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UPPER ORDOVICIAN BRACHIOPODS FROM POLAND AND BRITAIN

Abstract. — The brachiopods of the Upper Ordovician *Hirnantia* fauna from the Holy Cross Mountains of Poland (Góry Świętokrzyskie) are described. The fauna, which includes one new genus (*Plectothyrella*) and four new species (*Philhedra? stawyensis, Hirnantia? kielanae, Platymena? polonica, Plectothyrella platystrophoides*), is compared with occurrences from North Wales and the English Lake District.

INTRODUCTION

In this article are described the brachiopods of the *Hirnantia* fauna from the Upper Ordovician of the Holy Cross Mountains (Góry Świętokrzyskie), Poland. The descriptions are supplemented in some cases by reference to specimens from the Ashgill Shales of the English Lake District and the Hirnant Beds of North Wales.

The Polish material was collected by Dr. W. T. Dean, Mr. R. P. Tripp and myself during a visit to Poland in 1961 which was made possible by a grant from the Royal Society of London. During our visit we were received with great hospitality by Polish palaeontologists who gave up much time to showing us collections and accompanying us in the field. I am particularly indebted to Professor Zofia Kielan-Jaworowska (Palaeozoological Institute, Polish Academy of Sciences, Warsaw) for her kindness in making arrangements for our trip and for showing us the Ordovician sections of the Holy Cross Mountains. I am also very grateful to Professor Alwyn Williams for critically reading the manuscript and for much helpful advice; and to the following for the loan of specimens: Mr. A. G. Brighton (Sedgwick Museum, Cambridge), Dr. Dean (British Museum [Natural History]), Dr. V. Jaanusson and Dr. H. Mutvei (Riksmuseum, Stockholm), Professor C. Poulsen (Mineralogisk Museum, Copenhagen), Professor G. Regnéll (Palaeontological Institute, Lund), Dr. Vl. Zázvorka (Národní Muzeum, Prague). Dr. M. Levison and Mr. W. A. Sentance have been kind enough to obtain the eigenvalues and vectors of the matrices on the London University Atlas. I am grateful to Dr. B. Roberts for comments on some of the rock thin-sections. Field work in England and Wales was aided by a grant from the University of London Central Research Funds.

MATERIAL

The Polish fauna was collected from the Stawy section, near Łagow, in the Bardo syncline of the Holy Cross Mountains, from yellow sandy siltstones about 2 metres below graptolite shales forming the base of the Silurian (Kielan, 1960, p. 12, Text-fig. 1). The fauna includes trilobites, ostracods, bryozoans, worm tubes, a hyolithid, and crinoid and graptolite fragments in addition to brachiopods, but the latter are the predominant element. The fossils (excluding the graptolite fragments) are preserved as moulds stained yellow or brown and are usually undistorted. The preservation is good for internal features, but the matrix is rather coarse and friable and does not retain well the details of fine ribbing. The material was mostly collected in bulk and broken up in the laboratory.

Prefixes to the registration numbers of specimens are as follows: A — Sedgwick Museum, Cambridge; BB — British Museum (Natural History), London, where the Polish specimens are housed; Br — Riksmuseum, Stockholm; K — Geological Survey of India; LO — Palaeontological Institute, Lund. Suffixes a and b refer to part and counterpart. Except where explicitly stated otherwise, all descriptions, dimensions, illustrations, tables, etc., refer to specimens from Stawy. Dimensions of specimens in the systematic descriptions are quoted in mm. in the form: minimum, mean (variance), maximum. All measurements, including those of depth, have been made on internal moulds. The numbers of specimens in the collection from Stawy are listed in Table 10.

SYSTEMATIC DESCRIPTIONS

INARTICULATA

Superfamily **Lingulacea** Menke, 1828

Family **Obolidae** King, 1846

Genus *Lingulella* Salter, 1866

Lingulella sp.

(Pl. I, figs. 1—3)

Material[1] *and dimensions* (n mm.):

Pedicle valve (BB 30765): length 8.5; width 8.6

Pedicle valve (BB 30766): length 7.4; width 7.7

[1] Here, and elsewhere under this heading, „material" refers only to measured specimens.

Description. — Outline of pedicle valve sub-pentagonal to sub-triangular; width slightly greater than length, apical angle in two valves 99°, 103°. Proparea of pedicle valve striated, sloping antero-ventrally in front, prolonged forwards axially as a narrow tongue bearing pedicle groove; pedicle groove roundedly angular in section, not reaching umbo. Proparea of brachial (?) valve striated, not prolonged forwards axially, probably with a slight median ridge (in place of pedicle groove). Exteriors of shells with thin, concentric, evenly spaced fila (about 5 per mm. at 5 mm. from umbo, closer in immature parts) and apparently some concentric grooves in mature parts; interiors with faint concentric markings.

Remarks. — There is not sufficient material for a complete description of this form, especially as the identification and description of the brachial valve is only tentative. Although the general shape is linguloid it is rather wider than is usual in *Lingulella.*

Superfamily **Discinacea** Gray, 1840
Family **Discinidae** Gray, 1840
Genus *Orbiculoidea* d'Orbigny, 1847
Orbiculoidea radiata Troedsson, 1918
(Pl. I, figs. 4—7; Pl. II, figs. 1—2)

1918. *Discina (Orbiculoidea) radiata* Troedsson; G. T. Troedsson, Om Skånes..., p. 35, Pl. I, figs. 6—7.

Lectotype (here selected): Pedicle valve, LO 2867t, from Röstånga, Sweden (Troedsson, 1918, Pl. I, fig. 7), figured here on Pl. I, fig. 7.

Material and dimensions (in mm.):

4 pedicle valves:	length	2.1, 2.40 (0.09), 2.8
	width	2.0, 2.60 (0.17), 2.9
15 brachial valves:	length	1.7, 3.25 (3.63), 9.6
	width	2.1 3.52 (2.57), 8.5

Lectotype pedicle valve: length 4.5; width 5.0 (?)

Description. — *Pedicle valve* slightly conical, almost flat; outline sub-circular, possibly notched posteriorly even in largest form; umbo sub-central, slightly posterior; anterior and posterior slopes nearly flat, posterior slope slightly concave near umbo; pedicle slit extending from umbo (? to posterior margin), apparently filled; position of foramen obscure, probably near margin.

Brachial valve slightly more convex than pedicle valve, depth about one-sixth of length; outline sub-circular, umbo excentric, about one-ninth of length from posterior margin; anterior slope gently convex, posterior slope short, steep, concave.

Exteriors of both valves with fine fila concentric to umbones, the numbers of fila at any valve-length (about 19 at 2 mm., 28 at 4 mm.) the same in pedicle and brachial valves, although the spacing is different (more widely spaced on anterior slopes of brachial valves). Both valves occasionally show faint radial corrugations (about 14 and 18 radiating anteriorly from umbo in two brachial valves 3.9 and 9.6 mm. long).

Remarks. — Although the mean width is greater than the mean length for both pedicle and brachial valves, a two-tailed *t*-test on combined pedicle and brachial valves shows that the null hypothesis of equality of length and width cannot be confidently rejected ($.90 < p < .95$).

The correspondence of width/length and external fila/length plots for pedicle and brachial valves supports the reference of both valves to a single species, which is identified with *O. radiata*. The syntypes of the latter (Pl. I, figs. 6—7 here) are larger than most of the Stawy forms and this may account for the greater prominence of their radial corrugations, particularly on the pedicle valve; in other respects Troedsson's specimens agree well with ours.

Superfamily **Craniacea** Menke, 1828
Family **Craniidae** Menke, 1828
Genus *Philhedra* Koken, 1889
Philhedra? stawyensis n. sp.
(Pl. II, figs. 3—7)

Holotype: Internal and external moulds of brachial valve, BB 30760a, b, figured on Pl. II, fig. 3.

Type horizon and locality: Upper Ordovician, *Dalmanitina* beds, Stawy, Holy Cross Mountains, Poland.

Derivation of the name: *stawyensis* — from the name of the type locality Stawy.

Diagnosis. — A species of *Philhedra* with brachial valve of small size, usually with the ribbing of the host strongly impressed, radiating ribs on external surface very fine (probably bearing minute spines) and often apparently lacking, umbo less than one-third of length from posterior margin. Pedicle valve unknown and probably uncalcified.

Material and dimensions (in mm.):

29 brachial valves: length 1.7, 3.61 (0.64), 5.1

Holotype brachial valve: length 3.6

Description. — *Brachial valve*: Outline variable, usually sub-circular to sub-polygonal, often with straight or slightly indented posterior margin. Convexity variable, almost plane to sub-hemispherical with vertical edges, posterior slope from umbo concave, rarely reflexed. Umbo conical, excentric (distance from posterior margin variable but always less than one-third of length). Surface (external and internal) uneven, with large wrinkles, either with one or more concentric to umbo, or with impressions of ribbing of host running at any angle; posterior slope often smooth. Exterior with either fine radiating ribs (about 10 per mm. with broader rounded interspaces, the ribs in the best preserved specimens apparently bearing minute spines) or concentric growth-lines or both or apparently neither; no internal features can be distinguished with certainty. Shell sometimes split into layers peripherally.

Remarks. — This species, of which only the brachial valve is known, is interpreted widely to include forms of different convexity, with or without ribbing on the exterior, and with or without impressed ribbing of the host. The impressed ribbing is remarkably sharp and often suggests the asymmetrical ribbing of *Dalmanella testudinaria,* while finer ribbing may be that of *Hirnantia? kielanae* or *H. sagittifera,* and one specimen has very fine ribbing reminiscent of *Platymena? polonica.* Several valves at all stages of development, including the two smallest, have no clear traces of impressed ribbing, and it is not known what these were attached to. Most valves are sub-circular and probably represent individuals that lived alone, but the sub-polygonal outline of a few suggests that they may have lived aggregated, as illustrated by Cooper for *Acanthocrania subquadrata* (1956, Pl. 26, fig. 21). No pedicle valves have been found in the faunule and it seems likely that the pedicle valve was uncalcified, as Kozłowski demonstrated for *Philhedra umbrella* and *Philhedrella mimetica* (1929, Text-figs. 2, 3). This would account for the sharpness of the ribbing impressed on the brachial valve.

Generic reference of the species is difficult. *Philhedrella* (and to a lesser extent *Petrocrania*) agrees in taking up strongly the ribbing of the host, but lacks its own external ribs; *Philhedra,* which does have external radial ribs (though they are usually stronger than those of the Stawy species), does not usually take up the ribbing of the host (Kozłowski, 1929, p. 40); *Acanthocrania* has fine spines (sometimes arranged in a radial pattern) and may take up the ribbing of the host. It is clear that the species does not fit easily into any of these genera. On balance, despite the impressed ribbing of the host and in the absence of information about the muscle scars, the most convenient solution seems to be to refer it to *Philhedra.*

ARTICULATA

Superfamily **Enteletacea** Waagen, 1884
Family **Dalmanellidae** Schuchert & Le Vene, 1929
Genus *Dalmanella* Hall & Clarke, 1892
Dalmanella testudinaria (Dalman 1828)

(Pl. III, figs. 1—7; Pl. IV, figs. 1—6; Pl. V, figs. 1—7; Pl. VI, figs. 1—7; Text-fig. 1 a-c)

1828. *Orthis testudinaria* Dalman; pp. 115, 117, Pl. 2, fig. 4.

Material and dimensions (in mm.):

53 pedicle valves:	length	1.4, 5.26 (4.80), 10.0
	width	1.6, 6.26 (6.43), 12.4
63 brachial valves:	length	1.7, 5.73 (5.40), 13.8
	width	2.3, 6.91 (6.79), 16.2

Description. — *Pedicle valve*: Outline sub-circular; ratio of maximum width to length averages 1.2, constant during development. Convexity greater than that of brachial valve; depth averaging a little over a quarter of length. A broad fold gives a rather humped appearance to axial parts of valve. Cardinal area apsacline, curved (in large forms through about 90° with radius of curvature about 0.75 mm.).

Table 1

Width-distributions of 54 pedicle valves & 64 brachial valves of *Dalmanella testudinaria* from Stawy

Width (lower limit of class, in mm.)	0	1	2	3	4	5	6	7	8	9	10	11	12	13
No. of pedicle valves	0	2	6	3	3	8	10	10	5	4	1	1	1	0
No. of brachial valves	0	0	2	3	13	10	10	5	8	5	4	3	1	0

Delthyrium open, with pedicle collar (about 0.5 mm. long in large forms) which extends forwards as a short tapering flange on the wall of each dental plate. Inner walls of dental plates slant down to floor of valve at an angle greater than 45° to area. Teeth with crural fossettes. Bases of dental plates diverge in six specimens at 44°, 55°, 60° (twice), 65°, 80° (mean = 60.7°). Diductor scars extending to one-third length of valve, about as wide as anterior ends of dental plates; adductor scars expanding forwards, shorter than but not enclosed by diductors from which they are often not clearly separated. Indistinct mantle canals (?branches of *vascula media*) visible occasionally.

Brachial valve: Outline sub-circular, truncated by hinge-line; ratio of maximum width to length 1.2 at length 6 mm., decreasing throughout growth. Convexity slight, depth averaging about 12% of length. A broad, shallow, anteriorly-expanding median sulcus extends whole length of valve. Cardinal area anacline, slightly curved.

Notothyrium open. Inner walls of notothyrial cavity approximately vertical and in mature individuals closer together than edges of notothyrium which slope briefly obliquely down to them. Cardinal process more than half length of brachiophore supporting plates, narrowest at floor of valve where basal width varies from thin (slit-like in internal moulds) to nearly as wide as notothyrial cavity, the latter condition more common in forms above 6 mm. long; attachment surface usually simple, sometimes with traces of bilobation and crenulation; cardinal process tapers anteriorly and slopes usually steeply (sometimes vertically) down to floor of front part of notothyrial cavity where a broad, low swelling branches anteriorly. Brachiophore supporting plates short, not extending beyond ends of notothyrial cavity, their inner walls vertical and continuing inner walls of notothyrial cavity, their bases diverging forwards in nine specimens at 27°, 28° 30°, 34°, 40° (twice), 47° (twice), 52° (mean = 38.3°). Inner or outer faces of brachiophores occasionally grooved. Dental sockets sometimes showing one or two crenulations; sockets in three specimens make angles of 110°, 115°, 120° with each other; sockets defined by fulcral plates running obliquely

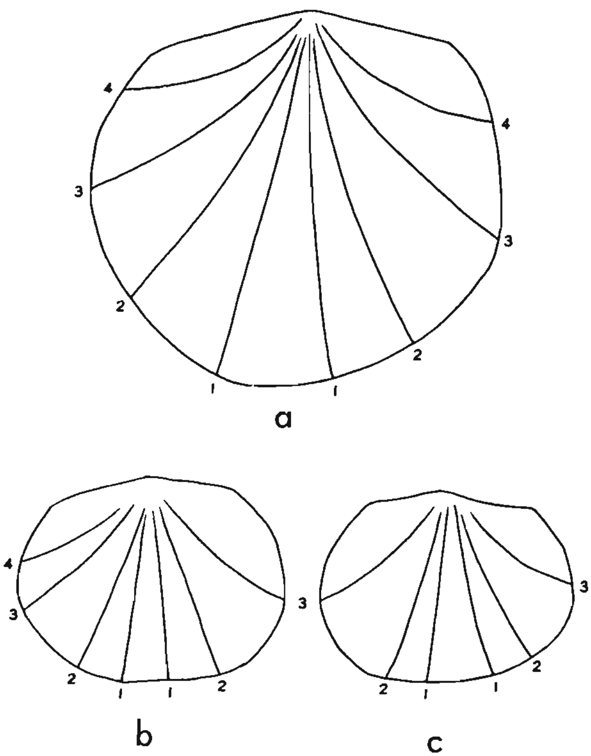

Fig. 1. — Disposition of primary ribs on brachial valves of *Dalmanella testudinaria* (Dalman): *a* from Borenshult, based on Br 1925; *b* from Stawy, based on BB 29588b, *c* from Stawy, based on BB 30012b; × 3.75.

outwards to hinge-line. Blunt, massive crural pits[2] usually present (and obscuring sockets in dorsal view of internal moulds), but sometimes much reduced or nearly absent. Adductor impressions well marked, reaching just over half length of shell (52% at 6 mm valve-length, decreasing slightly throughout growth), bounded distally by low

[2] Bancroft's term (see Williams & Wright, 1963, p. 5) is retained pending the appearance of the Brachiopoda volume of the *Treatise on Invertebrate Paleontology* in which, Professor Alwyn Williams tells me, its replacement will be proposed.

ridges which diverge obliquely from anterior ends of supporting plates, and separated axially by a broad ridge tapering forwards from the width of the notothyrial cavity. Anterior adductor longer and wider than posterior.

Ribbing: Ribbing costellate, some subsequent ribs remaining long grouped on flanks of parents, asymmetrically triangular in section. Primary interspaces bear thin fila apparently throughout their length; subsequent interspaces develop fila when they reach equal amplitude to primary interspaces. Some concentric growth-irregularities. Approximate numbers of ribs around commissures of six brachial valves as follows:

length (mm.)	2.9	4.0	5.4	6.9	7.0	9.1
no. of ribs	28	33	42	45	46	48

At 2 mm. from umbo 8, 9, 10, 11, 12 ribs per 2 mm. were counted in 4, 7, 1, 0, 1 brachial valves. Details of the ribbing system are given in Tables 2—3, the disposition of the primary ribs in Text-fig. 1. Ribbing clearly impressed only near margins of interiors of valves although faint traces extend inwards to edges of musculature.

Ontogeny. — The ribbing is rather strongly impressed on the smallest attributed internal mould of a brachial valve. Apart from slight differences in proportions (maximum width and adductor length relatively greater), brachial valves as small as 2.5 mm. do not differ markedly from larger forms. The smallest attributed pedicle valves (1.4 — 1.9 mm.) are very convex and strongly ribbed on internal moulds; valves of 2.4 mm. and longer do not differ appreciably from larger forms.

Variation. — There is variation in outline of both valves, and in convexity particularly of the brachial valve. The most apparent variation in internal moulds of the brachial valve is in the width of the cardinal process and the prominence of the crural pits, the two characters varying apparently independently. The angle of divergence of the bases of the dental plates and the prominence of the ventral umbo also vary. One specimen is unusual in having very massive dental plates.

Remarks. — The Polish specimens have been compared with a topotype sample of *D. testudinaria* from Borenshult, Sweden, and also with specimens from Hol Beck, Westmorland, in the English Lake District. The Swedish material is the same sample as that analysed by Williams & Wright (1963, p. 29), but it was not possible to distinguish the specimens called Form A by those authors, and the observations recorded here refer, therefore, to the whole sample.

The ribbing relations of the Polish and Swedish specimens are shown in Table 2. The only significant differences between the right sides of brachial valves (i.e. the left sides of external moulds of Stawy specimens) are in $2b^{-}/2a^{\circ}$ ($p = .02$) and $3a^{-}1^{-}a^{-}/2a^{\circ}$ ($p = .005$), indicating

Table 2

Rib relations of *D. testudinaria* based on 18 brachial valves from Stawy and 25 brachial valves from Borenshult, showing for each rib-pair the numbers of valves in which the first-named rib appears before : after : together with the second-named

	STAWY		BORENSHULT
	Left sides	Right sides	Right sides
$1a^{-}1^{-}/1b^{-}$	1 : 3 : 1	4 : 2 : 2	7 : 9 : 3
$2b^{-}1^{-}/2a^{\circ}$	0 : 11 : 0	1 : 7 : 0	1 : 1 : 0
$2c^{-}/2a^{\circ}$	0 : 11 : 0	1 : 7 : 0	3 : 1 : 0
$2b^{-}/2a^{\circ}$	4 : 9 : 1	7 : 3 : 3	24 : 0 : 0
$2a^{-}1^{-}/2b^{-}$	3 : 2 : 4	2 : 6 : 3	9 : 5 : 10
$3c^{-}/3a^{\circ}$	0 : 6 : 1	2 : 6 : 1	7 : 5 : 2
$3b^{-}/3a^{\circ}$	11 : 3 : 1	13 : 1 : 1	24 : 1 : 0
$3a^{-}1^{-}a^{-}/2a^{\circ}$	2 : 6 : 0	5 : 4 : 2	21 : 0 : 1

Table 3

Numbers of specimens among 18 brachial valves of *D. testudinaria* from Stawy in which the members of each rib-pair have the same relation (one appearing before the other, or both together) on the two sides of the valve : a demonstrably different relation on the two sides : an indeterminate relation (the pair being developed on one side only of the valve). The first condition is symmetrical, the second and third represent different kinds of asymmetry

$1a^{-}1^{-}/1b^{-}$	0 : 3 : 5
$2b^{-}1^{-}/2a^{\circ}$	5 : 1 : 5
$2c^{-}/2a^{\circ}$	5 : 1 : 5
$2b^{-}/2a^{\circ}$	4 : 7 : 2
$2a^{-}1^{-}/2b^{-}$	1 : 6 : 2
$3c^{-}/3a^{\circ}$	3 : 3 : 1
$3b^{-}/3a^{\circ}$	7 : 5 : 0
$3a^{-}1^{-}a^{-}/2a^{\circ}$	2 : 3 : 4

a tendency to earlier insertion of $2a^{\circ}$ at Stawy, and the non-significant difference in $2c^{-}/2a^{\circ}$ points in the same direction. The ribbing relations of the Stawy specimens seem closest, both in the early insertion of $2a^{\circ}$ and in the low frequency of $3c^{-}/3a^{\circ}$, to those of *D. wattsi* (Bancroft). The density of ribbing appears to be slightly higher at Stawy than at Borenshult where 7, 8, 9, 10, 11 ribs per 2 mm. were counted at 2 mm. from the umbo in 2, 5, 2, 1, 1 brachial valves (Williams & Wright, 1963, p. 31, also give counts per mm. for *D. testudinaria* and Form A).

Comparisons of brachial valves from Stawy and Borenshult have been made by measurements of:

(x_1) overall length,

(x_2) overall width,

(x_3) transverse separation of front ends of supporting plates (measured transversely between the same points as in x_4),

(x_4) length of supporting plate (measured along the plate from the umbo to the back of the front face of the plate — the latter point corresponds to the front edge of the slot left by the plate in internal moulds seen in dorsal view, and can be measured more objectively than the indefinite front foot of the plate),

(x_5) width of supporting plate (measured at right angles to its length at a point halfway along the crural pit).

Only one supporting plate (where possible the right) was measured on each specimen.

The resulting variance-covariance matrices (Table 4) differ significantly ($p > .995$), indicating differences in the scatter ellipsoids (dispersions). The first four principal components are of the same order of size, but only λ_1 (an index of overall size) can be equated with any confidence in the two samples. In both cases λ_5 appears from its large x_5 direction cosine to be an index of supporting plate width, but it is over 500 times as large (indicating much greater variation) in the Polish specimens and differently oriented with respect to x_3 and x_4. The correlation matrices (not reproduced here) show that r_{15}, r_{25}, and r_{45} are significantly less at Stawy (where they do not differ significantly from zero) than at Borenshult; r_{35} is positive and significant at both localities. Bivariate analysis (see below) shows that the mean supporting plate width is less at Stawy.

The Stawy specimens differ also in that the cardinal process is more sharply bounded anteriorly and the dorsal median ridge weaker. There are no apparent differences in pedicle valves.

There are clearly significant differences between the Stawy and Borenshult brachial valves, and if these two collections only were known the Stawy forms would be separated at least sub-specifically, mainly on the thinner supporting plates, weak dorsal ridge, and higher incidence of early insertion of 2a°. When the Lake District specimens are taken into account, however, the situation becomes more confused.

The Lake District specimens appear to be similar to Stawy specimens in the anterior bounding of the cardinal process and the weak median dorsal ridge. They are distorted by cleavage and it is not possible to get reliable readings on overall length, overall width, or supporting plate separation, or reliable data on ribbing relations. Nevertheless, a trivariate analysis of:

(x_4) length of supporting plate,

(x_5) width of supporting plate,

(x_6) depth of crural pit (measured along the length of the supporting plate)

was made of Polish and Lake District specimens (it is not possible to measure crural pit depth on the Borenshult specimens, as some of the brachial valves are too fragile for latex casts to be made). Again, the

Table 4

Multivariate analysis of overall length (x_1), overall width (x_2), transverse separation of supporting plates (x_3), length of supporting plate (x_4), and width of supporting plate (x_5) in brachial valves of *Dalmanella testudinaria* from Borenshult and Stawy (measurements in mm.)

				BORENSHULT		
Size of sample	n			6		
Means	$\bar{x}_1$			10.0167		
	$\bar{x}_2$			11.4500		
	$\bar{x}_3$			1.5417		
	$\bar{x}_4$			1.8333		
	$\bar{x}_5$			0.4500		
Variance-covariance matrix		3.9057	4.1850	0.7352	0.7173	0.1930
			4.5670	0.7775	0.7520	0.2070
				0.2344	0.1393	0.0395
					0.1667	0.0420
						0.0110
Principal components	λ_1			8.7101		
	λ_2			0.1010		
	λ_3			0.0512		
	λ_4			0.0224		
	λ_5			$0.0^{5}692$		
Transformation matrix		0.6681	0.7223	0.1264	0.1219	0.0332
		−0.0694	0.2579	−0.9508	−0.1506	−0.0432
		−0.4356	0.4776	0.2772	−0.7044	−0.0954
		−0.5977	0.4260	0.0475	0.6522	0.1834
		0.0439	−0.0465	−0.0282	−0.2020	0.9769
				STAWY		
Size of sample	n			17		
Means	$\bar{x}_1$			8.4529		
	$\bar{x}_2$			10.0118		
	$\bar{x}_3$			1.4676		
	$\bar{x}_4$			1.7500		
	$\bar{x}_5$			0.3324		
Variance-covariance matrix		3.1677	3.4943	0.1906	0.3003	0.0613
			4.4111	0.2535	0.3975	0.0718
				0.0553	0.0386	0.0235
					0.0600	0.0106
						0.0162
Principal components	λ_1			7.3876		
	λ_2			0.2447		
	λ_3			0.0571		
	λ_4			0.0172		
	λ_5			0.0037		
Transformation matrix		0.6398	0.7642	0.0435	0.0679	0.0130
		−0.7658	0.6252	0.0915	0.1198	0.0059
		0.0532	−0.1326	0.8081	0.3946	0.4134
		0.0348	−0.0868	−0.2409	0.8791	−0.4006
		−0.0145	0.0079	−0.5280	0.2292	0.8176

variance-covariance matrices (Table 5) are significantly different ($p > .995$), suggesting differences between the samples in these characters taken together. The principal components appear, though, to correspond fairly well in the two samples: λ_1 is probably an index of size despite its negative x_5 direction cosine at Stawy; λ_2 has direction cosines of opposite signs for x_4 and x_6 and contrasts supporting plate length (and also width at Stawy) with crural pit depth; λ_3, with its predominant x_5 direction cosine, is mainly an index of supporting plate width. The same principal components are recognisable in a trivariate analysis of *Hirnantia sagittifera* (see p. 399); and the same considerations of the effects of cleavage on the Lake District *D. testudinaria* apply as are discussed under that species.

Table 5

Trivariate analysis of supporting plate length (x_4), supporting plate width (x_5) and crural pit depth (x_6) in brachial valves of *Dalmanella testudinaria* from Stawy and Hol Beck (measurements in mm.)

		STAWY			HOL BECK	
Size of sample	n	14			13	
Means	$\bar{x}_4$	1.7179			1.7308	
	$\bar{x}_5$	0.3071			0.4115	
	$\bar{x}_6$	0.5464			0.7808	
Variance-covariance matrix	0.0245	−0.0049	0.0156	0.0573	0.0096	0.0123
		0.0111	−0.0188		0.0126	0.0119
			0.0409			0.0765
Principal components	λ_1	0.0579			0.0856	
	λ_2	0.0169			0.0515	
	λ_3	0.0017			0.0092	
Transformation matrix	0.4374	−0.3746	0.8175	0.4480	0.2011	0.8711
	0.8891	0.3162	−0.3308	0.8798	0.0736	−0.4695
	−0.1345	0.8716	0.4714	−0.1586	0.9768	−0.1440

Clearly, comparison of the three samples (Polish, Swedish, and Lake District) taken together is desirable, and a bivariate analysis was made of the only two characters among those studied that it is possible to measure accurately on specimens from all localities, i.e. (x_4) supporting plate length, and (x_5) supporting plate width. In this case the variance--covariance matrices (Table 6) do not differ significantly ($.10 < p < .90$), and it is possible to compare sample means along the axes corresponding to the principal components λ_1 and λ_2 of the pooled samples. Of the principal components, λ_1 represents the major axis of the ellipse (with both direction cosines positive) and could be used as a basis for a comparison of mean overall size (of the supporting plates), while λ_2 contrasts supporting plate width and length and is an indicator of shape. The transformed means $\bar{y}_1$ and $\bar{y}_2$ of the three samples relative to the pooled means and to the transformed axes corresponding to λ_1 and λ_2 are given in Table 6. It is clear that the Swedish and Lake District values of $\bar{y}_2$

Table 6

Bivariate analysis of length of supporting plate (x_4) and width of supporting plate (x_5) in brachial valves of *Dalmanella testudinaria* from Borenshult, Stawy, and Hol Beck (measurements in mm.)

	BORENSHULT	STAWY	HOL BECK
Size of sample n	8	17	13
Means $\bar{x}_4$ $\bar{x}_5$	$\begin{bmatrix}1.9750\\0.4625\end{bmatrix}$	$\begin{bmatrix}1.7500\\0.3324\end{bmatrix}$	$\begin{bmatrix}1.7308\\0.4115\end{bmatrix}$
Variance-covariance matrices	$\begin{bmatrix}0.1907 & 0.0389\\ & 0.0113\end{bmatrix}$	$\begin{bmatrix}0.0600 & 0.0106\\ & 0.0162\end{bmatrix}$	$\begin{bmatrix}0.0573 & 0.0096\\ & 0.0126\end{bmatrix}$
Variance-covariance matrix (pooled)		$\begin{bmatrix}0.0852 & 0.0159\\ & 0.0140\end{bmatrix}$	
Principal components (pooled)	λ_1 λ_2	0.0886 0.0106	
Transformation matrix (pooled)		$\begin{bmatrix}0.9779 & 0.2088\\ -0.2088 & 0.9779\end{bmatrix}$	
Transformed means $\bar{y}$ $\bar{y}$	$\begin{bmatrix}0.1960\\0.0355\end{bmatrix}$	$\begin{bmatrix}-0.0513\\-0.0448\end{bmatrix}$	$\begin{bmatrix}-0.0535\\0.0367\end{bmatrix}$

are very close and that both are considerably larger than the Polish. In fact, *t* tests show that Swedish and Lake District means do not differ significantly, Swedish and Polish differ probably significantly ($.95 < p < .975$), and Polish and Lake District differ more significantly ($.975 < p < .99$). In respect to the width of the supporting plates relative to their length the Lake District specimens are closer to the Swedish specimens than to the Polish, even though their general aspect is more like the latter.

There seems in this case, as in *Hirnantia sagittifera,* to be evidence of variation and difference between samples from all three areas. It is interesting that, also as in *H. sagittifera,* the Polish specimens are distinguished by the thinness of their supporting plates, and it may be that we are dealing here with an environmental character affecting more than one species at a particular locality. Until better specimens are available from the Lake District for comparison of more than two characters between all three samples, the Polish and Lake District specimens are provisionally referred to *D. testudinaria.* The case for at least subspecific separation of the Polish specimens is strong, but erection of a new (presumably geographical) subspecies must await a fuller assessment of the total variation within the species.

Dalmanella mansuyi Reed (1915, p. 73, Pl. 10, figs. 13, 16—19, ?20, ?21 — non figs. [4—15, see p. 394) from the "Llandovery" of Panghsa-pyé, Burma, is very similar to *D. testudinaria* from Stawy and may prove to be identical, although Reed's figure of the lectotype brachial valve (K 11.100 here chosen, the original of Reed's fig. 13) shows the adductor scars extending further forward than in the Polish forms. A small pedicle valve of *D. mansuyi* in the Sedgwick Museum (A 3190) is hardly distinguishable from Polish specimens of the same size.

Genus *Bancroftina* Sinclair, 1946

Bancroftina? cf. *bouceki* (Havlíček, 1950)

(Pl. VII, figs. 1—4, 6—7, ?5)

1950. cf. *Dalmanella boučeki* Havlíček; V. Havlíček, Ramenonožci..., p. 29(99), Pl. IV, figs. 7—8, Text-fig. 6.

Material and dimensions (in mm.):

6 pedicle valves:	length		3.4, 5.15 (1.90), 7.2
	width		3.7, 6.50 (4.44), 9.4
Brachial valves:	length	$[n = 6]$	1.9, 4.90 (2.47), 6.0
	width	$[n = 8]$	2.7, 6.53 (5.17), 10.0

Description. — *Pedicle valve*: Outline roundedly sub-quadrangular; convex, depth averaging about 20% of length, a strong axial fold extending to margin. Cardinal area curved, steeply apsacline at hinge to nearly orthocline at umbo.

Delthyrium open; apparently a small pedicle collar. Inner walls of dental plates slope steeply down to floor of valve, splayed only slightly outwards; teeth with crural fossettes. Bases of dental plates diverging only narrowly forwards; diductor scars bounded by low ridges converging forwards from ends of dental plates (in the best preserved specimen these ridges are almost straight, slightly concave outwards, turning slightly back before dying out near mid-line — Pl. VII, fig. 7); diductors reach an average of 27% length of shell and are separated by sub-parallel longitudinal ridges from central adductor area about as wide as each diductor; adductor area not bounded anteriorly.

Brachial valve: Outline roundedly sub-quadrangular, truncated by hinge-line. Ratio of maximum width to length about 1.3. Valve slightly convex, almost flat, with a broad, shallow, expanding median sulcus extending to anterior margin. Cardinal area steeply anacline, apparently flat or only slightly curved.

Notothyrium wide, open. Cardinal process (bilobed in one specimen) highest and widest posteriorly where it fills apex of notothyrium, extending forwards as a low ridge about as far as anterior ends of ancillary struts; in three out of five good dorsal interiors a very faint median septum continues forward to separate muscle scars. Brachiophore supporting plates widely splayed, their anterior ends sloping obliquely outwards and backwards to floor of valve, their bases slightly convex forwards, their distal ends subtending at the umbo a mean angle (and variance) of 113° (50.8) in 6 valves. Ancillary struts (bevelling bases of notothyrial cavity) slope inwards from supporting plates, their bases approximately parallel in front, their distal ends subtending at the umbo a mean angle (and variance) of 54° (339.2) in 6 valves; well-developed strut pits excavated between struts and floor of valve (the moulds of these pits are prominent slender processes reaching high into the umbo). Between bases of struts and for a short distance in front of them the floor of the valve is often raised. Dental sockets make angles of 126°, 130°, 135° with each other in three specimens. Muscle impressions faintly visible on three specimens: posterior adductor wider than long, limited anteriorly by a faint ridge almost parallel to supporting plate.

Ribbing: Ribbing multicostellate, angular; faint traces of fila in interspaces. Approximate numbers of ribs around commissures of two brachial valves as follows:

length (mm.)	4.5	5.8
no. of ribs	46	44

In 2 brachial valves 10, 11 ribs per 2 mm. at 2 mm. from umbo. Details of rib patterns rarely observed: $3a^{-}1^{-}$ is present (or absent) at 2 mm. from the umbo in 2(0) brachial valves, $2b^{-}$ appears before (after) $2a^{-}1^{-}$ in 1(1) valves, $3b^{-}$ before (after) $2b^{-}$ in 2(0) valves. A few widely-spaced growth-lines may be present externally and internally on both valves (up to 3 in a valve 6 mm. long). Ribbing impressed on interiors of valves, extending inwards to central regions of brachial valves, to edges of musculature in pedicle valves.

Ontogeny. — In the smallest referred brachial valve (Pl. VII, fig. 4) the strut pits are small.

Remarks. — The terminology of Williams & Wright (1963) has been adopted for the cardinal structures of the brachial valve as there seems little doubt that the widely splayed plates are the supporting plates and the inward sloping structures are ancillary struts. The most characteristic feature of the brachial valve is the strong development of pits (strut pits) between the struts and the floor of the valve. The pedicle valve is poorly represented in the collections: two of the best specimens have broken umbones, two of the others are crushed, and one wide flat valve (Pl. VII, fig. 5) is only tentatively included. Attribution of the pedicle valve to the better known and more easily diagnostic brachial valve is aided by a pair of conjoined valves from Aber Hirnant, North Wales, where the form is very abundant.

This form is closely related to *Dalmanella bouceki* Havlíček from the $d\varepsilon_{2c}$ beds of Bohemia, with which it agrees in the general features of its brachial interior (especially the long strut pits), in having the ribbing strongly impressed on the interiors of the valves, as well as in the general shape of the valves. The Polish brachial valves differ from topotype material of *bouceki* in their smaller size and in the disposition of the lines joining the distal ends of the supporting plates and the ancillary struts. These lines subtend posterior angles of 140°, 144°, 154°, 162°, 163°, 184° [sic] in 6 Polish specimens as against 80°, 107°, 117°, 121° in 4 specimens of *bouceki*, and a rank-sum test gives $p = .005$. This difference is probably due mainly to the wider divergence of the bases of the supporting plates in *bouceki*, where the distal ends subtend at the umbo a mean angle (and variance) of 122° (18.67) in 4 specimens, and the distal ends of the ancillary struts an angle of 51° (118.67). Pedicle valves of *bouceki* have not been available for study, but to judge from Havlíček's description and figures the pedicle valve is less convex than that of the Polish form and the dental plates are more divergent. These differences would justify at least sub-specific separation, but the Polish form is not here made the basis of a new taxon because of the small number of specimens and their often fragmentary preservation (particularly of the pedicle valve), and the lack of detailed information about the ribbing; the abundant North Welsh material will have to be used to supplement the Polish in a future description.

The differences between *bouceki* and cf. *bouceki* should not obscure the fact that, despite their disparity in horizon, they are more closely related to each other than to any other species. Their generic reference, however, is uncertain. They are referred provisionally to *Bancroftina* because of the widely divergent bases of the supporting plates and the development of ancillary struts (Williams & Wright, 1963, p. 10), but the long slender strut pits are not found in any other representatives of *Bancroftina*. The homologies of these structures are far from clear, but they seem to differ from crural pits in being mainly on the inside, not the outside, of the supporting plates, and may perhaps be related to the adductor pits of the Harknessellidae. They are so distinctively developed in *bouceki* and cf. *bouceki* that when the latter is described fully the two species will probably need to be referred to a new genus.

A brachial valve attributed by Reed (1915, Pl. 10, figs. 14—15) to *Dalmanella mansuyi* may belong to *B.* ? cf. *bouceki*.

Family **Schizophoriidae** Schuchert & Le Vene, 1929

Genus *Hirnantia* Lamont, 1935

Hirnantia sagittifera (M'Coy 1851)

(Pl. XI, fig. 8; Pl. XII, figs. 1—10; Pl. XIII, figs. 1—10, Pl. XIV, figs. 1—8; Text-fig. 2 a—b; Text-fig. 3 c—d)

1851. *Orthis sagittifera* M'Coy; F .M'Coy, On some new..., p. 398.

Lectotype (here selected): Internal mould of brachial valve, A 41217, from Aber Hirnant, North Wales (M'Coy, 1852, Pl. 1H, fig. 17), figured here on Pl. XI, fig. 8.

Material and dimensions (in mm.):

34 pedicle valves:	length 0.9,	8.47	(46.38),	24.4
	width 1.3,	10.60	(64.58),	29.6
38 brachial valves:	length 1.3,	6.47	(27.15),	21.5
	width 1.6,	8.75	(47.70),	28.5

Lectotype brachial valve: length 16.3; width 15.2 (?)

Description. — Pedicle valve: Outline transversely elongated with long hinge-line; commissure margin rounded. Ratio of maximum width to length decreasing throughout development: about 1.50 at length 1 mm., about 1.28 at length 10 mm. Convexity moderate, constant during development, depth averaging a little under one-quarter of length. A median fold extends for about 10 mm. from umbo. Cardinal area high, apsacline, curved (in large forms through about 90° with radius of curvature about 1.5 mm.).

Delthyrium narrow, open, with a pedicle collar (about 1 mm. long in large forms) which extends forwards as a short tapering flange on the wall of each dental plate. Inner walls of dental plates splayed outwards and downwards from edges of delthyrium at about 45° to surface of area, becoming vertical near floor of valve and finally inclining inwards. Teeth strong, triangular, with crural fossettes. Bases of dental plates diverge forwards in five specimens longer than 5 mm. at 52°, 55°, 62°, 74°, 82°, and pass forwards into low, converging ridges circumscribing the diductor scars anterolaterally. Diductor scars bounded posterolaterally by dental plates (or in some forms by low ridges at their bases) and separated from adductors by gently diverging (sometimes sub-parallel) ridges. Adductor scars not as long as diductors, reaching about a quarter the length of valve throughout growth, bounded anteriorly by a low ridge, surface about level with that of diductors; adductor area approximately as wide as each diductor, sometimes subdivided longitudinally by two fine ridges separating an axial strip less than a third the total width. In front of the adductor scars the floor of the valve is depressed (giving a distinctive hump in internal moulds), and in some large forms a pseudospondylium is developed, the front of the muscle area being bounded by a sharp vertical wall about 1 mm. high.

Brachial valve: Outline as pedicle valve but umbo less prominent. Ratio of maximum width to length about 1.35 at length 10 mm. and fairly constant during development. Convexity moderate, least in very small forms and increasing during development; depth constantly slightly less (about 0.2 — 0.3 mm.) than that of pedicle valve, the resulting difference in convexity being appreciable in the smallest forms, negligible in the largest. A broad, shallow, anteriorly expanding median sulcus occupying approximately Bancroftian rib sectors I—III does not extend beyond about 10 mm. from umbo. Cardinal area anacline, curved (in large forms through about 90° with radius of curvature about 1.0 mm.).

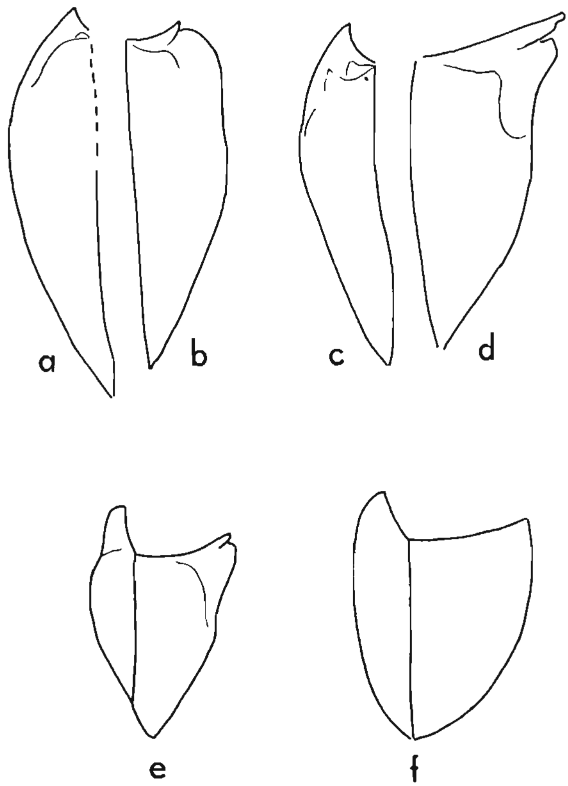

Fig. 2. — Profiles of *Hirnantia sagittifera* and *H.? kielanae*. *H. sagittifera* (M'Coy): *a* internal mould of brachial valve, based on BB 30007, *b* internal mould of pedicle valve, based on BB 29266; *H.? kielanae* n.sp.: *c* internal mould of brachial valve, based on holotype BB 29474, *d* internal mould of pedicle valve, based on BB 29445, *e* internal mould of conjoined valves, based on BB 29470, *f* exterior of conjoined valves, based on latex cast of BB 30785; × 8

Notothyrium open. Inner walls of notothyrial cavity vertical. Cardinal process short (decreasing from 15% of valve length in smallest forms to 7.5% in largest forms), narrow at floor of notothyrial cavity (like an inverted key-hole in internal moulds) but expanding ventrally so that bilobed, crenulated attachment surface often almost fills apex of cavity; cardinal process passing rapidly in front in mature individuals into a low median septum separating the adductor muscles. Dental sockets defined by fulcral plates, but in mature individuals the sockets and plates are obscured (in dorsal view of internal moulds) by very prominent massive crural pits. Brachiophores supported by long supporting plates, the bases of which diverge anteriorly in ten specimens 1.7 to 9.1 mm. long at 35°, 50° (twice), 52°, 54°, 55° (twice), 59° (twice), 60°

(mean = 52.9°), i.e. more acutely than the sides of the notothyrial cavity, giving a slightly "shouldered" appearance to internal moulds of the umbo in this size-range; in four specimens longer than 10 mm. the bases of the plates diverge at 68° (twice), 72°, 77° (mean = 71.3°). Bases of supporting plates extend usually not quite as far forwards as the maximum width of the adductor muscle scars, and are continued anteriorly into slight ridges which bound the muscle scars and run back into the anterior end of the median septum. Adductor scars ill defined, reaching about half-length of valve in small forms, about four-tenths in largest forms. Anterior and posterior scars separated approximately transversely near their maximum width by faint forwardly-concave ridges; anterior adductors larger and subcircular.

Ribbing: Ribbing fine, multicostellate; on small and medium-sized forms ribs and interspaces are subparallel-sided and rounded in section; on valves longer than about 10 mm. the ribs remain rounded in section but become much wider than the interspaces which become shallow and angular. On brachial valves up to about 10 mm. in length branching in Bancroftian sectors I—III is mainly internal, with external branches confined to distal sectors; on larger valves external branches develop also in the proximal sectors. Primary interspaces bear fila apparently throughout their length, subsequent interspaces usually develop fila later; the filum in the axial interspace of Pl. XIII, fig. 2 develops distally into an intercalated rib, but this is exceptional. Approximate numbers of ribs around the commissures of nine brachial valves as follows:

length (mm.)	1.7	2.1	2.8	4.2	4.5	5.6	7.5	10.0	21.5
no. of ribs	22	24	31	43	39	52	69	65	113(?)

Ribs hollow on both pedicle and brachial valves. A few widely-spaced concentric growth discontinuities. Ribbing impressed on interiors of both valves, often extending inwards to edges of musculature. (For further details see p. 406).

Ontogeny. — Small brachial valves are almost flat except for the median sulcus, have no median septum and only very small crural pits, and the muscle scars, although very ill defined, are proportionately longer than in larger forms. The convexity increases fairly rapidly around 3 mm. length and eventually becomes equal to that of the pedicle valve. The onset of the median septum is variable, but it is usually evident at a length of about 4 mm. The crural pits increase gradually in size (presumably by the continued forward growth of the fronts of the supporting plates) and are strongest in the largest individuals. The cardinal process decreases in relative length during growth.

In young pedicle valves the dental plates diverge widely and their inner walls are often very flatly splayed (at angles of less than 45° to area). The divergence of the dental plates (measured by the ratio of the transverse separation of their front ends to the maximum width of the pedicle valve) decreases during development from a little under 0.4 in the smallest forms to 0.25 at length 10 mm. and over. At a length of 0.9 mm. the pedicle collar is already present and the muscle scars well marked.

Variation. — The most noticeable variation is in the ratio of maximum width to length, and in the anterior divergence of the dental plates in the pedicle valve. The two characters vary apparently independently, as the partial correlation coefficient (after elimination of overall length) between transverse separation of dental plates and maximum overall width of pedicle value is 0.24, which is not significantly different from zero ($n = 31$).

Remarks. — The Polish specimens have been compared with topotype material of *H. sagittifera* from Aber Hirnant, North Wales, and also with material from Hol Beck, Westmorland. Comparison of overall

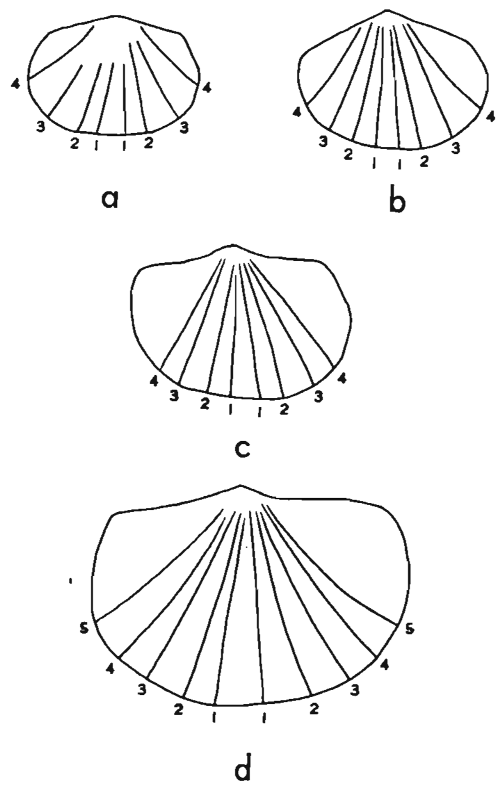

Fig. 3. — Disposition of primary ribs on brachial valves of *Hirnantia. H.? kielanae* n.sp.: *a* based on BB 29518b, *b* based on BB 30786; *H. sagittifera* (M'Coy): *c* based on BB 29668b, *d* based on BB 29245b; × 3.75.
The curvature of the dorsal umbo causes the ribs to appear to converge behind the umbo in dorso-ventral view, particularly in *H.? kielanae.*

dimensions, shape, and ribbing is made difficult by the distortion of the Welsh and Lake District specimens, but there do not appear to be any consistent differences except that the mean size of the Polish specimens is small. Internally, no differences are apparent in pedicle valves; the median septum in the brachial valve appears to be least prominent in the Polish specimens, but it is likely that the prominence of the septum in the other specimens is accentuated by cleavage. Comparisons have been made of the following measurements on brachial valves (the measurements being defined as for *Dalmanella testudinaria*):

(x_4) length of supporting plate,
(x_5) width of supporting plate,
(x_6) depth of crural pit.

Inspection of the specimens and the data suggests that Polish specimens have narrow supporting plates and deep crural pits, Welsh specimens wide supporting plates and shallow crural pits, and Lake District specimens wide supporting plates but deep crural pits. Quantitative comparison of the three samples was carried out by a trivariate analysis (Table 7). A test for equality of variance-covariance matrices shows that the samples differ in their dispersions ($.975 < p < .99$), and that this difference is due mainly to the Polish-Welsh pair ($.995 < p < .999$), the other pairs not differing significantly ($.60 < p < .70$ for Polish-Lake District, $.80 < p < .90$ for Lake District-Welsh). The principal components are the same as those recognised in *Dalmanella testudinaria*. Of them, λ_1 is clearly an index of size, λ_2 contrasts supporting plate length with crural pit depth, and λ_3 is an index of relative width of the supporting plate. Evidently both λ_2 and λ_3 are indicators of shape, despite the fact that they account for only a small proportion (very small indeed in the case of λ_3) of the total variance of the samples. A comparison of the means of the three samples along the transformed axis corresponding to λ_1 would be of little value, not only on general grounds (see p. 421) but also because the smallest Polish specimens were excluded from the Polish sample in order to minimise size-differences between samples. Comparisons of the sample means along the transformed axes corresponding to λ_2 and λ_3, however, are valid comparisons of shape, and can be made by pooling in turn the Polish-Lake District and Welsh-Lake District variance-covariance matrices (Polish-Welsh comparisons cannot be made in this manner because of the difference in dispersions). The relevant *t* tests show that for Polish-Lake District $\bar{y}_2^p - \bar{y}_2^l = 0.0707$ is not significant ($.80 < p < .90$), while $\bar{y}_3^p - \bar{y}_3^l = -0.0728$ is probably significant ($.975 < p < .99$); whereas for Welsh-Lake District $\bar{y}_2^w - \bar{y}_2^l = 0.3533$[3] is very significant ($.995 < p$), and $\bar{y}_3^w - \bar{y}_3^l = 0.0719$ is probably significant ($.975 < p < .99$). In other words, when the effects of overal size are

[3] The x_6 direction cosine of the pooled Welsh-Lake District λ_2 is negative, so that the positive difference here indicates that Welsh crural pits are shorter.

Table 7

Trivariate analysis of supporting plate length (x_4), supporting plate width (x_5), and crural pit depth (x_6) in brachial valves of *Hirnantia sagittifera* from Aber Hirnant, Hol Beck, and Stawy (measurements in mm.)

		ABER HIRNANT		
Size of sample	n		17	
Means	$\bar{x}_4$		2.7235	
	$\bar{x}_5$		0.3941	
	$\bar{x}_6$		0.9706	
Variance-covariance matrix	Σ	0.4469	0.0961	0.2051
			0.0268	0.0423
				0.2210
Principal components	λ_1		0.5875	
	λ_2		0.1013	
	λ_3		0.0059	
Transformation matrix	A	0.8488	0.1829	0.4961
		0.4802	0.1262	−0.8681
		−0.2214	0.9750	0.0193

	HOL BECK			STAWY		
n		17			17	
$\bar{x}_4$		3.0824			2.3059	
$\bar{x}_5$		0.3765			0.2118	
$\bar{x}_6$		1.5912			1.0118	
Σ	0.7878	0.1033	0.4620	0.5843	0.0524	0.3762
		0.0238	0.0657		0.0099	0.0317
			0.3191			0.2649
λ_1		1.0856			0.8378	
λ_2		0.0356			0.0165	
λ_3		0.0095			0.0048	
A	0.8464	0.1145	0.5200	0.8318	0.0738	0.5502
	−0.5293	0.0737	0.8452	0.5253	0.2159	−0.8231
	0.0585	−0.9907	0.1230	−0.1795	0.9736	0.1408

removed, Lake District specimens have deeper crural pits and probably narrower supporting plates than Welsh specimens, but probably wider supporting plates than Polish specimens. There are in fact significant differences in these characters between all three samples, least between Polish and Lake District and greatest between Polish and Welsh (where the dispersions themselves differ).

These results must be interpreted with caution. Both the Lake District and (to a lesser degree) the Welsh specimens are distorted, and although the cardinalia of *H. sagittifera* are massive, the relative dimensions of the supporting plates of individual specimens from these localities will have been altered from their original values. Only one (if possible the right) supporting plate was measured on each specimen, and the specimens seem to lie randomly with respect to the planes of deformation. It is likely therefore that in a sample of deformed specimens the mean values of the characters may not have been greatly altered, but the variances and co-variances will certainly have been altered. However, it is encouraging to observe that the greatest difference in dispersions is between the Polish and Welsh samples, and that the more deformed Lake District specimens have a dispersion matrix that does not differ significantly from either of the others. We may tentatively conclude that, although the alteration of the dispersion matrices of the Lake District and Welsh samples is likely to have affected the significance levels of the test, the overall pattern of the results may be accepted.

In respect to the characters measured, the Lake District specimens are morphologically intermediate between the Polish and Welsh specimens. It would be inappropriate in these circumstances to separate the samples taxonomically, and the variation is best considered intraspecific (or even intra-subspecific).

The reference of *Hirnantia* to the Schizophoriidae (Williams, 1951, p. 97; Cooper, 1956, p. 1005) is supported by the presence of hollow ribs. There is abundant evidence for these ribs in topotype material and specimens from the Lake District, but only one specimen (a brachial valve) from Stawy shows them. The difference may be preservational, but as hollow ribs are so readily observable in Stawy *H. ? kielanae* it seems possible that their rarity may be an original feature of the Stawy population of *H. sagittifera*. Cross sections of testate *H. sagittifera* from the Lake District have failed to show the existence of endopunctae, but this is probably a preservational feature due to the cleavage of the enclosing shales. *Hirnantia* seems to belong to the subfamily Draboviinae Havlíček (1950, p. 115), members of which were abundant in Bohemia from Llandeilian (dδ) to Ashgillian times (dξ_1).

Hirnantia? kielanae n. sp.

(Pl. VIII, figs. 1—7; Pl. IX, figs. 1—8; Pl. X, figs. 1—8; Pl. XI, figs. 1—7; Text-fig. 2 c—f; Text-fig. 3 a—b)

Holotype: Internal and external moulds of brachial valve, BB 29474 a, b, figured on Pl. VIII, figs. 5—6; Text-fig. 2c.

Type horizon and locality: Upper Ordovician, *Dalmanitina* beds, Stawy, Holy Cross Mountains, Poland.

Derivation of the name: *kielanae* — after Prof. Zofia Kielan-Jaworowska (Paleozoological Institute, Polish Academy of Sciences, Warsaw).

Diagnosis. — A species of *Hirnantia* of small size, with fine, bluntly angular, imbricate ribbing, high ventral cardinal area, widely divergent dental plates, approximately semicircular ventral muscle scars, prominent dorsal median septum, long dorsal adductor scars, massive sub--parallel supporting plates, blunt variably developed crural pits.

Material and dimensions (in mm.):

84 pedicle valves: length 1.1, 4.66 (3.64), 9.5
width 1.6, 6.20 (4.60), 11.9

173 brachial valves: length 0.8, 4.79 (3.27), 9.1
width 0.8, 6.15 (4.74), 11.6

Holotype brachial valve: length 5.7; width 7.5.

Description. — *Pedicle valve*: Umbo very prominent; commissure evenly rounded, sometimes slightly invaginated axially; ratio of maximum width to length about 1.3 at length 6 mm., higher in smaller forms; convexity greater in transverse than in longitudinal profile; in small forms transverse convexity is often greatest axially, producing a slight fold. Cardinal area very high (approximately half length of valve), very steeply apsacline to catacline, flat or only slightly curved, striated vertically and horizontally.

Table 8

Width-distributions of 87 pedicle valves & 179 brachial valves of *Hirnantia? kielanae* from Stawy

Width (lower limit of class, in mm.)	0	1	2	3	4	5	6	7	8	9	10	11	. 12
No. of pedicle valves	0	2	6	8	9	11	19	12	11	7	1	1	0
No. of brachial valves	1	6	9	9	20	31	34	26	24	11	6	2	0

Delthyrium narrow, high, open; pedicle collar up to 0.75 mm. long in largest forms, continued as a flange on inside of each dental plate near and parallel to edges of delthyrium; these flanges sometimes extend down to hinge-line. Inner edges of dental plates slope very flatly down from edges of delthyrium, becoming vertical near floor of valve; bases of dental plates diverge widely forwards, their anterior ends indenting internal moulds only slightly and bluntly. Teeth wide, triangular in section, with crural fossettes. Muscle scars outlined by a broad ridge extending approximately in a semicircle from the ends of the dental plates and reaching about two-fifths of the length of valve, sometimes indented axially. Combined adductor area less wide than each diductor and defined by a pair of thin sub-parallel ridges. Walls and floor of delthyrial cavity often much thickened by deposition of shell material within region bounded by muscle ridge.

Brachial valve: Outline subcircular, commissure evenly rounded; ratio of maximum width to length averaging 1.3, constant during development. Less convex than pedicle valve, depth averaging 20% of length. A shallow, often angular, median sulcus becoming inconspicuous before anterior margin in largest forms. Cardinal area high, slightly anacline (almost orthocline), curved (in large forms through about 90° with radius of curvature about 0.75 mm.), faintly striated parallel to hinge.

Notothyrium open. Inner walls of notothyrial cavity approximately vertical. Attachment area of cardinal process bilobed and crenulated, extending over half-way down notothyrium, sometimes to hinge-line; cardinal process narrowest at floor of valve, expanding anteriorly, sloping usually steeply down in front and passing into median septum which in large forms becomes a strong, broad ridge separating adductor scars. Dental sockets nearly parallel to hinge, thin proximally, deepening suddenly distally into prominent pits which project above hinge-line. Sockets defined by fulcral plates whose bases slope up and out to hinge-line. Brachiophores with short, wide supporting plates (their inner walls continuations of inner walls of notothyrial cavity) which continue into ridges around muscle scars; bases of supporting plates anteriorly diverging in small forms, subparallel in large forms. Crural pits usually blunt, sometimes obscuring sockets in dorsal view of internal moulds; no crural pits in smallest forms. Adductor scars extending about 60% of length, usually strongly outlined particularly posteriorly, separated by median septum or ridge; ridges between anterior and posterior scars situated near maximum width of scars and sloping obliquely forwards and outwards; anterior scars about twice as long as posterior, sometimes pointed in front.

Ribbing: Ribbing fine, multicostellate (very rarely, by strengthening of primaries, fascicostellate), of small amplitude, bluntly angular in section. On brachial valves branching in Bancroftian sectors I—III is mainly internal. A strong axial interspace in brachial valve, becoming inconspicuous before margin in largest forms. Rare traces of fila in interspaces (more commonly observed on pedicle valves). Approximate numbers of ribs around the commissures of ten brachial valves as follows:

length (mm.)	1.75	2.8	3.1	3.4	4.0	5.3	5.6	6.5	6.8	6.9
no. of ribs	23(?)	38	34	30	33	44	60	56	58	60

On brachial valves rib 2 and more distal ribs (both primary and subsequent) are hollow, with large exopunctae projecting obliquely and almost tangentially backwards into the centres of the ribs at growth-discontinuities; such large central exopunctae do not seem to occur on the proximal ribs of brachial valves or on any of the ribs of pedicle valves, these bearing only small exopunctae. Closely spaced growth-discontinuities produce a fine imbrication of the surface. Ribbing impressed for a short distance inwards from margins of interiors of both valves, and faint traces often extend to edges of musculature. (For further details see p. 406).

Ontogeny. — The smallest attributed brachial valve is poorly preserved but good valves are available from 1.0 mm. onwards. At the 1 mm. stage the valve is convex and deep, particularly in the region of the notothyrial cavity, there is a strong median sulcus and a prominent cardinal process; but the crural pits and median septum are either absent or represented only by the merest traces, and musculature cannot be made out. At 1.7 mm. crural pits may be well developed, the cardinal process is continued forwards into a short tapering median septum, and the musculature is evident. Crural pits increase in prominence with size, although their development is variable; in forms larger than about 5 mm. they are usually well developed. The median septum (which first appears in a specimen 1.1 mm. long although its onset is variable) is initially thin and distinct, but rapidly widens and lengthens to become prominent even by a length of 2.5 mm., while in forms larger than about 5 mm. the whole region between the muscle scars becomes much thickened and raised into a long and prominent ridge.

Small pedicle valves do not differ significantly from larger forms except in the axial profile of internal moulds, which is not convex but sinuous — almost straight but indented by a ridge around the muscle scar (which is strong even in the smallest forms) and slightly concave near the anterior margin. An overall convexity of this profile is not attained until a length of about 5 mm.

Variation. — The most noticeable variation in brachial valves concerns the development of the crural pits. When these are little developed the bases of the supporting plates diverge anteriorly and the notothyrial region appears triangular and prominent. This condition is characteristic of small and medium-sized forms but is also occasionally found in quite large forms. On the other hand, when the crural pits are well developed, as in most large forms, the bases of the supporting plates become nearly parallel in front. Another indication of this change is that the transverse separation of the front ends of the supporting plates, which increases with valve length up to about a valve length of 6 mm., remains stationary (though variable) at about 1.5 mm. thereafter. The crural pits themselves are sometimes more strongly developed on one than the other side of a specimen. Large individuals may show great deposition of shell material around the median ridge and behind the cardinal process, so as nearly to fill the notothyrial cavity, which is then defined only by a thin crack down each side.

The pedicle valve shows less apparent variation, apart from the usual variation in dimensions. And even this variation is greater than the inherent variability of the species, because the errors in measuring pedicle valves are unusually high: the tips of the umbones of internal moulds are often missing; the muscle boundary is broad and imprecise; small valves, particularly, are often crushed from side to side. Nevertheless the variance of pedicle valves is not significantly greater than that of brachial valves.

In large pedicle valves there may be great deposition of shell material within the delthyrial chamber. In one large pedicle valve (Pl. X, fig. 1) the inner parts of the diductor scars are raised and continued forwards and obliquely outwards into a pair of short rod-like processes projecting freely into the interior of the valve from just behind the ridge outlining the muscles. There is also a median ridge behind the pedicle collar, flanked by narrow elongated scars that may represent adjustors.

Remarks. — This elegant little species, the most abundant in the fauna, has a combination of features which are individually reminiscent of a number of unrelated orthoid and dalmanelloid brachiopods. The imbricate surface suggests comparison with glyptorthids, among which *Ptychopleurella,* although more coarsely ribbed, has a comparable profile and a dorsal sulcus; but the internal features of the brachial valve — strong supporting plates and the absence of a notothyrial platform — preclude close affinity with the glyptorthids. The confined musculature of the pedicle valve is similar to that of *Scaphorthis* and *Phragmorthis,* but in both these genera there is a cruralium and a very weak cardinal process.

The presence of hollow ribs suggests affinity with (among other families) the schizophoriids. Sections of testate specimens from the Lake District do not show endopunctae but this may be a preservational feature not necessarily precluding reference to the dalmanelloids. There are, despite the great differences in profile and size, a number of similarities to *Hirnantia sagittifera*: the ventral musculature and pedicle collar, the median septum and well developed supporting plates, the lack of a notothyrial platform, the general disposition of the ribs (see below). Indeed, at the 2—3 mm. stage of development it is difficult to distinguish *kielanae* brachial valves from those of *H. sagittifera* except on their ribbing and the stronger cardinal process and median septum. The brachial valve of *kielanae* differs in the earlier appearance during development of the median septum and its greater prominence in adults, the variable development of the crural pits, the more massive and less divergent supporting plates, the longer muscle scars, and the greater convexity in early stages of development. The pedicle valve differs in its high area, acute delthyrium, more oblique dental plates, and more concentrated musculature. Externally *kielanae* differs in its profile, smaller size, more marked dorsal sulcus, the form and detailed disposition of the ribs, the closer imbrication. The differences between the two species are striking, but several of them are probably dependent on the difference in profile of the pedicle valve. The similarities appear to be more fundamental, especially as they include features which exclude *kielanae* from other genera, and the species is provisionally referred to *Hirnantia*. Confirmatory evidence is needed, though, on whether or not the shell is punctate.

H.? kielanae may be conspecific with *Scenidium? medlicotti* Reed (1915, p. 75, Pl. 10, figs. 24—25, ?26) from the "Llandovery" of Panghsa--pyé, Burma, of which the internal mould of a pedicle valve K 11.97, the original, of Reed's fig. 25, is here selected as lectotype. Reed did not describe the interior of the brachial valve of his species, but it is most likely that the internal mould of a brachial valve from the same beds identified by him as *Orthis* aff. *canaliculata* Lindström (1915, p. 75, Pl. 10, fig. 23) should be associated with *S.? medlicotti*. The type material of these forms has not been available for study, but in the Sedgwick Museum there is an internal mould (on A 3195) and a fragmentary external mould (on A 3191), both of pedicle valves and apparently referable to *S.? medlicotti*, which are very similar to pedicle valves of *H.? kielanae*, and Reed's descriptions and figures of both pedicle and brachial valves suggest that he was dealing with a form very like that from Stawy. However, as the Burmese species is not well known whereas the Polish material is extremely abundant and can be described in detail, it is considered best that the latter should form the basis of a new species.

Table 9

A & B — Distribution of subsequent ribs at 2 mm. stage in 15 brachial valves each of (a) *Hirnantia sagittifera* and (b) *H.? kielanae*, showing for each rib (A) the number of specimens in which the rib is developed on one or both sides : neither side, and (B) the number of specimens in which the rib is symmetrically developed (present or absent on both sides) : asymmetrically developed (present on one side but absent on the other)

		1a⁻	1a°	2a⁻	2a°	3a⁻1⁻	3a⁻	3b⁻	3a°	4a⁻	4a°
A	(a)	8 : 7	2 : 13	12 : 3	2 : 13	5 : 9	14 : 0	2 : 12	5 : 9	12 : 0	3 : 5
	(b)	13 : 0	0 : 13	15 : 0	1 : 12	9 : 3	14 : 0	2 : 8	0 : 9	12 : 0	3 : 1
B	(a)	10 : 5	13 : 2	12 : 3	15 : 0	12 : 2	14 : 0	12 : 2	10 : 4	4 : 2	6 : 0
	(b)	8 : 4	13 : 0	11 : 2	12 : 1	5 : 3	9 : 0	8 : 0	9 : 0	4 : 0	1 : 3

Ribbing of H. sagittifera and *H.? kielanae*: Detailed comparison of the ribbing is handicapped by the relatively small numbers of *sagittifera* and by the often poor preservation of the ribbing of *kielanae* which makes difficult an objective recognition of the primary ribs, particularly the distal primaries (there is usually little doubt about 1, 2 and 3). As regards the form of the ribbing, the ribs and interspaces of *kielanae* are of small amplitude and bluntly angular in section, while those of *sagittifera* at the same valve length are of greater amplitude, parallel-sided and round-topped; furthermore, the ribs in large specimens of *sagittifera* (admittedly larger than any specimens of *kielanae*) change character and become much wider than the interspaces. The ribbing of *kielanae* (with 10, 11, and 12 ribs per 2 mm. at 2 mm. from the umbo in 3, 3, and 4 brachial valves) is finer than that of *sagittifera* (with 8, 9, and 10 ribs in 2, 2, and 3 brachial valves) at least in the early stages, although the numbers of ribs around the commissures appear to be the same.

The disposition of ribs is broadly similar in the two species (Text-fig. 3). In the brachial valves of both, primaries 1 to 4 are weakly curved and narrowly divergent, slightly more curved and divergent in *kielanae* than in *sagittifera*: at the 4 mm. stage the ends of the primaries 4 subtend at the umbo angles of 77°, 79°, and 96° in three specimens of *kielanae*, and of 64°, 67°, and 69° in three specimens of *sagittifera*. At the 2 mm. stage the pattern of ribs present is also similar (Table 9A), the only significant difference being the earlier appearance of $1a^-$ in *kielanae* ($p = .005$) There is also evidence that $1a^-1^-$ appears earlier in *kielanae*, where it is present at the 4 mm. stage on one or both sides in 8 out of 10 specimens, compared with 1 out of 7 for *sagittifera* ($p = .013$). This accelerated internal branching in sector I may be due in part to the stronger development of the dorsal sulcus in *kielanae*. The general pattern of branching (mainly internal on brachial valves in sectors I—III) and the degree of asymmetry (Table 9B) are also similar in the two species. $2b^-$ is inserted before, after, at the same time as $2a^-1^-$ in 4, 1, 0 right halves (of external moulds) and 1, 2, 1 left halves of *sagittifera*, and in 2, 9, 0 right halves and 2, 7, 2 left halves of *kielanae*; for right halves the probability is .036, but this cannot be considered significant, especially as the left halves do not support a null hypothesis of earlier insertion of $2a^-1^-$ in *kielanae*.

Superfamily **Strophomenacea** King, 1846
Family **Strophomenidae** King, 1846
Genus *Platymena* Cooper, 1956
Platymena? polonica n. sp.

(Pl. XV, figs. 1—4; Pl. XVI, figs. 1—5)

Holotype: Internal and external moulds of brachial valve, BB 30009 a, b, figured on Pl. XV, fig. 2.

Type horizon and locality: Upper Ordovician, *Dalmanitina* beds; Stawy, Holy Cross Mountains, Poland.

Derivation of the name: *polonica* — occurring in Poland.

Diagnosis. — A species of *Platymena* distinguished by transversely elongated outline, the presence of dental plates, and the absence of a thickened border around the visceral regions of the valves.

Material and dimensions (in mm.):

10 pedicle valves:	length	2.0,	5.88	(7.30),	12.1
	width	2.8,	9.69	(23.84),	18.4
14 brachial valves:	length	1.6,	6.28	(5.93),	9.9
	width	2.2,	10.07	(18.28),	18.0

Holotype brachial valve: length 7.0; width 10.1

Description. — *Pedicle valve:* Outline usually strongly elongated transversely (ratio of maximum width to length about 1.6), postero-lateral angles approximately right-angled (sometimes slightly acute or obtuse), non-mucronate; commissure margin evenly rounded, rarely sub-quadrate. Valve probably very slightly convex. Cardinal area anacline, curved near umbo, horizontally striated.

Pseudodeltidium convex, extending apparently half-way down delthyrium axially, to base laterally. Strong pedicle foramen. Dental plates thin, sloping steeply outwards (or vertical) from edges of delthyrium to floor of valve, their bases diverging anteriorly at about 115°. Muscle scars rarely visible, small, extending laterally only slightly beyond ends of dental plates, ill defined anteriorly; diductors sub-triangular, their inner parts deepened, separated usually by longitudinal ridges from parallel-sided raised adductor area less wide (from one-third to two--thirds) than each diductor; in the best preserved specimen (Pl. XVI, fig. 5) the muscle scar is three-quarters as long as wide and extends about one-third length of valve, the diductors are flabellate. Pseudopunctae as in brachial valve.

Brachial valve: Outline as of pedicle valve. Valve apparently plane. Cardinal area steeply anacline, plane.

Chilidium filling notothyrium, convex, medially grooved (other details not visible). Cardinal process lobes small, close together in notothyrium, directed antero-ventrally, their bases transversely elliptical to circular in section, usually joined at floor of valve by shell material that continues into socket plates. A deep pit medially in front of cardinal process lobes, directed postero-dorsally under bases of lobes (and often obscuring them in dorsal view of internal moulds). Sockets conical, short, not reaching nearer than about their own length to edges of notothyrium, their posterior edges close to hinge-line; socket plates straight or slightly concave posteriorly, their bases diverging forwards in three specimens at 113°, 115°, 116°; posterior faces of socket plates occasionally with traces of crenulations; in front of and within socket plates faint traces occasionally visible of paired low broad ridges, highest distally where they end abruptly (in one specimen projecting freely forwards into interior a short distance) almost in exsagittal line with distal ends of socket plates, and diverging forwards less widely (at about 90°) than socket plates. Muscle scars not visible. Pseudopunctae small, arranged apparently along interspaces (at about 5 per mm.) to produce a uniform distribution extending over whole valve in small forms but exclusive of cardinal regions in larger forms.

Ribbing: Ribbing fine, multicostellate (rarely unequally parvicostellate); fine concentric growth-lines often as strong or stronger than ribbing, particularly apically; both valves occasionally stepped down (inwards) distally at some growth-lines. Approximate numbers of ribs around the commissures of four brachial valves as follows:

length (mm.)	3.2	5.9	6.0	7.6
no. of ribs	51	77	75	119

At 2 mm. from the umbo 13, 14 ribs were counted in 2 mm. on 2, 2 brachial valves. Ribbing and growth-lines impressed on interiors of both valves almost to umbones.

Variation. — The outlines of two brachial valves are anteriorly elongated, but as both valves are much wrinkled this may be due to (presumably post-mortem) distortion. Another brachial valve is geniculated ventrally through about 1 mm. along a growth-line, becoming flat again distally. The ribbing is unusually strongly impressed on two internal moulds of pedicle valves, and in one of these the cardinal area is almost catacline. The moulds of the umbonal chambers are very fragile and easily broken, in which condition there appear to be no discrete dental plates (Pl. XV, fig. 1); but this is a purely preservational feature, in contrast to the partial obliteration of the umbonal chambers by deposition of calcite in *Eostropheodonta hirnantensis.*

Remarks. — This species agrees with *Platymena* Cooper in the flatness of its valves, the small size of the muscle area, and the delicacy of its cardinalia and ribbing, but it differs from *P. plana* Cooper (1956, p. 880 — the only species of which the interior is known) not only in outline but in possessing dental plates and in lacking a thickened border around the visceral regions of the valves. There is a general similarity in outline and profile to the monotypic *Foliomena* Havlíček (1952, p. 413), but *F. folium* (Barrande) lacks radial ribs and dental plates and has long socket plates and a pair of strong sub-median septa in the brachial valve. On the other hand our species shows some similarities to *Eostropheodonta,* but in both *E. hirnantensis* and the Llandovery *E. mullochensis* (Reed) the delthyrium is open, and although a pseudodeltidium is developed in other (later) stropheodontids it does not occur together with dental plates. It seems best to refer the species provisionally to *Platymena.*

The Polish species is very similar in most features to *Platymena? mcmahoni* (Reed, 1915, p. 76, Pl. 11, figs. 1—9) from the "Llandovery" of

Panghsa-pyé, Burma, of which the internal and external moulds of a brachial valve K 11.102 (the originals of Reed's figs. 1—2) are hereby selected as lectotype. The original material of Reed's species has not been available for study, but there is a slab in the Sedgwick Museum (A 3191) with several fragments of both valves labelled by Reed and agreeing with his description although showing no traces of denticulation on the hinge-line (cf. 1915, p. 76). The Burmese form is much larger than the Polish (Reed's quoted dimensions are length 18 mm., width 26 mm., and the Sedgwick Museum fragments are about this size), and differs in having more robust cardinalia, stronger oblique ridges in the brachial valve and a median septum in the pedicle valve. These morphological differences may, however, be dependent on size, and size difference by itself is a doubtfully valid criterion for distinguishing allopatric fossil populations (see p. 421). In the absence of smaller forms from Burma with which comparisons can be made, the Polish material is referred to a new species, but there is no doubt that *polonica* and *mcmahoni* are very closely related, if not conspecific.

Family **Stropheodontidae** Caster, 1939

Genus *Eostropheodonta* Bancroft, 1949

Eostropheodonta hirnantensis (M'Coy 1851)

(Pl. XVII, figs. 1—6; Pl. XVIII, figs. 1—7; Pl. XIX, figs. 1—5)

1851. *Orthis Hirnantensis* M'Coy; F. M'Coy, On some new..., p. 395.

Lectotype (here selected): Internal mould of pedicle valve, A 28831, from Aber Hirnant, North Wales (M'Coy, 1852, Pl. 1H, fig. 11c), figured here on Pl. XIX, fig. 1.

Material and dimensions (in mm.):

20 pedicle valves:	length	2.6,	10.76	(25.06),	21.3
	width	3.7,	13.82	(41.85),	24.2
9 brachial valves:	length	1,8,	10.39	(39.56),	20.0
	width	2.0,	14.51	(89.71),	27.6

Lectotype pedicle valve: length 20.5 (?); width 25.7

Description. — *Pedicle valve*: Commissure outline evenly rounded, sides straight or slightly convex, hinge usually slightly mucronate; ratio of maximum width (excluding ears) to length about 1.35. Valve slightly convex with a median fold near umbo; convexity greatest near umbo. Cardinal area orthocline to gently anacline, flat or slightly curved (at apex). horizontally striated.

Delthyrium wide, open, with small apical pedicle collar. Inner walls of dental plates vertical, their bases diverging forwards in four specimens longer than 10 mm. at 75°, 80°, 90°, 96°. Teeth sometimes separated from hinge-line by thin oblique accessory sockets; inner walls of dental plates and posterior faces of teeth with denticles (up to nine in number but only about six commonly visible). Muscle scars cannot be distinguished.

Pseudopunctae large, fairly evenly spaced (about 2 per mm.) along distal parts (about half-lengths) of interspaces, sometimes forming rough concentric pattern.

Brachial valve: Outline as pedicle valve. Valve nearly plane, slightly concave near hinge, with a very slight median sulcus extending about 5 mm. from umbo. Cardinal area steeply anacline, flat, horizontally striated.

Chilidium filling notothyrium, convex, with a median groove and on each side (two?) flanking radiating grooves. Cardinal process lobes directed ventrally, their bases elliptical with axes diverging forwards at 60° to 90° and sometimes joined posteriorly. Dental sockets conical, reaching inwards about to edges of notothyrium, their posterior edges close and parallel to hinge-line, defined anteriorly by straight or posteriorly concave socket plates, the bases of which diverge forwards in three specimens longer than 10 mm. at 97°, 99°, 101°; posterior faces of socket plates with apparently up to about six denticles (posterior faces of sockets themselves cannot be seen). A depression on floor of valve between anterior ends of cardinal process lobes. Adductor scars (visible on two large specimens) antero-proximally elongated, well defined postero-proximally where their somewhat scallopped edges define with the socket plates and notothyrium a diamond-shaped raised area; separated axially by a broad ridge about as long as notothyrium; ill defined antero--distally. Pseudopunctae as in pedicle valve.

Ribbing: Ribbing strong, close, parallel-sided, rounded in section, unequally parvicostellate (becoming evenly multicostellate in largest forms); a strong primary rib axially on small pedicle valves; subsequent ribs arising apparently by intercalation in interspaces in both valves. Fine, close growth-lines and occasional growth-irregularities. Approximate numbers of ribs around the commissures of four pedicle valves as follows:

length (mm.)	4.8	7.4	10.7	13.0
no. of ribs	48	57	106	78

At 2 mm. from umbo, 7, 8, 9, 10 ribs were counted in 2 mm. on 2, 2, 2, 1 pedicle valves. Ribbing impressed on interiors of both valves, traces extending to umbo in pedicle valve and to edges of musculature in brachial valve.

Ontogeny. — Several small pedicle valves (Pl. XIX, figs. 2—4) are available and show a rather acute delthyrium and prominent primary ribs (especially the median rib), but do not otherwise differ greatly from older forms. The smallest internal mould of a brachial valve (Pl. XIX, fig. 5) shows anteriorly a strong, septum-like, median rib-interspace, passing rapidly behind into a deep, narrow, median depression on the floor of the valve extending from the notothyrium one-third of the valve--length, widest and deepest at its own mid-length and tapering towards both ends. The external mould of another small brachial valve shows that the flanking grooves on the chilidium do not reach to its apex.

Variation. — Variation in the ratio of length to width causes considerable differences in shape: one small, transversely elongated brachial valve has unusually oblique cardinalia (Pl. XVIII, fig. 4). The moulds of the umbonal chambers vary in prominence; accessory sockets may or may not occur.

Remarks. — So far as it is possible to judge by comparison with crushed topotype material, the Polish specimens are identical with M'Coy's species. The lectotype, a large distorted internal mould of a pedicle valve, is illustrated (Pl. XIX, fig. 1).

Williams (1951, p. 122; 1953, p. 8) has called the tooth-structures of early stropheodontids "denticular plates", which form with the dental plates composite "hollow cones". This usage is not followed here as it obscures the apparently complete homology of these structures with true teeth and dental plates. Apart from denticulation, an unusual feature of the interior of the pedicle valve is the prominence of the accessory sockets; these probably articulated with ridges on the hinge-sides of the dental sockets, although such ridges have not been observed on brachial valves.

The method of rib multiplication by intercalation in the interspaces in both valves, which Williams (1953, p. 7) considers characteristic of stropheodontids, is such that ribs and interspaces of opposite valves do not correspond and the commissures cannot interlock.

?Superfamily **Athyridacea** M'Coy, 1844
?Family **Meristellidae** Hall & Clarke, 1895
Genus *Plectothyrella* nov.

Type species: Plectothyrella platystrophoides n. sp.

Derivation of the name: Plectothyrella — Gr. πλεκω (I plait) — referring to the external ribbing which is a feature distinguishing the genus from *Meristina* and *Cryptothyrella.*

Diagnosis. — A genus of (?) Meristellidae with fold and sulcus, strong ribbing, wide dental plates with adjustor scars impressed on their anterior faces, a deep geniculated depression in front of ventral platform, dorsal median septum not supporting the divided hinge-plate. Brachidium unknown.

Plectothyrella platystrophoides n. sp.
(Pl. XX, figs. 1—5; Pl. XXI, figs. 1—10)

Holotype: Internal mould and portion of external mould of conjoined valves, A 52001, figured on Pl. XX, fig. 3.

Type horizon and locality: Ashgill Shales (Upper Ordovician), Hol Beck, 850 m. NE of High Skelghyll farm, near Ambleside, Westmorland, England.

Derivation of the name: platystrophoides — recalling *Platystrophia.*

Diagnosis. — *P. platystrophoides* being the only known species, its diagnosis is provisionally as for the genus.

Material and dimensions (in mm.):

12 Hol Beck pedicle valves: length (to front of ventral platform) 2.5, 5.79 (4.02), 10.0

Holotype conjoined valves: length (to front of ventral platform) 6.5; width 16.4

Stawy conjoined valves, BB 30019: length (total) 16.5; width (est.) 17.4

Description. — *Exterior*: Both valves very convex proximally, pedicle valve apparently more so than brachial valve; distal parts of valves much less convex and apparently thin-shelled (but only rarely preserved). A broad, anteriorly expanding, flat-topped fold on brachial valve (commencing about 3 mm. from umbo and replacing a faint apical sulcus), and corresponding sulcus on pedicle valve. Ribbing strong, rounded; 3 ribs in sulcus, 4 on fold (the two inner ones branching off internally at about 5 mm. from umbo), up to 10 on each side laterally; median interspace on brachial valve with strong filum. Surface variably imbricate, particularly in distal parts of valves. Ribbing strongly impressed on interiors of valves.

Pedicle valve: Umbo high; interareas not clearly delimited, curved. Delthyrium open; pedicle chamber concave in longitudinal section, rising anteriorly to sinuous bounding ridge, in front of which floor of valve drops vertically (dorso-ventrally) forming a ventral platform, anteriorly convex in longitudinal profile, widening anteriorly and bearing a low median ridge or septum; platform bounded in front by a sharp, approximately right-angled, deeply impressed geniculation; in front of geniculation median part of valve floor runs more or less horizontally to anterior margin of valve and is flanked laterally by deep grooves (corresponding to ribs bounding external sulcus).

Teeth strong, curved; dental plates long and prominent in small forms, thickened in larger forms, widening anteriorly, their front faces forming a pair of ridge-bounded, approximately oval adjustor scars of variable width flanking posterior part of ventral platform. Other muscle scars obscure; faint chevron-shaped ridges on median part of valve in front of geniculation probably represent diductors; adductors probably occupied ventral platform. Coarse genital punctations antero-lateral to adjustors.

Brachial valve: Interareas very small. Notothyrium open; notothyrial walls massive, their posterior faces concave and facing obliquely inwards and backwards to form a divided hinge-plate, their anterior faces often slightly notched by crural pits. Notothyrial chamber narrow, its opening constricted by hinge-plate, usually with a low median ridge; inner parts of hinge-plate continued anteriorly as crural bases. Thin, tapering dental sockets outside notothyrial walls, reaching only a short distance towards umbo. A median septum begins about twice the length of notothyrial chamber from umbo and extends (as the accentuated median rib-interspace) to anterior margin of valve. A pair of short, broad, postero-laterally concave grooves usually distinguishable, branching forwards and outwards from posterior end of septum, may divide anterior and posterior adductors, but muscle scars not distinguishable with certainty. Coarse genital punctations antero-lateral to cardinalia, with short sinuses running postero-distally towards hinge-line.

Ontogeny. — In pedicle valves during growth there is an increase in the length of the ventral platform and in the prominence of the geniculation: in the smallest available form the platform is barely distinguishable, while in the largest it is about twice as long as the pedicle chamber. The dental plates and umbonal chambers, which are well marked in young forms, become almost obliterated in large forms by the deposition of adventitious tissue in the hinge region. In small brachial valves the dental sockets are long and the notothyrial chamber is broad, anteriorly expanding and without a median ridge; in larger forms the sockets are shorter, and the notothyrial chamber becomes much restricted by widening of the walls and may be reduced to a thin, parallel-sided cleft in the massive hinge-plate.

Remarks. — *Plectothyrella platystrophoides* is rare at Stawy and the description is based largely on specimens from the Ashgill Shales of the English Lake District. These specimens, although distorted by cleavage, are well preserved in the thick proximal parts of the valves, but the thinner distal parts are poorly preserved and the complete outline is rarely observable. However, the external mould of a pair of conjoined valves from Stawy (Pl. XX, fig. 5) shows the outline to be anteriorly elongated. The overall dimensions of Hol Beck specimens cannot be measured, but for comparative purposes the length from the umbo of the pedicle valve to the front of the ventral platform (about one-third of the total length of the valve) is quoted. A point of interest is the high proportion of conjoined valves.

The affinities of this species are difficult to evaluate, especially as nothing is known about the disposition — or even the existence — of spires in the brachial valve. Discounting the strong superficial resemblance to *Platystrophia* (under which name the British specimens have probably been earlier recorded), we may remark similarities to atrypoid, meristelloid and rhynchonelloid brachiopods. The presence of ribbing and of a fold and sulcus recall *Plectatrypa*[4], although the ribbing is rather coarser than is common in *Plectatrypa* and, possibly as a result of this, the fold and sulcus are more clearly delimited (with no ribs on

[4] The current concept of this genus is based on *P. imbricata* of Davidson (1867, p. 135, Pl. 15, figs. 3—8) which differs from Sowerby's original material in being more strongly imbricate.

the flanks of the fold); furthermore, *Plectatrypa* typically has a deltidium and an apical pedicle foramen, not an open delthyrium. The internal features of topotype material of *P. imbricata* have not been described, but if we may judge from the Gotland specimens figured by Schuchert & Cooper (1930, p. 279, Pl. 2, figs. 20—21) the ventral muscle scars are "small and confined to the umbonal region", while the dorsal interior lacks a median septum. *P. marginalis* (Dalman) resembles our species in having a divided hinge-plate with a median ridge in the notothyrial chamber and well marked adjustors in the pedicle valve; but there is no ventral platform and the ventral musculature is very compact, with diductors immediately in front of the adjustors, and adductors forming an oval depression surrounded by adjustors and diductors (Poulsen, 1943, Text-figs. 18-I, 20).

The strong, sparse ribbing and clear-cut fold and sulcus are also suggestive of rhynchonelloids, and although most Palaeozoic rhynchonelloids have a cruralium in the brachial valve there are some without. Among these is *Drepanorhyncha* Cooper (1956, p. 627) which has a divided hinge-plate with concave faces, an open delthyrium, and long sub-parallel dental plates defining a muscle space subdivided by a median septum. A similar ventral interior is found in *Orthorhynchuloides* Williams (1962, p. 240) which has, however, a cruralium. Neither of these genera, though, has a ventral platform and geniculated depression.

Among meristellids, *Meristina crassa* (J. de C. Sowerby) and *M. crassa incipiens* Williams (1951, p. 111, Pl. 6, figs. 14—20, text-figs. 15—16), which have recently been referred by Boucot, Johnson & Staton (1964, p. 817) to *Cryptothyrella* Cooper, are very similar to our species in several respects. They have an open delthyrium, a ventral platform, a geniculated depression and an anteriorly placed muscle scar in the pedicle valve, and a median septum or myophragm in the brachial valve; but they lack external ribbing, as does the type species *M. maria* Hall. The adjustor scars flanking the ventral platform in our species do not seem to occur in *Meristina,* where the dental plates are thinner and run close to the ventral platform in positions that correspond to the inner margins of the adjustors, although Hall & Clarke (1894, Pl. 42, figs. 7, 32) illustrated what may be adjustors in *Merista* and *Pentagonia.*

On balance, the closest resemblances of the species, particularly its ventral interior, seem to be with meristellids. The strong external ribbing necessitates the erection of a new genus.

GENERAL DISCUSSION

Numbers of specimens and conditions of accumulation

Table 10 is based on a count of all recognisable internal moulds in the collection from Stawy, and excludes (except in the case of conjoined valves) specimens preserved only as external moulds. It is not thought that this procedure, which is necessary in order to avoid duplication in the counting of specimens, introduces bias into the counts, but bias may be present because of other factors. Identification of poorly preserved specimens involves the possibility of error: it is for instance difficult to

Table 10

Numbers of specimens from Stawy

	Brachial	Pedicle	Conjoined	In-determinate	Total
Lingulella sp.	2	3	0	10	15
Orbiculoidea radiata	24	7	0	2	33
Philhedra? stawyensis	91	0*	0	0	182*
Dalmanella testudinaria	99	99	1	0	200
Bancroftina? cf. *bouceki*	10	8**	0	0	18
Hirnantia sagittifera	76	78	1	1	157
H.? kielanae	375	291	5	0	676
Platymena? polonica	35	13	0	6	54
Eostropheodonta hirnantensis	13	25	0	6	44
Plectothyrella platystrophoides	1	0	3	1	8

* The pedicle valve of this species is probably uncalcified and the figure given in the totals column has been doubled for comparison with totals of other species.

** Includes one valve only tentatively referred to the species.

distinguish at certain stages of growth between pedicle valves of *Hirnantia sagittifera* and *Dalmanella testudinaria*, and (particularly in small forms) between brachial valves of *H. sagittifera* and *H.? kielanae*. Some specimens may be overlooked and not counted: the ribbing of *Plectothyrella platystrophoides* is very coarse and distinctive and it is unlikely that any fragments would be missed, whereas *Philhedra? stawyensis*, which either takes up the ribbing of its host or has no ornament, could easily be overlooked. The method of collection, by the breaking up in the laboratory of fairly small blocks of siltstone, is likely to produce more small specimens than large and so to be biased against large species. The diagnostic features of small species are more likely to be visible in fragmented specimens than are those of large species. Despite these reservations it is likely that the table gives a fairly true picture of the relative abundance of the different valves.

Hirnantia? kielanae is by far the commonest species at Stawy, over three times as abundant as the next commonest, *Dalmanella testudinaria* and *Philhedra? stawyensis*. The numbers of pedicle and brachial valves are sensibly equal in *D. testudinaria*, *Bancroftina?* cf. *bouceki* and *H. sagittifera*, doubtfully different in *Eostropheodonta hirnantensis* ($p = .036$), and significantly different in *Orbiculoidea radiata* ($p = .002$), *H.? kielanae* ($p < .001$) and *Platymena? polonica* ($p < .003$). In both *P.? polonica* and *E. hirnantensis* there is a high proportion of poorly preserved or fragmentary valves that are indeterminate. There is no reason to believe that these are not equally divided between pedicle and brachial valves, in which case the pattern of significance is not changed. If, however, all the indeterminate *E. hirnantensis* were brachial the difference in valve numbers would no longer be significant, whereas if all the indeterminate *P.? polonica* were pedicle the difference in numbers would still probably be significant ($p = .020$).

These differences in valve numbers suggest that *O. radiata, H.? kielanae, P.? polonica* and perhaps *E. hirnantensis* have been affected by some selective process such as winnowing or drifting. It is not unexpected that the two valves of *H.? kielanae* should be differently affected by currents as they differ greatly in shape and presumably in buoyancy, but there are no obvious differences between the pedicle and brachial valves of the other species, particularly *E. hirnantensis* and *P.? polonica.* The selective process in *H.? kielanae* seems to have been independent of size, for the means and variances of width-distributions in samples of pedicle and brachial valves of this species do not differ significantly, and a chi-square homogeneity test shows that the distributions themselves (Table 8) do not differ ($.10 < p < .25$).

The rarity of conjoined valves of all species suggests some current action, but it does not seem likely that this can have been very vigorous. The abundance of small specimens of all species, the small proportion of broken valves, the intact preservation of the fragile valves of *P.? polonica,* the unsorted nature of the matrix which contains quartz fragments of a wide range of sizes and often angular: all these imply relatively quiet conditions of deposition.

Comparisons

The Stawy brachiopods belong to the *Hirnantia* fauna of North Wales, the English Lake District, and the Northern Shan States of Burma. The age of this fauna is still uncertain, but it is conventionally referred to the top-most Ordovician since it is everywhere succeeded by graptolite-bearing beds of the Llandovery.

Tables 11 and 12 are based on counts made under similar conditions to those of Table 10 on collections of the *Hirnantia* fauna from Aber Hirnant, North Wales, and Hol Beck, Westmorland, in the Lake District. The same factors of possible bias and error in counting operate as in the Stawy collection, but an additional factor is the strong cleavage of the sediments, and the virtual absence of inarticulate horny brachiopods at

Table 11
Numbers of specimens from Aber Hirnant, North Wales

	Brachial	Pedicle	Conjoined	Indeterminate	Total
Lingulella sp.	0	0	0	0	0
Orbiculoidea radiata	0	0	0	0	0
Philhedra? stawyensis	0	0	0	0	0
Dalmanella testudinaria	3	0	0	0	3
Bancroftina? cf. *bouceki*	58	21	1	0	81
Hirnantia sagittifera	30	26	0	0	56
H.? kielanae	2	5	0	0	7
Platymena? polonica	0	0	0	0	0
Eostropheodonta hirnantensis	31	42	0	6	79
Plectothyrella platystrophoides	4	7	0	0	11
Others	0	1	0	0	1

Table 12
Numbers of specimens from Hol Beck, Westmorland

	Brachial	Pedicle	Conjoined	Indeterminate	Total
Lingulella sp.	0	0	0	2	2
Orbiculoidea radiata	0	0	0	0	0
Philhedra? stawyensis	1	0	0	0	2
Dalmanella testudinaria	20	11	1	0	33
Bancroftina? cf. *bouceki*	0	0	0	0	0
Hirnantia sagittifera	49	40	0	2	91
H.? kielanae	45	52	1	0	99
Platymena? polonica	10	1	0	2	13
Eostropheodonta hirnantensis	7	10	2	4	25
Plectothyrella platystrophoides	15	17	8	0	48

Aber Hirnant and Hol Beck [5] may be due to their not having recognisably survived the deformation of the sediments. The relative frequencies of the species are clearly different in the three samples, and are summarised in Table 13 as percentages of the total number of articulate brachiopods (the inarticulate brachiopods — including *Philhedra* which is abundant at Stawy — being omitted for this purpose). The most striking differences are between Stawy and Aber Hirnant, particularly in the relative numbers of *H.? kielanae* and *B.?* cf. *bouceki*. When one of these species is abundant (*H.? kielanae* at Stawy and Hol Beck, *B.?* cf. *bouceki* at Aber Hirnant) it is the predominant element of the fauna and the other is very rare. The two species appear to be alternatives, and as they

[5] A fragment probably referable to *Orbiculoidea* has been recognised from Hol Beck since this section was written and the tables drawn up.

are similar in size it is possible that they may have been competitors for the same ecological niche. *D. testudinaria* seems to vary in abundance concomitantly with *H.? kielanae*, as does *E. hirnantensis* with *B.?* cf. *bouceki*, although the number of samples is too small for a significant correlation coefficient in either case. An inverse correlation appears to exist between the *H.? kielanae* — *D. testudinaria* pair and the *B.?* cf. *bouceki* — *E. hirnantensis* pair. *H. sagittifera* and *P. platystrophoides* are both locally most abundant at Hol Beck, but otherwise the Lake District faunule is characterised (except for the absence of *B.?* cf. *bouceki*) by frequencies intermediate between those of Stawy and Aber Hirnant, and it will be recalled that the Hol Beck *H. sagittifera* are morphologically intermediate between the Polish and Welsh forms of that species.

Table 13

Percentage frequencies of articulate brachiopods in collections from Aber Hirnant (A), Hol Beck (B), and Stawy (C)

	A	B	C
Dalmanella testudinaria	1.27	10.68	17.29
Bancroftina? cf. *bouceki*	34.18	0.00	1.56
Hirnantia sagittifera	23.63	29.45	13.57
H.? kielanae	2.95	32.04	58.43
Platymena? polonica	0.00	4.21	4.67
Eostropheodonta hirnantensis	33.33	8.09	3.80
Plectothyrella platystrophoides	4.64	15.53	0.69

As regards the numbers of pedicle and brachial valves, the most notable feature of the Welsh faunule is the preponderance of brachial valves of *B.?* cf. *bouceki* ($p < .003$). This disparity is probably accentuated by the ease of recognition of small fragments of the dorsal hinge-line of this species, but as with *H.? kielanae* at Stawy, it may imply a winnowing effect on the most abundant element of the fauna. At Hol Beck, on the other hand, the frequencies of pedicle and brachial valves do not differ significantly in either of the two most abundant species *H.? kielanae* and *H. sagittifera*, although there are more brachial than pedicle valves of the rather rare and thin-shelled *P.? polonica* ($p = .006$). There is therefore very little evidence of winnowing at Hol Beck, and the fine-grained nature of the sediment is consistent with quiet undisturbed deposition. In all three faunules pedicle valves of *E. hirnantensis* are more frequent than brachial valves, and although individually not significant, cumulatively the difference is probably significant ($.01 < p < .02$ for one-tailed test).

Table 14 shows the ranked abundance of all brachiopod species in the three localities. The distributions at Aber Hirnant and Hol Beck are

Table 14

Ranked abundance of brachiopod species at Stawy, Aber Hirnant, and Hol Beck, compared with the abundance predicted by MacArthur's formulas on the assumptions of (a) non-overlapping niches, (b) overlapping niches

	Observed	Predicted			Observed	Predicted	
		a	b			a	b
ABER HIRNANT	81	88.2	90.0	STAWY	200	267.6	181.7
	79	54.2	37.3		182	198.2	139.4
	56	37.2	28.6		54	117.3	103.6
	11	25.8	24.1		44	89.6	93.6
	7	17.2	21.2		33	66.4	86.1
	3	10.5	19.2		18	46.6	80.1
	1	4.9	17.7		15	29.3	75.3
HOL BECK	99	106.4	110.7				
	91	67.2	45.8				
	48	47.7	35.2				
	33	34.6	29.7				
	25	24.8	26.1				
	13	17.0	23.6				
	2	10.5	21.7				
	2	4.9	20.2				

similar in that the first and second species are nearly equally abundant, whereas at Stawy the first species is over three times as abundant as the second. The observed frequencies are compared in the second and third columns with those estimated from the formulas suggested by MacArthur (1960) for species in population equilibrium. It will be seen that in all cases agreement is better with the values predicted on the assumption of non-overlapping niches, and in fact for Hol Beck the differences from expectation are only just significant ($.975 < p < .99$). The fit is poor, though, in the case of Stawy, where the first species is much more abundant than expected, and in all localities rare species are rarer than expected. It is perhaps not surprising that the best fit is at Flol Beck, where there is least evidence that the frequencies have been affected by sorting.

For a comparison of the diversity of the three faunules we may use an informational measure and calculate $-\Sigma p_i \log_e p_i$ where p_i is the frequency (out of unity) of the i^{th} most abundant species (MacArthur & MacArthur, 1961). For articulate brachiopods alone the diversities for Stawy, Aber Hirnant, and Hol Beck are respectively 1.2548, 1.3762, 1.5893, indicating increasing approach to equality of numbers of species (represented for 7 species by a diversity of 1.9459). There does not seem to be available a test for the comparison of these diversities.

Borings in the larger shells, particularly *H. sagittifera* and *E. hirnantensis* (see Pl. XVIII, figs. 5—6), are found in all three localities, relatively rarely at Stawy and Hol Beck, but very commonly at Aber Hirnant where some shells may be riddled with borings.

The most characteristic feature of the Burmese occurrence of the *Hirnantia* fauna, as far as it is possible to judge from a small collection in the Sedgwick Museum and from Reed's 1915 descriptions and figures, is the abundance of *Platymena? mcmahoni* in contrast to the rarity of *P.? polonica* in Europe.

It is noteworthy that many of the species from Stawy are represented by individuals smaller on the average than those from other localities. It is difficult in dealing with fossil assemblages to know what taxonomic importance to attach to such size-differences. Certainly, very small individuals (not only brachiopods but also small trilobite growth-stages) appear to be more common at Stawy than elsewhere, but this may be due to the conditions of deposition having been more favourable to their preservation; conversely, large individuals are relatively rare at Stawy, although this effect may have been exaggerated by the method of collecting (see above). Size-difference can be a valid specific criterion for two species from the same locality, as in the case of *H. sagittifera* and *H.? kielanae*, but in comparing samples from different localities it is extremely hazardous to argue from an observed size-difference in what is presumably a much-altered death assemblage to an original size-difference at corresponding growth-stages in the living animals. Accordingly size by itself has not been used here as a specific criterion, and the smaller Stawy forms of for instance *H. sagittifera* and *O. radiata* are not separated from the larger topotype specimens.

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GÓRNO-ORDOWICKIE BRACHIOPODY Z POLSKI I BRYTANII

Streszczenie

WSTĘP

Opisane w niniejszej pracy brachiopody pochodzą z górnego ordowiku Gór Świętokrzyskich. Opisy niektórych gatunków są uzupełnione obserwacjami okazów z łupków aszgilskich z English Lake District i z warstw Hirnant (Walia Płn.).

Fauna polska pochodzi z profilu Stawy okolic Łagowa w Górach Świętokrzyskich (synklina bardziańska), zebrana z żółtych, piaszczystych mułowców, leżących około 2 m poniżej łupków graptolitowych, tworzących spąg syluru (Kielan, 1960, p. 12, Text-fig. 1).

Materiał dotyczący *Dalmanella testudinaria* został porównany z topotypowym materiałem pochodzącym z Borenshult, (Szwecja), oraz z Hol Beck (Lake District). Dla porównania z okazami z Borenshult zastosowano multiwariantną analizę 5 cech skorupki grzbietowej. Otrzymany wzór variance-covariance dla dwóch prób znacznie się różni. W przypadku okazów z miejscowości Stawy i Hol Beck zastosowano trójwariantną analizę, opartą na pewnych wymiarach kardynalii; tutaj również wzory variance-covariance różnią się. Przy zastosowaniu analizy biwariantnej dla trzech prób (długość i szerokość płytek podpierających) wzory variance-covariance, nie różnią się bardzo i porównanie przeciętnych λ_2 wykazuje, że okazy polskie mają prawdopodobnie znacznie cieńsze płytki podpierające, niż okazy szwedzkie lub angielskie, pochodzące z Lake District, przy czym u okazów z tych dwóch miejscowości element ten jest niemalże identyczny. Chociaż okazy polskie różnią się w pewnych innych cechach, wariacja ta, warunkowo, jest uważana za wewnątrzgatunkową.

Kolekcja okazów *Hirnantia sagittifera* z miejscowości Stawy została porównana z topotypowym materiałem okazów z Aber Hirnant (Walia Płn.) i z okazami z Hol Beck. Analiza pewnych rozmiarów kardynalii wykazuje, że okazy z tych miejscowości różnią się znacznie, a ich wzory variance-covariance są różne. Okazy z Hol Beck mają głębsze dołki kruralne i prawdopodobnie szersze płytki podpierające, niż okazy z miejscowości Stawy. Wariacja ta jest uważana za wewnątrzgatunkową.

DIAGNOZY NOWYCH GATUNKÓW

Philhedra? stawyensis n.sp.

Przedstawiciel rodzaju *Philhedra* o skorupce dorsalnej małych rozmiarów, z dość wyraźnie zaznaczonym urzeźbieniem skorupki służącej za podłoże; powierzchniowe żeberka promieniste, bardzo delikatne (prawdopodobnie pokryte delikatnymi kolcami), lub często brak ich; dziób mniejszy niż 1/3 długości skorupki, licząc od brzegu tylnego. Skorupka wentralna nie zachowana, prawdopodobnie nie była skalcytowana.

Hirnantia? kielanae n.sp.

Hirnantia małych rozmiarów, o wąskich, tępo kanciastych, dachówkowatych żeberkach; area wentralna wysoka, płytki zębowe mocno dywergentne; wentralne odciski mięśniowe o prawie półokrągłym zarysie; septum dorsalne środkowe dość wysokie; odciski adduktorów w skorupce dorsalnej wydłużone; płytki podpierające zgrubiałe, ułożone prawie równolegle; dołki kruralne różnie wykształcone.

Platymena? polonica n.sp.

Gatunek rodzaju *Platymena* charakteryzuje się poprzecznie wydłużonym zarysem zewnętrznym muszli, obecnością płytek zębowych i brakiem zgrubiałego wałeczka, obrzeżającego wisceralne części skorupek.

Plectothyrella n.gen.

Przedstawiciel rodziny Meristellidae, mający wykształcone siodło i zatokę; żeberka grube; płytki zębowe szerokie, zachowujące na przednich powierzchniach ślady odcisków adiustorów; ku przodowi, od platformy wentralnej, zaznacza się głębokie kolankowate przegięcie skorupki; septum dorsalne środkowe nie podpiera dwudzielnej płytki zawiasowej. Brachidium nie znane.

Genotyp: *Plectothyrella platystrophoides* n.sp. — diagnoza jak dla rodzaju.

DYSKUSJA

Ilość okazów pochodzących z miejscowości Stawy, Aber Hirnant i Hol Beck podana jest w Tabelach 10—12 (s. 416, 418). W toku badań stwierdzono znaczne różnice w ilościach skorupek wentralnych i dorsalnych w obrębie najliczniejszych gatunków, pochodzących z miejscowości Stawy (*Hirnantia? kielanae*) i z Aber Hirnant (*Bancroftina?* cf. *bouceki*). Na tej podstawie można przypuszczać, że fauna tych dwóch miejscowości została przemieszczona na pewną odległość od miejsca przyżyciowego. Natomiast w Hol Beck nie stwierdzono tak znacznych różnic w ilościach skorupek wentralnych i dorsalnych w obrębie najliczniejszych gatunków (*H.? kielanae* i *H. sagittifera*), można więc sądzić, że fauna tutaj nie uległa dalszemu transportowi.

Względna częstotliwość gatunków w trzech próbach jest różna (Tabl. 13, s. 419). Wydaje się, że duże ilości okazów *H.? kielanae* i *Dalmanella testudinaria* są odwrotnie skorelowane z okazami *Bancroftina?* cf. *bouceki* i *Eostropheodonta hirnantensis*. Częstotliwość występowania gatunków w każdej z miejscowości jest porównywana (Tab. 14, s. 420) z częstotliwością, przewidzianą wzorem MacArthura (1960). We wszystkich przypadkach istnieje duża zgodność z wartościami przewidzianymi wspomnianym wzorem, co świadczyłoby o istnieniu nie zachodzących na siebie nisz, w których zwierzęta te żyły. Najlepiej wzór ten stosuje się dla Hol Beck, najgorzej dla miejscowości Stawy i wszędzie gatunki te są rzadsze, niż można by przewidywać.

Rozpatrywany jest również problem brachiopodów o przeciętnie małych rozmiarach muszli, pochodzących z miejscowości Stawy. Uważa się, że taksonomiczne różnice dla form pochodzących z różnych miejscowości powinny być oparte raczej na kształcie muszli, niż na jej rozmiarach.

ДЖОН Т. ТЭМПЛ

ВЕРХНЕ-ОРДОВИКСКИЕ БРАХИОПОДЫ ИЗ ПОЛЬШИ и ВЕЛИКОБРИТАНИИ

Резюме

В настоящей работе дано описание брахиопод из верхне-ордовикских отложений Свентокржиских Гор. Описание некоторых видов дополнено данными, полученными из наблюдений над некоторыми экземплярами брахиопод из эшгильских сланцев (область Lake District), а также из слоев Гирнант (Hirnant, северный Уэльс).

Польскую фауну, происходящую из разреза Ставы (бардзианская синклиналь, в окрестностях города Лагув, в Свентокржиских Горах) извлечено из желтых аргилитов, выступающих в разрезе около 2 метров ниже граптолитовых сланцев, образующих здесь нижний слой силура (Kielan, 1960, с. 12, фиг. 1).

Материал содержащий *Dalmanella testudinaria* сравнено с топотиповым материалом происходящим из Боренщульт (Borenshult) в Швеции, а также из Голь Бек (Hol Beck-Lake District). Для сравнения польских экземпляров с формами из Боренщульт применяется многовариантный анализ 5 признаков спинной створки. Полученная формула варианс-ковариaнс (variance-covariance) в случае двух образцов значительно различается. К образцам происходящим из местностей Ставы и Голь Бек применяется тройвариантный анализ, основанный на некоторых размерах кардинальев, но и здесь также формулы варианс-ковариaнс различаются. В случае применения двухвариантного анализа для трёх образцов — длина и ширина зубных пластин — формулы варианс-ковариaнс значительно не различаются. Сравнение средних λ_2 показывает, что образцы из Польши обладают более тонкими зубными пластинами, чем образцы из Швеции либо из Великобритании (Lake District), причём в образцах из двух последних местностей элемент этот является почти идентичным. Хотя польские образцы различаются по некоторым другим признакам, вариацию эту условно считается внутривидовой.

Коллекцию образцов *Hirnantia sagittifera* из местности Ставы сравнено с топотиповым материалом из Абер Гирнант в северном Уэльсе, а также с образцами из Голь Бек. Анализ некоторых размеров кардинальев показывает, что образцы из двух вышеупомянутых местностей значительно между собой различаются, а характеризующие её формулы варианс-ковариaнс являются тоже различными. Образцы из Голь Бек имеют более глубокие круральные ямки и вероятно более широкие зубные пластины, чем образцы из местности Ставы. Вариацию эту считается внутри-видовой.

ДИАГНОЗЫ

Philhedra? stawyensis n. sp.

Представитель рода *Philhedra* характеризуется спинной створкой маленьких размеров, с умеренно отчетливой скульптурой раковины, служащей как субстрат; на поверхности створки видны очень тонкие радиальные рёбра (вероятно покрыты тонкими шипами), которые часто отсутствуют; макушка короче 1/3 длины створки, считая с заднего её края. Брюшная створка не сохранилась; по всей вероятности не подверглась кальцитизации.

Hirnantia? kielanae n. sp.

Hirnantia маленьких размеров, с узкими, тупоугловатыми черепичными рёбрышками; арея высокая, зубные пластины сильно расходящиеся; отпечатки мускулов почти полукруглого очертания; срединная септа спинной створки умеренно высокая. Отпечатки закрывателей спинной створки удлиненные, уложенные почти параллельно; круральные ямки различно образованные.

Platymena? polonica n. sp.

Вид рода *Platymena* характеризуется поперечно удлиненным внешним очертанием раковины, наличием зубных пластин и отсутствием утолщенного валика, окаймляющего висцериальные части створок.

Plectothyrella n. gen.

Представитель семейства *Meristellidae* имеет четко образованные седло и синус. Рёбрышки толстые; зубные пластины широкие, с сохраненными на передних поверхностях следами отпечатков адиюсторов; впереди, около брюшной платформы, наблюдается глубокий коленчатый изгиб; срединная септа спинной створки не поддерживает разделенной замочной площадки. Брахидиум не известное.

Генотип: *Plectothyrella platystrophoides* n. sp. Диагноз — как для рода.

ДИСКУССИЯ

Количество экземпляров происходящих из местностей Ставы, Абер Гирнант, а также Голь Бек приводится в таб. 10—12. В ходе исследований, в пределах наиболее многочисленных видов, происходящих из местности Ставы (*H.? kielanae*), а также из Абер Гирнант (*B.?* cf. *bouceki*), удостоверено значительное различие в количестве спинных и брюшных створок. Основываясь на этом, можно предполагать, что фауна из двух вышеупомянутых местностей не находится сейчас на месте прижизненного обитания, а по всей вероятности была перемещена после смерти на некоторое расстояние. В Голь Бек зато, в пределах наиболее многочисленных видов (*H.? kielanae* и *H. sagittifera*) не удостоверяется значительного различия в количестве брюшных и спинных створок. Судя из этого, присутствующая здесь фауна брахиопод не была подвергнута длинному перемещению.

Относительная частота видов в трёх пробах является разной (таб. 13). Кажется, что множество экземпляров *H.? kielanae* и *D. testudinaria* есть обратно коррелировано с экземплярами *B.?* cf. *bouceki* и *E. hirnantensis*. Частоту появления видов в каждой местности сравнено (таб. 14) с частотой предположенной формулой МакАртура (MacArthur, 1960). Во всех случаях имеет место соответствие с величинами предположенными упомянутой формулой, что свидетельствует о существовании не охватывающих друг друга ниш, в которых обитали эти формы. Наилучшим образом формула эта применяется для Голь Бек; хуже всего — для местности Ставы, и везде редко выступающие виды являются более редкими, чем можно бы предусматривать.

Обсуждается также вопрос брахиопод со средне маленькими раковинами, происходящими из местности Ставы. Считается, что таксономические различия в экземплярах, происходящих с различных местностей ,должны скорее всего основываться на форме раковины, чем на её величине.

PLATES

Plate I

Lingulella sp.

Fig. 1. Internal mould of pedicle valve (BB 29248a); × 5.
Fig. 2. External mould of same specimen (BB 29248b), × 5.
Fig. 3. Internal mould of pedicle valve (BB 30766); × 5.

Orbiculoidea radiata Troedsson

Fig. 4. External mould of brachial valve (BB 30774b); × 10.
Fig. 5. Internal mould of large brachial valve (BB 29578); × 5.
Fig. 6. Brachial valve from Röstånga, Sweden, figured by Troedsson, 1918, Pl. 1, fig. 6 (LO 2866T); × 10.
Fig. 7. Pedicle valve, lectotype, from Röstånga, Sweden, figured by Troedsson, 1918, Pl. 1, fig. 7 (LO 2867t); × 10.

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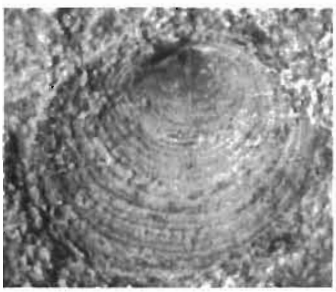

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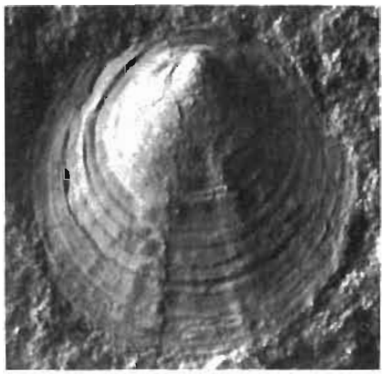

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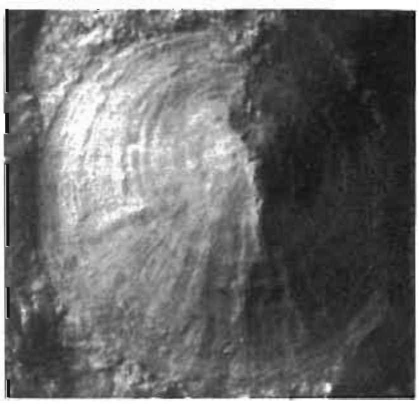

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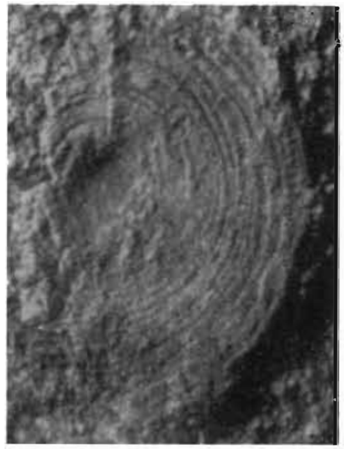

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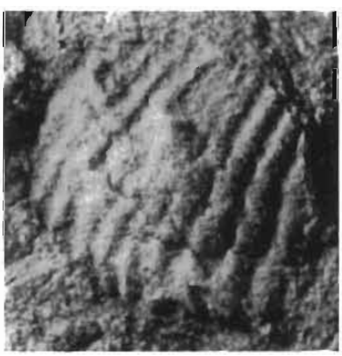

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Plate II

Orbiculoidea radiata Troedsson

Fig. 1. Internal mould of pedicle valve (BB 30769a); × 20.
Fig. 2. External mould of same specimen (BB 30769b); × 20.

Philhedra? stawyensis n. sp.

Fig. 3 Internal mould of brachial valve, holotype (BB 30760a); × 10.
Fig. 4. External mould of same specimen (BB 30760b); × 10.
Fig. 5. Internal mould of brachial valve (BB 30745); × 10.
Fig. 6. Internal mould of brachial valve (BB 30740); × 10.
Fig. 7. Right lateral view of internal mould of brachial valve (BB 29381); × 10.

Plate III

Dalmanella testudinaria (Dalman)

Fig. 1. Internal mould of pedicle valve (BB 29299); × 5.
Fig. 2. Anterior view of same specimen; × 5.
Fig. 3. Internal mould of pedicle valve (BB 29630); × 5.
Fig. 4. Right lateral view of same specimen; × 5.
Fig. 5. Internal mould of brachial valve (BB 29613); × 5.
Fig. 6. Internal mould of brachial valve (BB 29320); × 5.
Fig. 7. Internal mould of brachial valve (BB 29972); × 5.

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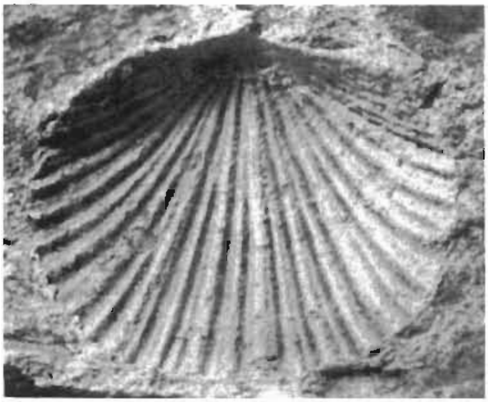
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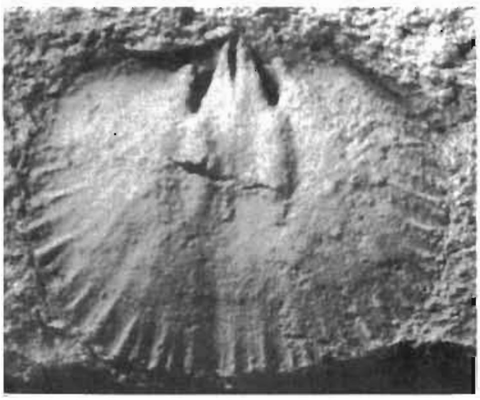
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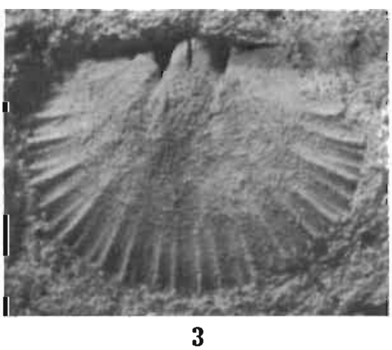
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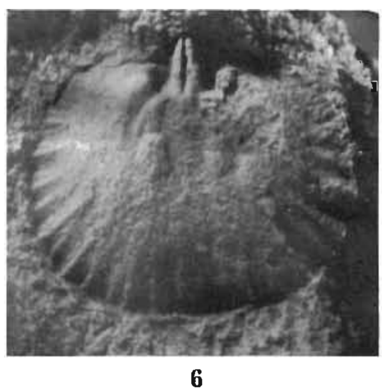
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Plate IV

Dalmanella testudinaria (Dalman)

Fig. 1. External mould of brachial valve (BB 30012b); × 6.6.
Fig. 2. Internal mould of same specimen (BB 30012a); × 6.6.
Fig. 3. Internal mould of brachial valve (BB 29327); × 6.6.
Fig. 4. Latex cast of interior of brachial valve (BB 29367); × 6.6.
Fig. 5. Internal mould of brachial valve (BB 30059); × 6.6.
Fig. 6. Internal mould of brachial valve (BB 29351); × 6.6.

Plate V

Dalmanella testudinaria (Dalman)

Fig. 1. Internal mould of brachial valve (BB 29323); × 13.2.
Fig. 2. Internal mould of brachial valve (BB 29373); × 13.2.
Fig. 3. Internal mould of brachial valve (BB 29973); × 13.2.
Fig. 4. Internal mould of brachial valve (BB 29681); × 13.2.
Fig. 5. Internal mould of pedicle valve (BB 29586); × 13.2.
Fig. 6. Internal mould of pedicle valve (BB 29603); × 13.2.
Fig. 7. Internal mould of pedicle valve (BB 29977); × 13.2.

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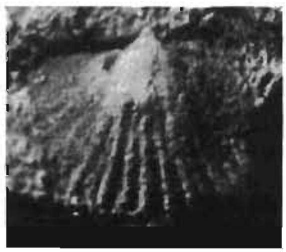

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Plate VI

Dalmanella testudinaria (Dalman)

Fig. 1. Internal mould of pedicle valve (BB 29629); × 6.6.
Fig. 2. Internal mould of pedicle valve (BB 29989); × 6.6.
Fig. 3. Internal mould of pedicle valve (BB 30032); × 6.6.
Fig. 4. Internal mould of pedicle valve (BB 29631); × 6.6.
Fig. 5. Internal mould of pelicle valve (BB 29333); × 6.6.
Fig. 6. Internal mould of pedicle valve (BB 29996); × 6.6.
Fig. 7. Posterior view of same specimen; × 6.6.

Plate VII

Bancroftina? cf. *bouceki* (Havlíček)

Fig. 1. Internal mould of brachial valve (BB 29568); × 6.6.

Fig. 2. Internal mould of brachial valve (BB 29348); × 6.6.

Fig. 3. Internal mould of brachial valve (BB 29362); × 6.6.

Fig. 4. Internal mould of small brachial valve (BB 29637); × 6.6.

Fig. 5. Internal mould of pedicle valve doubtfully attributed to this species (BB 29277); × 6.6.

Fig. 6. Internal mould of pedicle valve (BB 29303); × 6.6.

Fig. 7. Internal mould of large pedicle valve (BB 30055); × 6.6.

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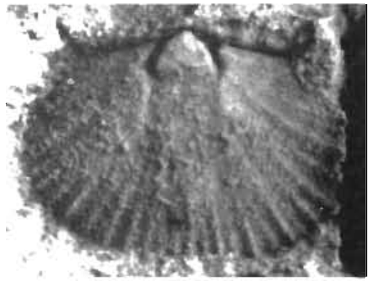

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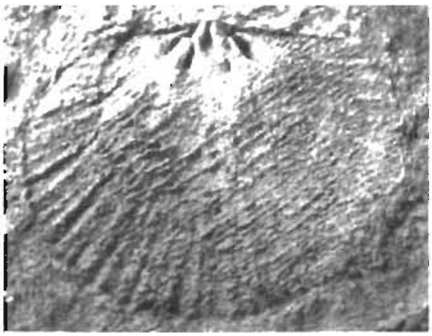

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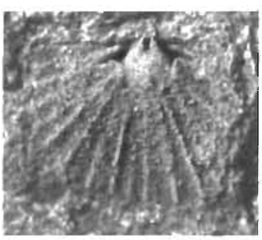

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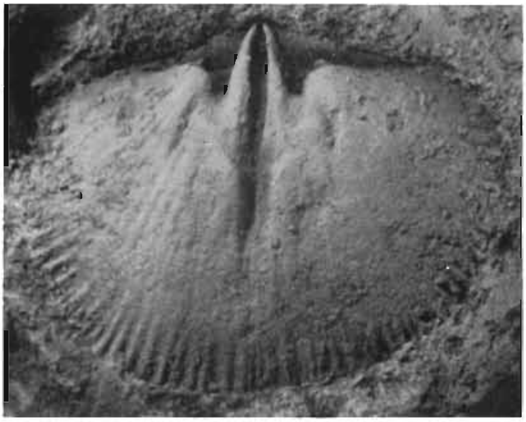

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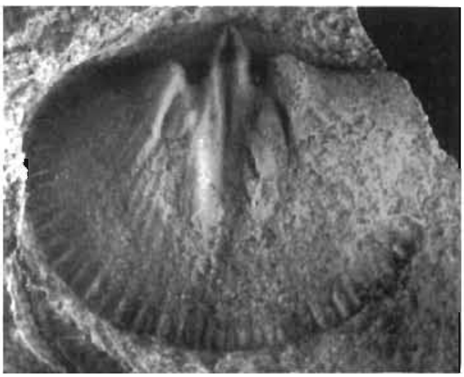

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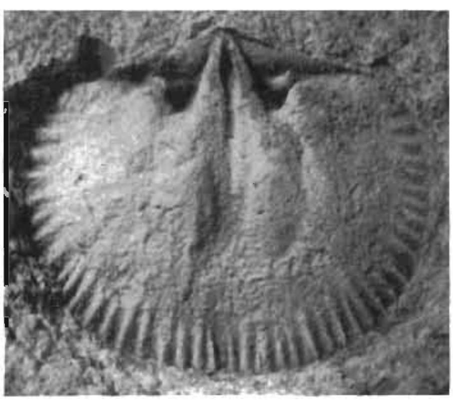

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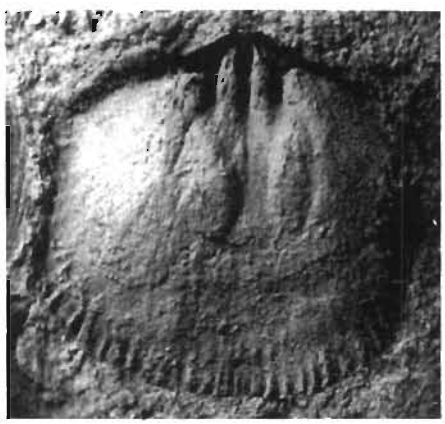

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Plate VIII

Hirnantia? kielanae n. sp.

Fig. 1. Internal mould of brachial valve (BB 29501); × 6.6.
Fig. 2. Internal mould of brachial valve (BB 29468); × 6.6.
Fig. 3. Internal mould of brachial valve (BB 29507); × 6.6.
Fig. 4. Internal mould of brachial valve (BB 29518); × 6.6.
Fig. 5. Right lateral view of internal mould of brachial valve, holotype (BB 29474); × 6.6.
Fig. 6. Dorsal view of holotype; × 6.6.
Fig. 7. Internal mould of brachial valve (BB 29402); × 6.6.

Plate IX

Hirnantia? kielanae n. sp.

Fig. 1. Internal mould of brachial valve (BB 29519); × 13.2.
Fig. 2. Internal mould of brachial valve (BB 29269); × 13.2.
Fig. 3. Internal mould of brachial valve (BB 29998); × 13.2.
Fig. 4. Internal mould of brachial valve (BB 29625); × 13.2.
Fig. 5. Internal mould of brachial valve (BB 29655); × 13.2.
Fig. 6. Internal mould of brachial valve (BB 29988); × 13.2.
Fig. 7. Internal mould of brachial valve (BB 29395); × 13.2.
Fig. 8. External mould of brachial valve, showing hollow spines on primaries 2 and distal ribs (BB 29468b); × 6.6.

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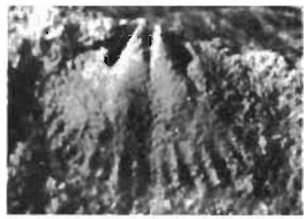

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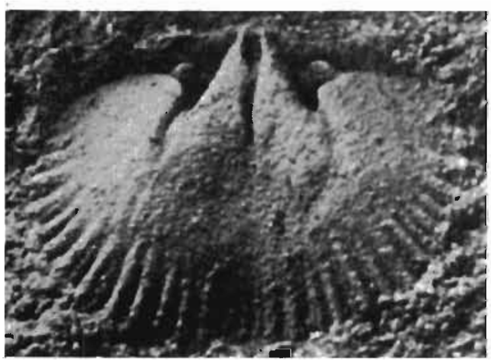

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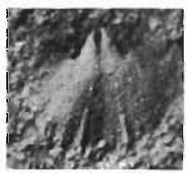

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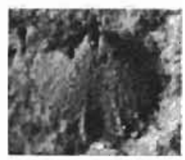

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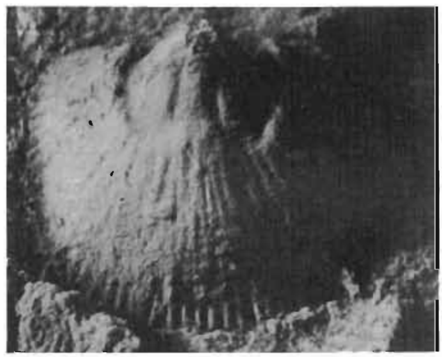

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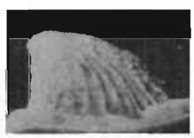

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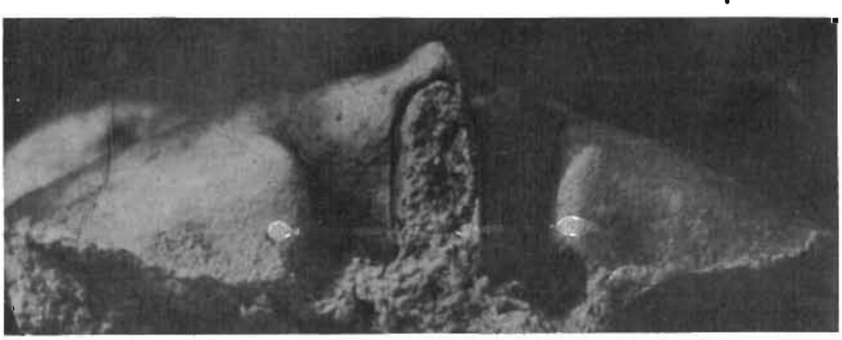

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Plate X

Hirnantia? kielanae n. sp.

Fig. 1. Internal mould of pedicle valve, showing rod-like processes projecting into interior of valve (BB 30015); × 6.6.

Fig. 2. Internal mould of pedicle valve (BB 29467); × 6.6.

Fig. 3. Latex cast of external mould of brachial valve (BB 30787); × 6.6.

Fig. 4. Internal mould of pedicle valve (BB 29406); × 6.6.

Fig. 5. Latex cast of external mould of pedicle valve (BB 30726b); × 6.6.

Fig. 6. Left lateral view of same; × 6.6.

Fig. 7. Cardinal area of same; × 6.6.

Fig. 8. Posterior view of internal mould of pedicle valve, showing pedicle collar passing into flange (BB 30003); × 13.2.

Plate XI

Hirnantia? kielanae n. sp.

Fig. 1. Internal mould of pedicle valve (BB 29445); × 6.6.
Fig. 2. Internal mould of pedicle valve (BB 30726); × 6.6.
Fig. 3. Internal mould of pedicle valve (BB 29635); × 6.6.
Fig. 4. Latex cast of interior of brachial valve (BB 29509); × 6.6.
Fig. 5. Internal mould of pedicle valve (BB 29575); × 13.2.
Fig. 6. Internal mould of pedicle valve (BB 29433); × 13.2.
Fig. 7. Internal mould of pedicle valve (BB 30042); × 13.2.

Hirnantia sagittifera (M'Coy)

Fig. 8. Internal mould of brachial valve, lectotype, from Aber Hirnant, North Wales (A 41217); × 3.3.


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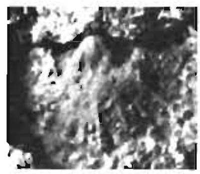
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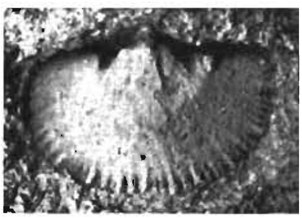
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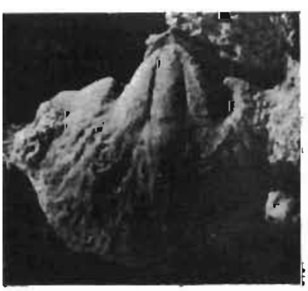

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Plate XII

Hirnantia sagittifera (M'Coy)

Fig. 1. Internal mould of brachial valve (BB 29194); × 1.6.
Fig. 2. Internal mould of brachial valve (BB 29198); × 3.3.
Fig. 3. Internal mould of brachial valve (BB 29196); × 1.6.
Fig. 4. Internal mould of brachial valve (BB 29199); × 3.3.
Fig. 5. Postero-dorsal view of internal mould of brachial valve (BB 29242); × 3.3.
Fig. 6. Left lateral view of same specimen; × 3.3.
Fig. 7. Dorsal view of same specimen; × 3.3.
Fig. 8. Internal mould of pedicle valve (BB 30024); × 3.3.
Fig. 9. Right lateral view of internal mould of pedicle valve (BB 29621); × 3.3.
Fig. 10. Ventral view of same specimen; × 3.3.

Plate XIII

Hirnantia sagittifera (M'Coy)

Fig. 1. Internal mould of brachial valve (BB 29193); × 3.3.
Fig. 2. External mould of brachial valve (BB 29245b); × 3.3.
Fig. 3. Internal mould of same specimen (BB 29245a); × 3.3.
Fig. 4. Internal mould of brachial valve (BB 30007); × 3.3.
Fig. 5. Internal mould of brachial valve (BB 29646); × 13.2.
Fig. 6. Internal mould of brachial valve (BB 29590); × 13.2.
Fig. 7. Internal mould of brachial valve (BB 29668); × 6.6.
Fig. 8. Internal mould of brachial valve (BB 29611); × 6.6.
Fig. 9. Internal mould of brachial valve (BB 29236); × 6.6.
Fig. 10. Internal mould of brachial valve (BB 29569); × 6.6.

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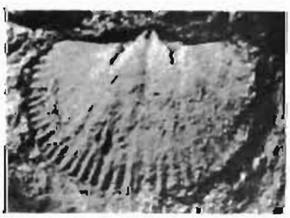

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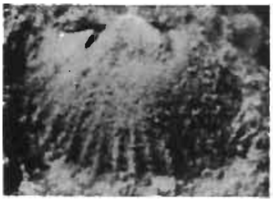

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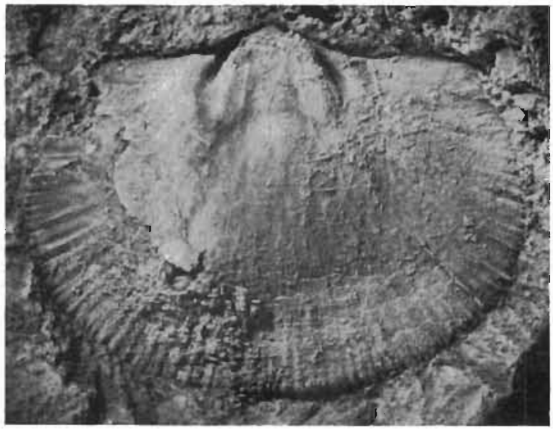

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Plate XIV

Hirnantia sagittifera (M'Coy)

Fig. 1. Internal mould of pedicle valve (BB 29308); × 13.2.
Fig. 2. Internal mould of pedicle valve (BB 29653); × 13.2.
Fig. 3. Internal mould of pedicle valve (BB 30025); × 13.2.
Fig. 4. Internal mould of pedicle valve (BB 29282); × 13.2.
Fig. 5. Internal mould of pedicle valve (BB 29200); × 3.3.
Fig. 6. Internal mould of pedicle valve (BB 29266); × 6.6.
Fig. 7. Internal mould of pedicle valve (BB 29280); × 6.6.
Fig. 8. Internal mould of pedicle valve (BB 29680); × 6.6.

Plate XV

Platymena? polonica n. sp.

Fig. 1. Internal mould of pedicle valve (BB 30010); × 6.6.

Fig. 2. Internal mould of brachial valve, holotype (BB 30009); × 6.6.

Fig. 3. Internal mould of brachial valve (BB 29216a): × 6.6 (see also Pl. XVI, fig. 3).

Fig. 4. Internal mould of brachial valve (BB 29666); × 6.6.

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Plate XVI

Platymena? polonica n. sp.

Fig. 1. Postero-ventral view of internal mould of pedicle valve (BB 29649); × 6.6.
Fig. 2. Ventral view of same specimen; × 6.6.
Fig. 3. External mould of brachial valve (BB 29216b); × 3.3. (see also Pl. XV, fig. 3)
Fig. 4. Internal mould of brachial valve (BB 29636); × 6.6.
Fig. 5. Internal mould of pedicle valve (BB 30784); × 6.6.

Plate XVII

Eostropheodonta hirnantensis (M'Coy)

Fig. 1. Internal mould of pedicle valve (BB 29689); × 3.3.
Fig. 2. Right lateral view of internal mould of pedicle valve (BB 29230); × 3.3.
Fig. 3. Internal mould of pedicle valve (BB 29608a); × 3.3.
Fig. 4. Internal mould of pedicle valve (BB 29257); × 3.3.
Fig. 5. Latex cast of interior of same specimen; × 3.3.
Fig. 6. External mould of same specimen as fig. 3 (BB 29608b); × 3.3.


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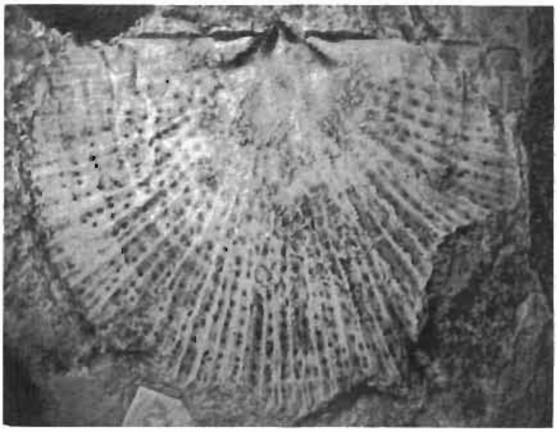

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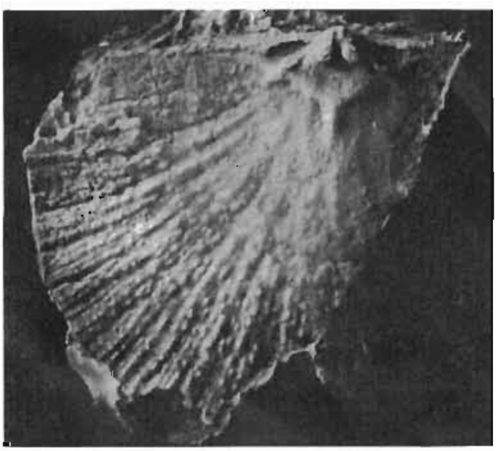

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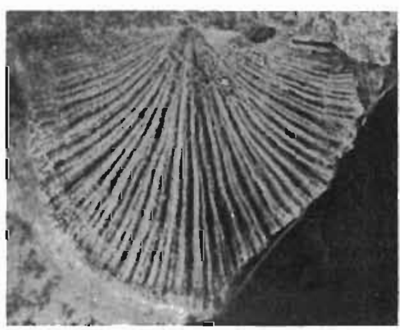

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Plate XVIII

Eostropheodonta hirnantensis (M'Coy)

Fig. 1. Internal mould of brachial valve (BB 29268); × 3.3.
Fig. 2. Internal mould of brachial valve (BB 29272); × 3.3.
Fig. 3. Latex cast of interior of same specimen; × 3.3.
Fig. 4. Internal mould of brachial valve (BB 30014); × 3.3.
Fig. 5. Internal mould of pedicle valve with borings in shell (BB 29672); × 3.3.
Fig. 6. Internal mould of pedicle valve with borings in shell (BB 29633a); × 3.3.
Fig. 7. External mould of same specimen (BB 29633b); × 3.3.

Plate XIX

Eostropheodonta hirnantensis (M'Coy)

Fig. 1. Internal mould of pedicle valve, lectotype, from Aber Hirnant, North Wales (A 28831); × 3.3.

Fig. 2. Internal mould of pedicle valve (BB 29991); × 6.6.

Fig. 3. Internal mould of pedicle valve (BB 30011); × 6.6.

Fig. 4. Internal mould of smallest pedicle valve, showing pronounced median rib (BB 29975); × 13.2.

Fig. 5. Internal mould of smallest brachial valve, showing deep axial depression and strong median interspace (BB 30783); × 20.

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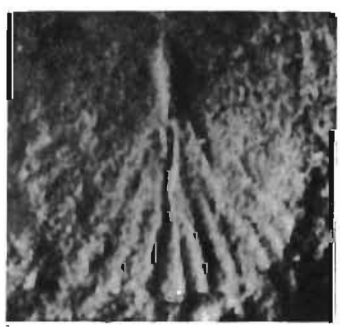

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Plate XX

Plectothyrella platystrophoides n. gen., n. sp.

Fig. 1. Posterior view of internal mould of conjoined valves (A 52002); × 3.3.

Fig. 2. Lateral view of same specimen; × 3.3.

Fig. 3. Posterior view of internal mould of conjoined valves, holotype (A 52001); × 3.3.

Fig. 4. Internal mould of brachial valve (BB 29974); × 3.3.

Fig. 5. Dorsal external mould of conjoined valves (BB 30019b); × 3.3.

Figs. 1—3 from Hol Beck, Westmorland, England.
Figs. 4—5 from Stawy, Poland.

Plate XXI

Plectothyrella platystrophoides n. gen., n. sp.

Fig. 1. Internal mould of brachial valve (A 52005); × 3.3.
Fig. 2. Latex cast of same specimen; × 3.3.
Fig. 3. Antero-ventral view of same; × 3.3.
Fig. 4. Internal mould of brachial valve (A 52004); × 1.6.
Fig. 5. Left lateral view of same specimen; × 1.6.
Fig. 6. Internal mould of brachial valve (A 52101); × 1.6.
Fig. 7. Internal mould of small brachial valve (A 52007); × 6.6.
Fig. 8 Internal mould of pedicle valve (A 52003); × 3.3.
Fig. 9. Anterior view of same specimen; × 3.3.
Fig. 10. Internal mould of small pedicle valve (A 52006); × 6.6.

Figs. 1—5, 7—10 from Hol Beck, Westmorland, England.
Fig. 6 from Aber Hirnant, North Wales.

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