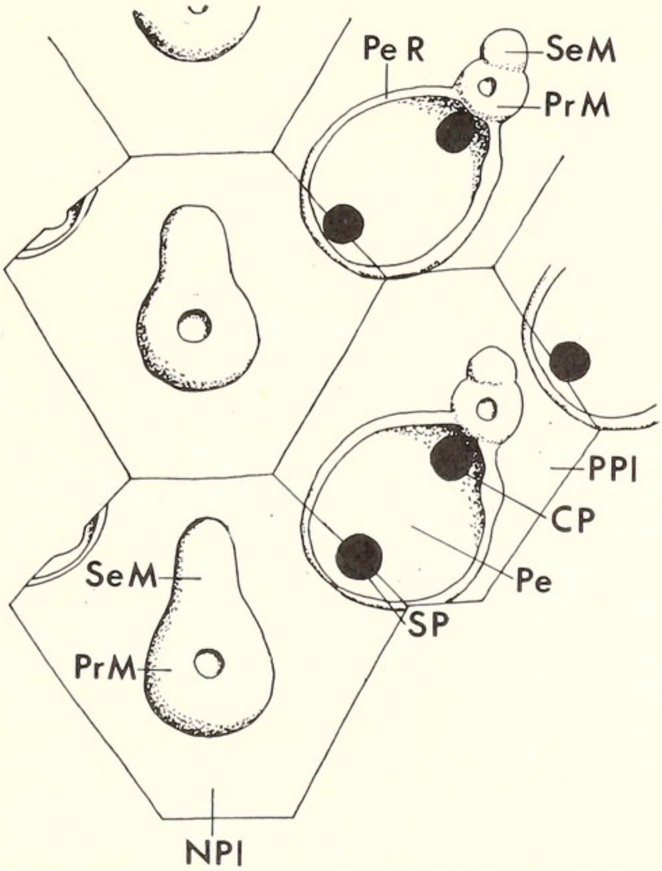


TEXT-FIG. 3. A sketch of the ornament of the plates of BMNH E 42523. CP, central pore; NPl, non-poriferous plates; Pe, peripodium; PeR, peripodium rim; PPl, poriferous plates; PrM, primary spine mamelon; Ri, ridge; SeM, secondary spine mamelon. Figs. 3 and 4 are in this orientation for ready comparison with the plates of *Bothriocidaris*. It is quite possible, however, that Figs. 2–4 and 6 are inverted.

The internal mould. This is almost complete but the surface is worn, obscuring some details. It is slightly compressed and measures 15×10 mm., with a height of 11 mm. Five columns of imperforate plates and five inter-radial sutures could be detected after coating with ammonium chloride sublimate. They converge towards the top of the mould. Unfortunately this region is worn and no details can be distinguished. There is no indication of a large aperture, such as the peristome, and this may be the apical region. If so, the chevra were inverted in life. At the opposite pole the matrix still obscures the plates so neither peristome nor apical system can be recognized definitely.

There are regularly four perforate plates in each row and thus any two adjacent radii are separated by eight perforate plates. Occasionally accessory plates without pores appear near the inter-radial sutures. The maximum number of imperforate plates distinguished in a column was seven. The maximum diameter of these plates averages 1·0 mm. In two cases fragmentary casts of radial water vessels have been preserved. The perforate plates reach 1·35 mm. and the arrangement of the pore-pairs is as in the two previous specimens.

The external mould (Pl. 85, fig. 6). Only one fragment is well preserved and shows one radius with seven or eight imperforate plates and one inter-radial suture. Both approximate towards one edge of the mould which was near a pole. Near the position of the



TEXT-FIG. 4. A sketch of the ornament of the plates of HM E 1247. Symbols as in text-fig. 3.

pole there are two large imperforate plates, one measuring 1·35 × 1·0 mm. and bearing three large mamela. These two plates may have been part of the apical system but as the column of imperforate plates terminates before reaching them this seems unlikely. In addition the chevra are the right way up in this orientation which contradicts the evidence of the internal mould.

Near the pole the inter-radial suture follows a zigzag course with perforate plates alternating on either side. Near the ambitus the perforate plates are opposite each other and four sutures meet in a distinct pit in the external surface. The inter-radial suture has become an almost straight line. Each pore-pair consists of a sutural, and a central, pore opening in a rimmed peripodium. The rim bears one perforate mamelon adjacent to which is a smaller imperforate mamelon. Below these is a marked pit in the plate surface. The imperforate plates have a central perforate mamelon and one appears to have a single secondary mamelon but the details are obscured by the brown deposit.

E. The Lamont Specimen

This specimen was briefly examined before it was returned to Dr. Lamont. It is an internal mould showing a large area of articulated plates but neither pole. It adds nothing new to the description of these specimens. In one row of perforate plates each plate has one less lateral vessel passing through it than the immediately ad-radial plate, thus confirming the reconstruction of the water vascular system given in text-fig. 6.

AFFINITIES OF THE SPECIMENS

Assuming the latter four specimens were congeneric this genus is characterized by five single columns of imperforate plates; perforate plates arranged in rows forming chevra; pore pairs set in a deep peripodium with a perforate mamelon on its rim; one pore of each pore-pair shared by two plates.

As far as the present writer is aware there are only three genera of Palaeozoic echinoids with single columns of imperforate plates. These are *Bothriocidaris* Eichwald 1860, *Cravenechinus* Hawkins 1946, and *Xenechinus* Kier 1958. The Girvan specimens resemble the latter two genera, which together form the Cravenechinidae, in having many plates between columns of imperforate plates. In the Cravenechinidae the perforate plates are arranged in columns (eight in *Cravenechinus* and four in *Xenechinus*) not rows, and each pair of pores is entirely within one plate. *Xenechinus* has radial water vessels covered internally by a calcitic deposit and lateral vessels in shallow grooves (Kier 1958, 1965). Superficially this resembles the condition in the BMNH specimen but in *Xenechinus* the radial water vessels are beneath the radial sutures and the single columns of imperforate plates are inter-radial. This was probably the case in *Cravenechinus* also but the internal surface is unknown.

The Girvan specimens resemble *Bothriocidaris* in having pore-pairs set in peripodia with spine mamela on the peripodium rims. They differ, however, in the arrangement and number of the perforate plates and in having one pore of each pore-pair shared by two plates. The positions of the radial water vessels in the BMNH specimen and *Xenechinus* prevents assigning the Girvan material to the Cravenechinidae. The strong resemblance between the pore-pairs and peripodia of the Girvan specimens and *Bothriocidaris*, however, suggests they are closely related.

Männil (1962) has accepted four species of *Bothriocidaris* separated on the details of the peripodium rim. The BMNH specimen has one large primary mamelon on the peripodium rim and two smaller mamela on the plate surface (text-fig. 3). The imperforate plates have one large perforate mamelon and two smaller mamela, one above and one below. The Hunterian specimen has one primary and one secondary mamelon on both types of plate (text-fig. 4).

Apart from these differences the peripodium rim is less distinct and occasionally shared by three plates; the peripodium is deeper and the pores nearer the margins on the Hunterian specimen than on the BMNH specimen. The plates of the Hunterian specimen are smaller and there are more of them in a row suggesting their small size is not a feature of growth. These two specimens are considered to belong to separate species.

SYSTEMATIC PALAEONTOLOGY

Family Bothriocidaridae Klem 1904

Diagnosis. A family of regular echinoids with single columns of imperforate plates; with pore-pairs opening externally in distinct peripodia surrounded by a rim on which perforate spine mamela are developed.

Genus *Neobothriocidaris* nov.

Type species. N. peculiaris gen. et sp. nov.

Diagnosis. A genus of Bothriocidaridae with single radial columns of imperforate plates; with perforate plates arranged in rows forming chevra with their axes coincident with the radial columns; with one pore of each pore-pair shared by two adjacent plates.

Regional distribution. Craighead Inlier, Girvan, Ayrshire.

Stratigraphic Range. Ordovician. Craighead Kiln Mudstones (Upper Caradoc) to Starfish Bed (Middle or Upper Ashgill).

N. peculiaris gen. et sp. nov.

Holotype. BMNH E 42523 a–d.

Type locality. Locality 7 (Lamont, 1935), Threave Glen, Girvan.

Type Stratum. Starfish Bed, Upper Drummock Group. According to Ingham (1966, p. 495) this is on the boundary of the Middle and Upper Ashgill. *N. peculiaris* is only known from the type locality.

Diagnosis. A species of *Neobothriocidaris* with one primary and two secondary spine mamela on the imperforate plates; with one primary mamelon on the peripodium rim; and two secondary mamela on the plate surface of the perforate plates.

N. minor gen. et sp. nov.

Holotype. HM E 1427.

Type locality and stratum as for *N. peculiaris.*

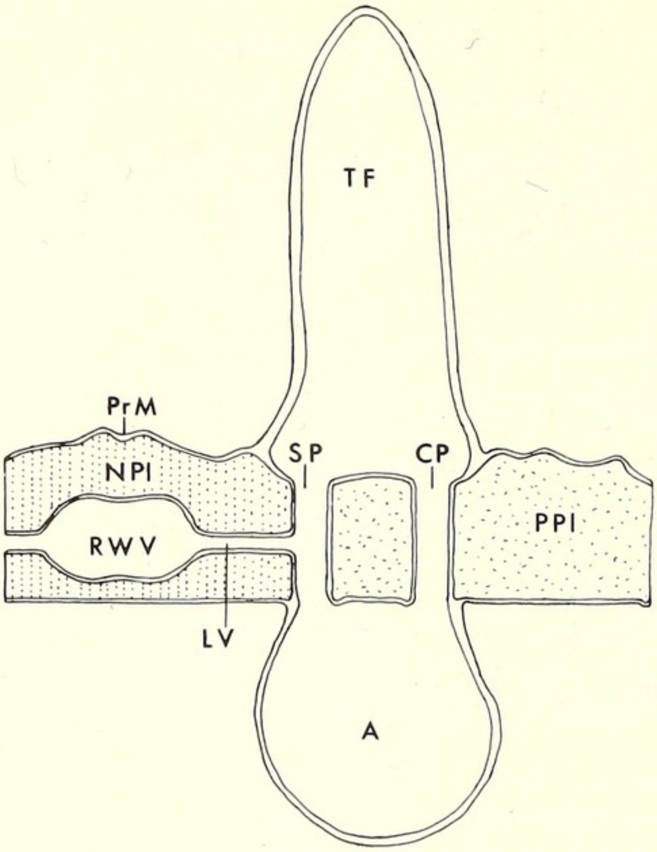
Diagnosis. A species of *Neobothriocidaris* with one primary and one secondary spine mamelon on the imperforate plates; with one primary mamelon on the peripodium rim; and one secondary mamelon on the plate surface of the perforate plates.

N. minor (the Lund specimen) is recorded from the Craighead Kiln Mudstones, below the kilns at Craighead Quarry, Girvan, as well as from the type locality.

The full complement of mamela is only developed on large perforate plates of which those adjacent to the inter-radial suture are taken as typical. Lamont's specimen cannot yet be assigned to either species above. It is from the Starfish Bed.

RECONSTRUCTION OF THE WATER VASCULAR SYSTEM IN *NEOBOTHRIOCIDARIS*

It is assumed that the madreporite in *Neobothriocidaris* gave rise to a stone canal leading to a circumoesophageal ring canal off which five radial water vessels arose, as in all other sea urchins. The radial vessels may have been partly or completely within the coronal plates. This was the case in at least two radii of the BMNH specimen as is



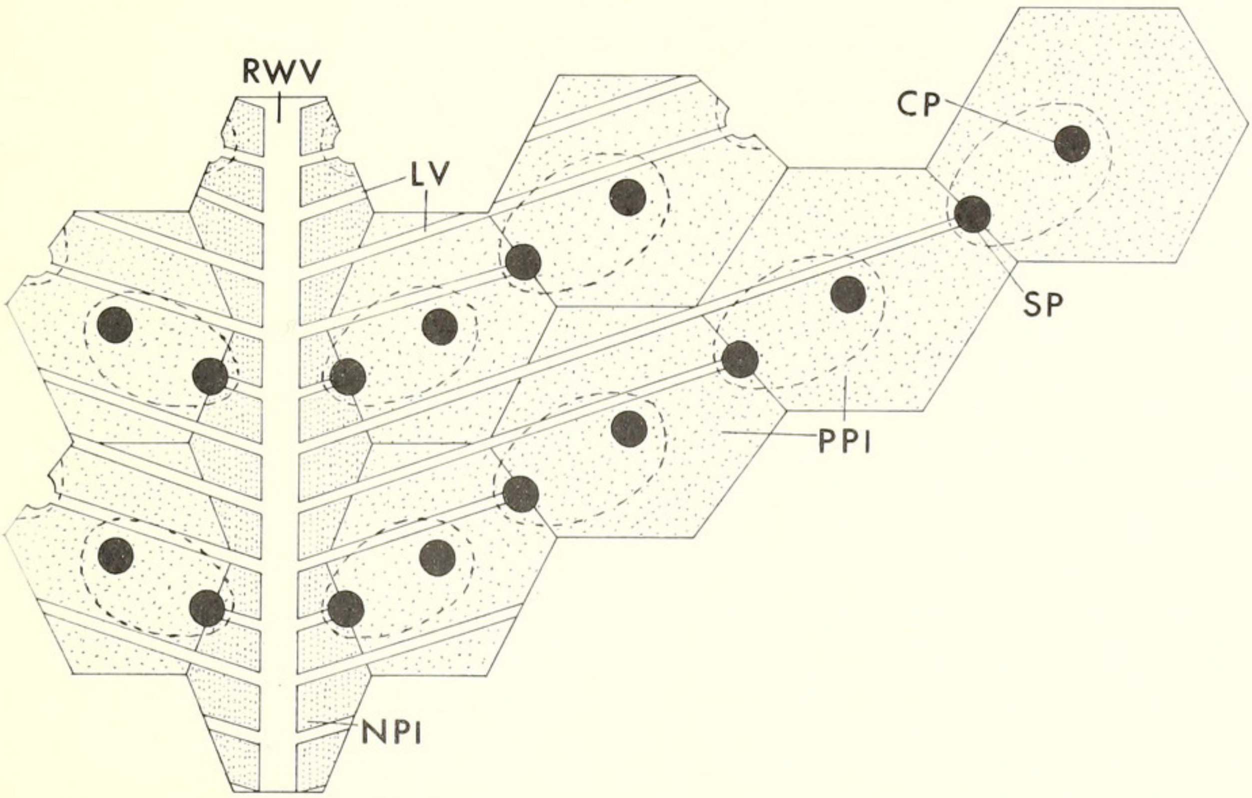
TEXT-FIG. 5. Reconstructed transverse section through a radial water vessel (RWV) and a tube-foot (TF) of *Neobothriocidaris* gen. nov. showing a lateral vessel (LV) feeding the sutural pore (SP) within the plate of the corona. A, ampulla; CP, central pore; NPl, non-poriferous plate; PPl, poriferous plate; PrM, primary spine mamelon.

shown by the casts seen on E 42523 b. There was no evidence of the radial vessel of the third radius however nor in the majority of plates in the five radii of the Lund specimen. If the radial vessels were entirely within the coronal plates in life casts would be formed only when the covering was damaged after death. The radial vessels were probably within the plates since the casts of the lateral vessels are in the BMNH and Hunterian specimens. Casts of radial vessels are only preserved in the Lund specimen where the plates are slightly damaged. Text-fig. 5 shows the interpretation adopted here.

In plan view (text-fig. 6) the perforate plates are arranged in chevra with their axes coincident with the radial column of imperforate plates. In all cases the lateral vessels are also arranged in chevra at a slightly greater angle to the radial line. This arrangement allows lateral vessels to feed tube-feet in perforate plates not adjacent to the column of imperforate plates, and is preserved in Lamont's specimen.

RE-INTERPRETATION OF BOTHRIOCIDARIS

The internal mould of *Neobothriocidaris peculiaris* gen. et sp. nov. (BMNH E42523 b) has casts of radial and lateral water vessels preserved. By definition the plates bearing radial water vessels are radial in position but in this specimen they are imperforate



TEXT-FIG. 6. Diagrammatic reconstruction of part of the water vascular system of *Neobothriocidaris* gen. nov. CP, central pore; LV, lateral vessel; NPl, non-poriferous plates; PPl, poriferous plates; RWV, radial water vessel; SP, sutural pore.

plates which have previously been regarded as inter-radial in *Bothriocidaris*. Assuming *Neobothriocidaris* and *Bothriocidaris* are closely related it seems advisable to reinterpret the latter with the imperforate plates radial. Lack of knowledge of the apical system and peristome in *Neobothriocidaris* unfortunately prevents a complete comparison. The main effect of the proposed re-interpretation is that all radial features became inter-radial and vice versa. To reduce confusion in the following account radial and inter-radial are italicized when referring to the re-interpretation.

The Apical System. The apical system of *Bothriocidaris* is unique in lacking genital and terminal pores and in consisting of five, not ten plates. The five plates were regarded as radial and therefore as ocular plates, one of which was modified as a madreporite. These plates now become *inter-radial*, genital plates with one a madreporite, as in later echinoids. The madreporite is used to orientate the test and lies in inter-radius 2. It is assumed this was the case in *Bothriocidaris*. Where were the oculars if the apical plates