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Source: *Irish Journal of Earth Sciences*, Vol. 12 (1993), pp. 155-189
Published by: Royal Irish Academy
Stable URL: https://www.jstor.org/stable/30002353
Accessed: 01-11-2023 19:53 +00:00

THE CEPHALOPOD FAUNA OF THE KILLEY BRIDGE FORMATION (ORDOVICIAN, ASHGILL), POMEROY, COUNTY TYRONE

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(Received 19 April 1993)

Abstract

The cephalopod fauna described by Portlock from the Killey Bridge Formation is revised, and more recently discovered material described. Although poorly preserved, the fauna is diverse and represented by endocerids, orthocerids, ascocerids, oncocerids, discosoriids, and tarphycerids, all of an upper Ordovician aspect. The abundance of orthocerids representative of the Orthoceratidae in the fauna suggests a relatively offshore site. Evidence is provided for suggesting that other elements of the cephalopod fauna may have been transported (probably during sediment mass-movement) from more inshore sites. The fauna falls within the North American – North European province and, although lacking many elements, appears to show stronger affinities with the 'Arctic' faunas of the Canadian archipelago and the western United States, although factors such as the similar ages of these faunas may also contribute to their apparent affinity.

Introduction

Cephalopods were first described from the Killey Bridge Formation by Portlock (1837; 1843). Portlock recognised several species described by Munster and Sowerby as well as describing a number of species himself — in all, 32 taxa originating from the Bardahessaigh (Caradoc Series) and Killey Bridge (Ashgill Series) Formations. Although some fossil groups from the Killey Bridge Formation have been revised this century (e.g. bivalves and gastropods, Reed 1952; brachiopods, Mitchell 1977), the only substantial review of the cephalopod fauna was carried out by Blake (1882). Tunnicliff (1982) showed that *Koleoceras* Portlock was a sedimentary or diagenetic structure, thus reducing the number of species represented in the fauna.

Much of the material that Portlock described from the Killey Bridge Formation consists of flattened external and internal moulds normally lacking evidence of the siphuncle or cameral deposits. Perhaps today such a fauna would be described, but not used as the basis for erecting new species. However, in Portlock's time, understanding of the importance of internal morphology in the taxonomy of ectocochliate cephalopods was still in its infancy. Consequently, there could have been little or no foreknowledge of the problems that would be created by the naming of such material. A

Irish Journal of Earth Sciences **12** (1993), 155–189.

number of Portlock's species have been quoted in subsequent British and Irish literature and faunal lists. In many cases these species now have extremely large stratigraphical ranges. These records must be treated with suspicion until topotype material is more fully understood and material referred to by later authors has been restudied.

Very little is known about the cephalopod faunas of the North-west Terrane of Ireland. Teichert (1940) described a fauna from the contiguous north-eastern extension of the terrane in Scotland. This fauna came from the Starfish Beds (Upper Drummuck Group) of Girvan, Strathclyde. Very little is known of the upper Ordovician cephalopod faunas of the terranes forming the outer margins of Laurentia. The previously described cephalopod taxa of the Killey Bridge Formation are reviewed (in some cases with the help of comparative material from elsewhere), and more recently collected material is described. An interpretation of the stratigraphical and palaeogeographical relationships of the fauna is attempted.

Material and locations

The following prefixes refer to museum collections of relevant cephalopods:
GSM = British Geological Survey;
TCD = Trinity College, Dublin;
BELUM K = Ulster Museum, Belfast;
NMS = National Museums of Scotland;
NMINGF = National Museum of Ireland;
SMA = Sedgwick Museum, Cambridge;
NMW = National Museum of Wales.

Many of the specimens from the GSM and

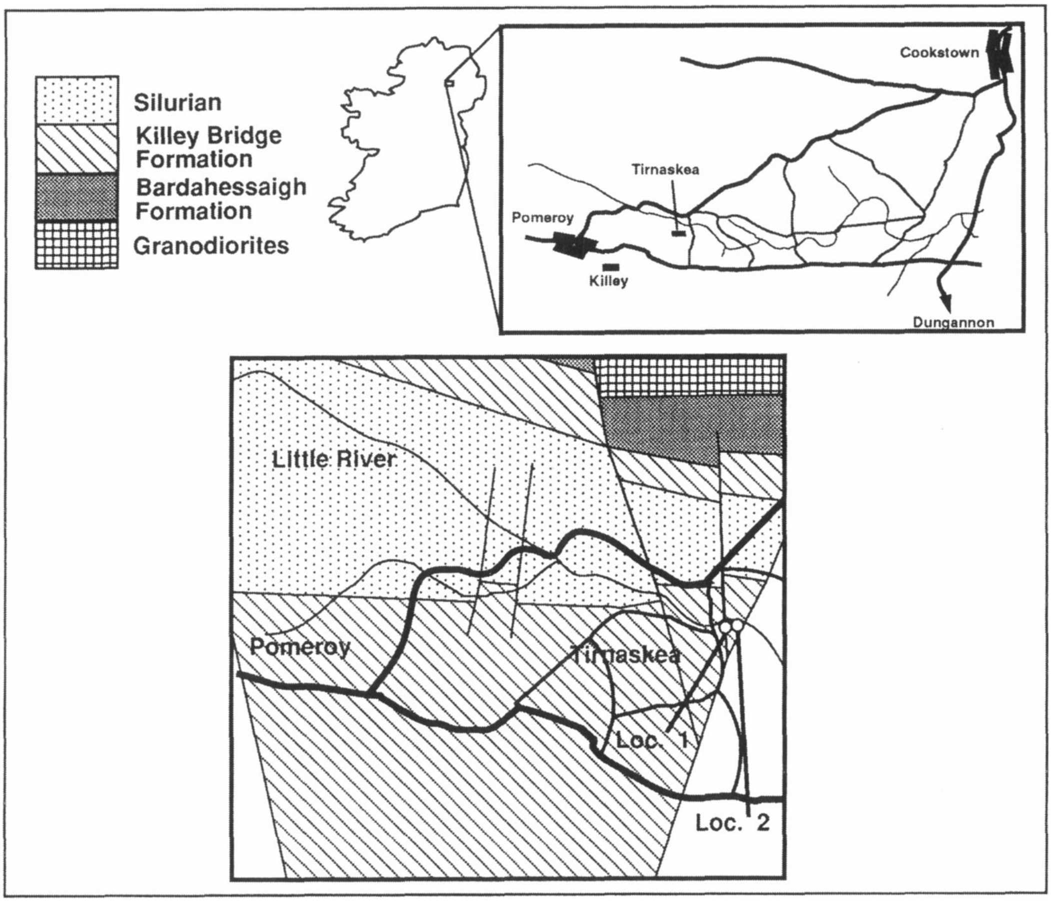


Fig. 1 — Sketch map showing the location of the sites.

Ulster Museum collections represent material from the Portlock Collection. The Lower Palaeozoic portion of the Portlock Collection was catalogued by Tunnicliff (1980). Using specimen labels, information from Portlock's report (1843), and evidence from the lithologies of the matrix, Tunnicliff was able to locate the probable origin of the specimens. All the cephalopods originating from the Killey Bridge Formation in the Portlock Collection appear to have come from Little River. This is locality 3 of Mitchell (1977), '3.6km East of Pomeroy Square, 1.6km SSE of Craigbardahessaigh, 160m E of Slate Quarry Bridge [H 7297 7268]'. This was considered to be the probable site of Portlock's locality 2 (Tunnicliff 1980, 12). The original site consists of an old overgrown quarry. This is locality 1 herein. Recently collected material has come from an excavation on the south bank of the Little River about 15m east of the old quarry (locality 2 herein). Material originating from this site comes from a horizon approximately 8m higher in the succession than at locality 1.

Stratigraphy

The early history of the elucidation of the stratigraphy of the Pomeroy area was summarised by Fearnsides *et al.* (1907), who noted the probable equivalence of the Desertcreat Group with the Drummuck Group of the Girvan area of Scotland (*ibid.*, 116–17). They further noted the likely equivalence of the Trinucleus Mudstones (= the Drummuck Group in the current sense) with the Killey Bridge Beds. Mitchell (1977, 15–17) discussed the age of the Killey Bridge Formation, noting

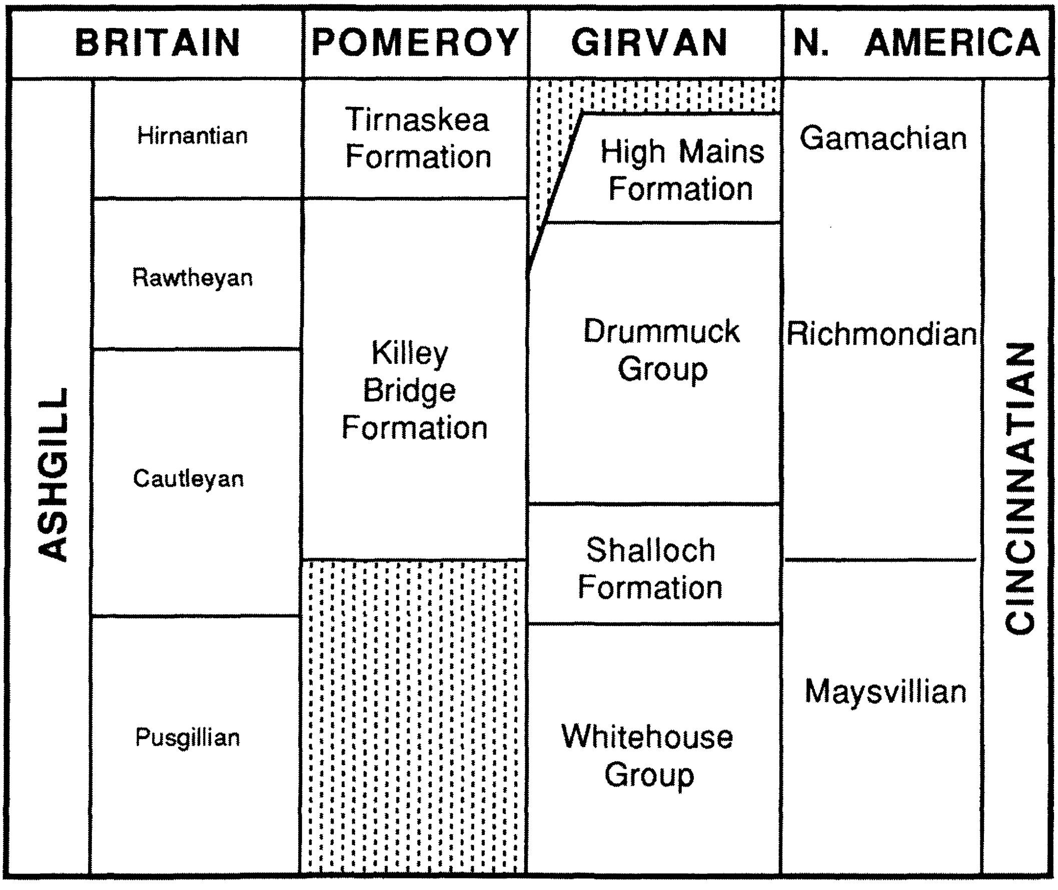


Fig. 2 — Stratigraphy of Killey Bridge area.

that the graptolite fauna indicated the lower part of the *anceps* Biozone. The cryptolithid and tretaspid species were noted to be identical to those from the Lower Drummuck Group and stated to be distinct from Upper Drummuck Group species. Similar conclusions were reached by Harper (1982), who noted the similarity of the Lower Drummuck Group brachiopod faunas to those of the Killey Bridge Formation.

Preservation

As much of the material used in the study comes from museum collections, unknown biases may be built into the observations made below. This results from selective collecting in the past and leads to an over-abundance of certain taxa in the fauna (Fig. 3). It may also lead to a distorted interpretation of preservational modes and taphonomy.

The cephalopods are preserved in slightly cleaved micaceous mudstones and siltstones, as well as more calcareous horizons. Shells are distributed throughout these sediments although they appear to be frequently concentrated in patches. Apart from occasional horizons containing *Zoophycos,* the sediments appear to be devoid of primary structures. Many of the cephalopods are preserved flattened as compression moulds. Some individuals are less flattened and may have originated from more carbonate-rich horizons. In a few cases, where carbonate is still present within the conch, shells retain their original shape.

Orthocones consist mostly of fragments ranging between 20mm and 300mm in length, the larger fragments generally belonging to phragmocones of a larger diameter. Breviconic forms (notably *Diestoceras* and the ascocerids) have relatively complete conchs. The planispiral *Characteroceras* appears to be represented entirely by body-chambers coupled with the most adoral part of the phragmocone. Both latter observations may be subject to bias as these taxa appear to have been preferentially collected (see Fig. 3).

Septa are recognisable in some specimens but, on the whole, phragmocones appear to contain only sediment. It is not possible to attribute the disappearance of septa to any particular event.

Although most fragments of shell appear to lie parallel to the bedding, some are in subvertical to subhorizontal positions. This can be demonstrated in specimens such as GSM103524, where the plane of flattening is strongly oblique to the plane of coiling (Fig. 4). As discussed below, the compression of these beds appears to have been high. This means that some specimens which may have been at low angles to bedding could have been rotated during compression to lie parallel to the bedding. Patterns of cracks (many of which are longitudinal) on the compression moulds are consistent with breakage of the shell during compression. This indicates that shell dissolution may have taken place at a late stage of compaction.

The structure *Koleoceras* generally takes the form of curved surfaces parallel to and surrounding shells, forming a cylindrical to ellipsoidal body. The surfaces are covered with slickensides oriented normal to the conch axis. These structures are associated with specimens retaining a degree of solidity, but may also occur with flattened shells, although the structure itself is flattened in such cases. The structures appear to be mainly associated with the apical parts of shells and concretions.

The structure described above is interpreted as resulting from the lateral movement of matrix around resistant objects. It seems likely that the apparent association of these structures with the apical parts of phragmocones is related to the high mechanical strength of such fragments through the low radii of curvature involved, combined with the investment of camerae with cameral deposits. Flattened *Koleoceras* structures may represent continued compaction after the dissolution of the shell.

One specimen, TCD7933 (*Pleurorthoceras subcostatum*), shows part of an internal mould of a phragmocone with a *Koleoceras* structure at the apical end. Part of the phragmocone contained cameral deposits, now evident as moulds. The surfaces of these moulds have striae running along their length which correspond to the shell sculpture, indicating that the

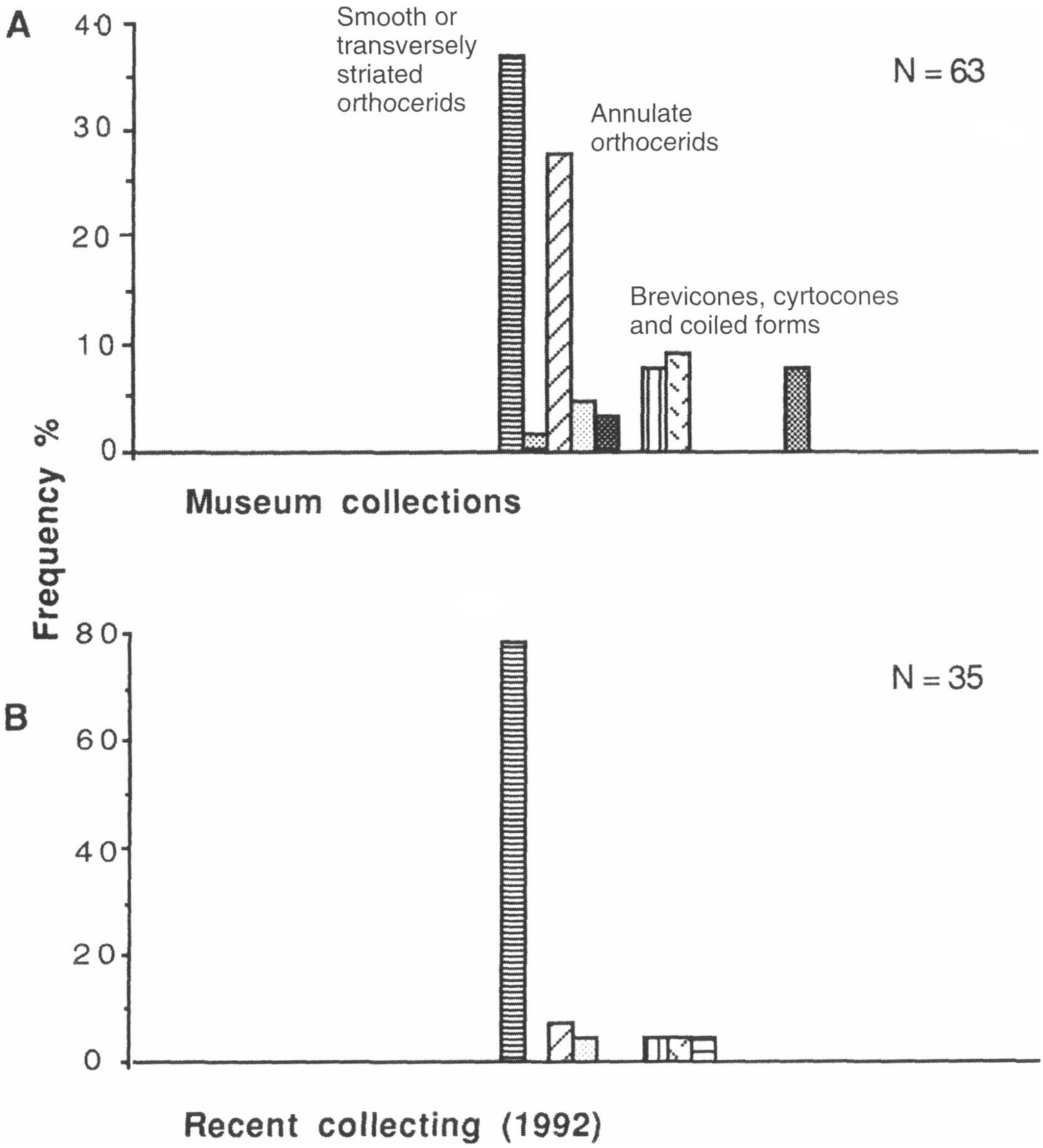


Fig. 3 — A. Frequency distribution of different cephalopod morphologies in museum collections dating back to the early nineteenth century. B. Frequency distribution of morphologies collected from locality 2 during 1992.

external mould has been impressed upon the internal mould concurrently with the dissolution of the shell, producing a composite mould. This also suggests that shell dissolution occurred at a late stage.

The cleavage developed is weak and parallel to the bedding in all specimens. A slight shear is evident in some specimens. Using the method described by Ramsay and Huber (1983, 128–30) the axes of the strain ellipse for several specimens within the plane of bedding were calculated. The axes of the strain ellipse normal to the bedding plane and principal lineation were calculated directly from the width and thickness of the flattened phragmocones. No markers were available which would allow estimation of absolute extension. Despite this, the very high y/z values and low

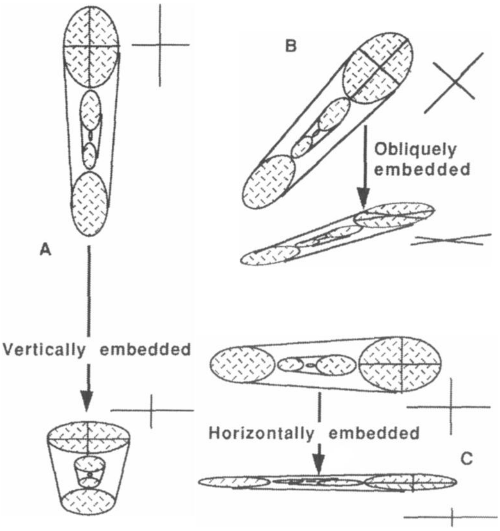


Fig. 4 — Effect of compression on differently poised coiled cephalopods. A. Vertical burial. B. Oblique burial, with minor tortion of coil. C. Horizontal burial.

x/y values plotted on a Flinn diagram (Fig. 5) suggest that the tectonic component of strain is very small, most of the strain being accounted for by compression and de-watering during burial. Although tectonic strain does not appear to have been significant (and should not affect measurements made for taxonomic purposes), the strain resulting from burial was. While shell material remained, deformation was inhomogeneous and was initially expressed by the cracking of the shell. Once the shell was dissolved deformation may have become homogeneous. A number of specimens indicate that once this had taken place, shortening reduced the circumference of shells in the plane normal to the bedding. Evidence of this is seen in specimens possessing a longitudinal sculpture. Whereas the elements of the sculpture should be evenly spaced, the spacing actually decreases at the margins. It is clear that deformation has affected the dimensions of cephalopods during burial. Measurements of circumference are probably particularly affected and in turn will affect estimates of cameral depth and the rate of expansion of the conch — probably increasing the former and decreasing the latter.

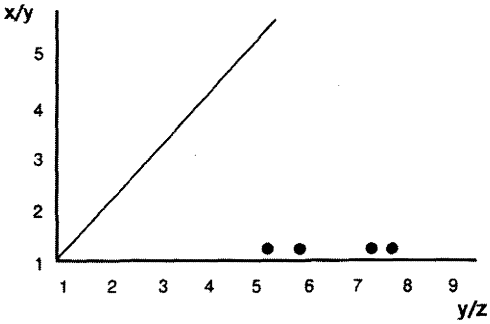


Fig. 5 — Flinn diagram showing strain of four cephalopods from the Killey Bridge Formation. Specimens are well away from the area of slaty cleavage and much of the compression may be attributed to sediment dewatering and compaction.

Palaeoecology

The Killey Bridge Formation consists of micaceous mudstones and siltstones which may in some cases be calcareous. A sandstone, possibly turbiditic, occurs near the top of the succession (Mitchell 1977). Several thin conglomerates are interbedded in the succession (A. Jeram, pers. comm.). Mitchell (1977, 10–11) noted that the size frequency distributions of pedicle and brachial valves of brachiopods were similar and that there was evidence for a fairly constant mortality rate. This was taken to suggest (Mitchell 1977) quiet conditions with very small currents.

A preliminary list of trilobites from the Killey Bridge Formation was provided by Ingham and Tripp (in Thomas *et al.* 1984). Many of the trilobites reported do not occur in Wales and northern England. Those trilobites that do occur in Wales and northern England were often restricted to the shelf to slope associations or communities described and deduced by Price (1980; 1981) and Price and Magor (1984). In the Killey Bridge Formation trilobites considered restricted to one or a number of associations appear to be occurring together. Thus elements of the Illaenid–Cheirurid–Lichid, *Encrinuroides–Ceraurinella,* and *Opsimasaphus–Nankinolithus* associations of Price and Magor (1984) occur together in the Killey Bridge Formation. Faunas of mixed affinities are known from the Upper

Drummuck Group and the mixing has been attributed to downslope transport (Owen *et al.* 1991, 187). A similar explanation seems probable for the Killey Bridge Formation trilobites.

Although the museum collections reflect the diversity of the cephalopod fauna, the overall proportions of the different morphologies indicate the strong collecting bias (Fig. 3a). Collecting carried out during 1992 (Fig. 3b) probably comes closer to the true situation. The dominant element of the fauna consists of smooth to transversely striated longiconic orthocones. Other morphologies are rare by contrast. Hewitt and Stait (1984), in discussing *Bactroceras* and 'small, smooth or transverse lirate longicones', noted a general increase in abundance in offshore mudstones. In the type Onnian and Tetragraptus Shales (Pontifenni Formation) examples given by Hewitt and Stait (1984, 239), the diversities are extremely low (limited to two species, one of which is dominant by at least a magnitude (Evans 1988)). The domination of the Killey Bridge Formation cephalopod fauna by this morphology suggests a more distal offshore position. Some of the rarer elements of the diverse fauna are thought likely to be representative of more inshore environments. For example, most records of ascocerids in North America and northern Europe are from what are probably shallow shelf environments such as the Slade and Redhill Mudstone Formation (Evans 1988), the Boda Limestone (Frye 1982), and the Wainsville Formation (Frey 1987). Cephalopod diversity appears to have reached a maximum in mid-shelf environments (Hewitt and Watkins 1980; Evans 1988). The presence of cephalopods which probably lived in inner shelf to mid-shelf environments in sediments containing other taxa suggesting a more distal environment may be explained either by post-mortem drifting or downslope transport. The oblique deformation which many specimens show suggests that they were not in natural positions of rest while being compressed during burial. It is suggested that the shells were transported downslope with muddy sediments and came to rest chaotically within the sediment. Similar rotations of shells within the sediment might be attained through bioturbation. The large size of some of the shells involved suggests that rotation through bioturbation is unlikely, but the possibility cannot be entirely ruled out. Therefore, the possibility of post-mortem drift on this evidence alone cannot be entirely rejected. However, much of the evidence described above tends to suggest that mass transport has taken place.

On balance, it is considered that the cephalopod fauna may represent a mixture of inner to mid-shelf elements which have been introduced into a more distal shelf environment probably through mass transport processes.

Palaeogeographical relationships

The brachiopod faunas of the Killey Bridge Formation have been placed in the context of a North European Province (Williams 1973). Mitchell (1977, 16–17) noted that the Killey Bridge Formation contains brachiopods which were previously considered endemic to the Mid-American Province, North American Province or Bohemian Province of Williams (1973).

The palaeogeography of upper Ordovician cephalopod faunas in a North American – north European context was discussed by Flower (1976), who recognised a tropical fauna dominated by discosorids, actinocerids, ascocerids and barrandeocerids with few endocerids, oncocerids or orthocerids. This tropical fauna was largely restricted to the Arctic region. An eastern temperate fauna was typified by proteocerids, oncocerids and generalised endocerids. Some mixing between the two faunas was observed. Flower considered that temperate elements characterised the faunas of Wales and southern Scotland.

On the basis of the genera it contains, similarities may be drawn between the Killey Bridge fauna and the faunas of Mid-North America and the Arctic in the presence of *Billingsites, Probillingsites,* and *Pleurorthoceras.* The possible presence of *Tyrioceras* provides a link with Baltic faunas, while the presence of *Characteroceras* and *Endoceras* in the Killey Bridge fauna, as well as in many other Baltic and North American faunas, again suggests links with those latter faunas whilst distinguishing them from those of England and Wales. In marked contrast with all faunas except those of England and Wales, Percé, and the Boda Limestone, there is an apparent (and probably real) lack of actinocerids.

Most of these faunas are united by the presence of *Gorbyoceras*, and a number of oncocerids which provide underlying similarities between all faunas and indicate a large province consisting of parts of North America and northern Europe, containing a number of sub-provinces.

The Killey Bridge cephalopod fauna was compared with several north European and North American faunas using cluster analysis (Table 1 and Fig. 6). This approach has required manipulation of faunal lists in order to remove material assigned to 'dustbin' genera such as *Spyroceras* that cannot reasonably be transferred to other taxa. Because of their indeterminate nature, such taxa are excluded from the study as far as possible.

Nine cephalopod faunas of broadly Ashgill Series age from northern Europe and North America were selected for comparison with the Killey Bridge Formation. The faunas were compared in pairs (Table 1) using the coefficient of association of Williams (1973):

$$\frac{\text{Sum of genera common to both assemblages}}{\text{Sum of genera in smaller assemblage}}$$

The table generated was processed by single linked cluster analysis to produce the dendrogram (Fig. 6). The dendrogram consists of two main clusters, one broadly consisting of the Baltic, England and Wales, and the Canadian Atlantic seaboard, and the other consisting of Wyoming, Baffin Island and Pomeroy. The coefficient of association of these two clusters with each other is 0.6. These two clusters group to form a cluster markedly discriminated from both the Boda Limestone and Kazahkstan assemblages. The results show some similarities to those of Williams (1973, 257) for mid-Ashgillian brachiopods. There appear to be two main differences. The first is in the smaller coefficient of association between the two major clusters (0.6 as opposed to values of 0.94 for northern Europe compared with North America and 0.91 for northern Europe compared with the mid-American province brachiopod assemblages (Williams 1973, 259)). The second difference is in the clustering of the Killey Bridge fauna with the Baffin Island and Bighorn faunas. Williams's study (1973, text-fig. 8) shows the Baffin Island brachiopod fauna to be most strongly associated with mid-American faunas. The

Table 1 — Coefficients of association for pairs of Upper Ordovician cephalopod faunas from northern Europe and North America. Ew: England and Wales (Evans 1988). Po: Killey Bridge Formation (this paper). Pe: Percé, Quebec (Foerste 1936). Ka: Kazahkstan (Barskov 1972). Bo: Boda Limestone, Sweden (Frye 1982; Strand 1934). Os: Oslo (Strand 1934). An: Anticosti Island (Foerste 1928a, b). BI: Baffin Island (Miller *et al.* 1954). Wy: Bighorn Mountains, Wyoming (Foerste 1935). Es: Lyckholm Stuffe, Estonia (Teichert 1930).

Ew	**Po**	**Pe**	**Ka**	**Bo**	**Os**	**An**	**BI**	**Wy**	**Es**	
	.36	.57	.21	.33	.73	.47	.33	.4	.6	**Ew**
		.27	.27	.18	.64	.45	.55	.64	.55	**Po**
			.29	.17	.71	.71	.28	.57	.43	**Pe**
				.001	.21	.21	.14	.21	.19	**Ka**
					.67	.5	.16	.2	.17	**Bo**
						.55	.48	.6	.69	**Os**
							.38	.32	.31	**An**
								.62	.31	**BI**
									.19	**Wy**
										Es

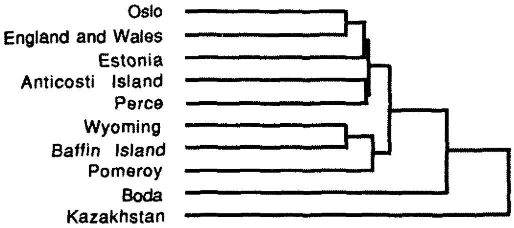


Fig. 6 — Dendrogram of cluster analysis carried out on the data from Table 1.

analysis here suggests the presence of a mid-American group through the pairing of the Baffin Island and Wyoming faunas.

These differences require explanation. The results that might be expected would show greater similarity to Williams's (1973) brachiopod distributions and also show stronger relationships to the faunas of Percé and Anticosti. The exclusion of a number of taxa from the analysis may have caused some error, but inclusion of 'dustbin' genera would probably cause other errors. The small number of genera comprising some of the faunas make the ánalysis sensitive to large changes in coefficients of association where the difference may only be one genus. This happens with the Killey Bridge fauna. Addition of one or two genera common to the Welsh Basin or Oslo could cause the fauna to cluster with the north European group. Nevertheless, comparison of the composition of the fauna collected recently (Fig. 3a–b) with that in previous collections suggest that more extensive collecting might significantly increase the number of taxa recovered. Thus a significant change in the pattern could easily occur.

The Killey Bridge fauna is a single fauna representing a limited time-range and provenance. This fauna is in some cases (e.g. Oslo, Anticosti and England and Wales) being compared with a composite fauna spread over a substantial stratigraphical range. It should be noted that the cluster formed by that of the Killey Bridge fauna with Baffin Island and Wyoming involves faunas which are much more constrained in terms of their age and may be broadly similar in age. Very possibly, the only safe conclusion that can be drawn is that the combined North American and north European faunas are quite strongly discriminated from the Boda Limestone and Kazahkstan assemblages. On these grounds, they may be seen as a relatively homogeneous group. Discrimination from the Boda Limestone may in part be a product of the small size of the fauna, but may also reflect unusual facies (limestone mud-mounds). In the case of the Khazahkstan fauna the composition is distinctly different from all others in this comparison and probably reflects geographical distance and differing conditions. Increasing provinciality of Kazakhstania was noted by Crick (1990, 155).

Systematic palaeontology

Where type material described by Portlock is concerned, the syntype series and probable type locations determined by Tunnicliff (1980) are accepted here.

Class Nautiloidea Agassiz, 1847
Order Endocerida Teichert, 1933
Family Endoceratidae Hyatt, 1883
Genus *Endoceras* Hall, 1847

Type species. Endoceras annulatum Hall, 1847; by subsequent designation Miller, 1889.

Endoceras perannulatum (Portlock). Fig. 7.1–3.

v* 1843. *Orthoceras per-annulatum* Portlock, p. 367, pl. 25, figs 5?, 6.

v* 1882. *Orthoceras perannulatum,* Portlock, pl. 3, fig. 4.

Lectotype. GSM103545. Figured, Portlock, pl. 25, fig. 6. Locality 1.

Paralectotypes. GSM103546; figured Portlock, pl. 25, fig. 5. GSM103547. GSM104153; figured Blake, pl. 3, fig. 4. K4385. All from locality 1.

Additional material. TCD7885, Portlock Collection, probably locality 1.

Description. All specimens are flattened. Obtainable measurements are given in Table 2. All specimens show low (0.5mm high) annulations which in the larger specimens appear to undulate to a certain extent. The annulations are not directly transverse in the flattened specimens, instead curving adapically on one surface and adorally on the other. This suggests that the annulations were originally

Table 2 — Morphological data for *Endoceras perannulatum*. Length = length of shell fragment; Dia. = diameter of shell; Dist. annul. = distance between culminations of annulations; Dist. septa = distance between septa.

Spec. no.	*Length*	*Dia.*	*Dist. annul.*	*Dist. septa*
GSM103545	165mm	57mm	5mm	5mm
GSM103547	48mm	>25mm	4.5mm	4.5mm
GSM104153	130mm	46mm	5.5mm	5.5mm
TCD7885	70mm	29mm	4mm	—
K4385	57mm	—	6mm	6mm

oblique. Septa are very closely spaced, indicating cameral depths ranging from 8% to 12% of the phragmocone diameter. Sutures are also oblique and appear largely to follow the annulations, but intersect annulations in the presumed dorso-ventral axis. A number of the specimens (GSM103547, TCD7885 and K4385) may show remains of the wrinkle layer of the shell.

Remarks. Despite the poor preservation of the material and the lack of diagnostic features, there are compelling reasons for referring *Orthoceras perannulatum* to *Endoceras*. These specimens are (apart from *Orthoceras pomeroense*) the largest conchs in the fauna, and possess the shallowest camerae. Both the large size of the conch and the very shallow camera are suggestive of the Actinocerida or Endocerida. When comparisons are made with approximately coeval faunas in North America there is a clear and strong resemblance to the many species of *Endoceras* described: for example, *Endoceras longum* (Miller), *E. abundum* (Miller), *E. expansum* (Miller), *E. depressum* (Miller) from the Lander Sandstone of Wyoming (Miller 1932) (approximately early Pusgillian in age); *E. baffinense* Foerste from the Upper Ordovician of Baffin Island (Miller *et al.* 1954); *E. fulgar* (Billings), illustrated by Foerste (1928a) from the English Head and Vaureal Formations (Pusgillian to Rawtheyan) of Anticosti Island. *Endoceras norvegicum* (Strand) was described by Strand (1934) from horizons in the Gastropod Limestone at various locations in the Oslo area. Strand described a number of specimens referable to *Endoceras* from the Upper Ordovician of the Oslo region. The similarity of the external form of these species to *Orthoceras perannulatum* Portlock is held to be strong evidence that the species is correctly assigned to *Endoceras*. No comment can be made on its relationship to these other species.

The paralectotype of *Orthoceras perannulatum* is regarded here as belonging to some other genus. It is considered unlikely to be an endocerid, but its true nature is uncertain.

Orthoceras perannulatum was recorded from several parts of Wales (Blake 1882, 85), both from the Ashgill Series and from the Llanvirn and Arenig Series. These latter citations resulted from the recognition of *Orthoceras encrinale* Salter as a junior synonym. *O. encrinale* is best placed in *Protocycloceras* (Evans, in prep.) and is closely related to the early orthocerids and rod-bearing baltoceratids. The Ashgill Series material mentioned by Blake cannot be traced. Pugh (1923, 523) recorded *Orthoceras perannulatum* from the Abercorris Group of southern Snowdonia. This is represented by a suite of specimens (National Museum of Wales 27.110G.508–10; NMW24.164GR.7a–c). The relationship of this material is enigmatic, as no sutures are known. Annulations are generally sharper and wider than those of Killey Bridge Formation specimens and it is thought that they represent a different taxon. It is impossible to ascertain the nature of the Abercorris Group specimens below class level, although they may be orthocerids.

Order Orthocerida Kuhn 1940
Superfamily Orthocerataceae M'Coy 1844
Family Orthoceratidae M'Coy 1844
Subfamily Michelinoceratinae Flower 1945
Genus *'Orthoceras'*

'Orthoceras' elongatocinctum (Portlock). Figs 7.6, 7, 9; 8; 10.2.

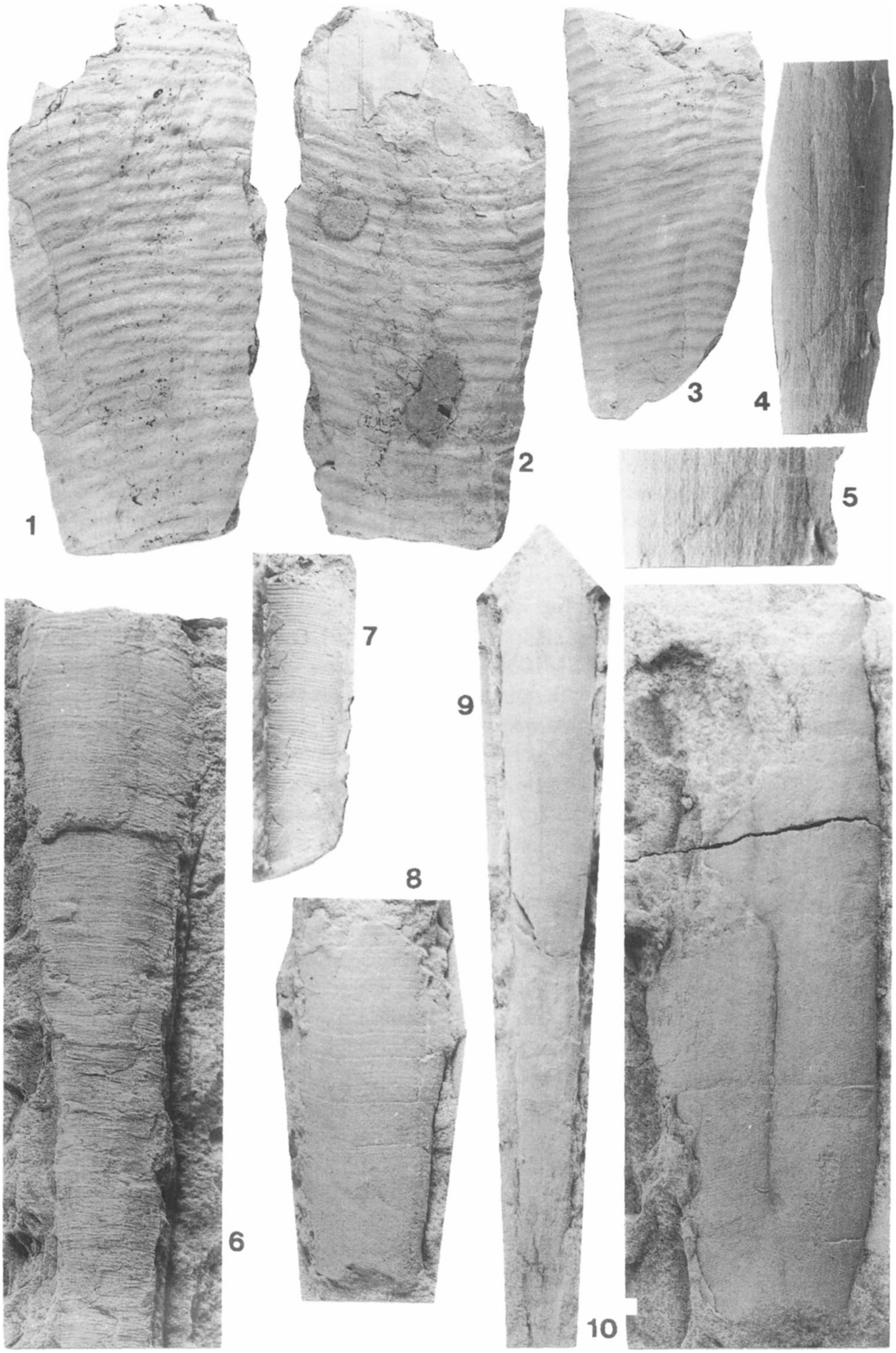


Fig. 7 — 1–3, *Endoceras perannulatum* (Portlock). 1 and 2, GSM103545; 3, GSM104153 (all x 0.5). 6, 7, and 9, *'Orthoceras' elongatocinctum* (Portlock). 6, GSM103562 (x 2); 7, TCD15886 (x 2.5); 9, GSM103564 (x 2). 4 and 5, *Pleurorthoceras subcostatum* Portlock, GSM103512 (4, x 4; 5, x 5), showing details of the shell sculpture. 8, *Tyrioceras subundulatum* (Portlock), GSM54308 (x 2.3). 10, *'Orthoceras' expansum* (Blake), GSM103511 (x 2).

v* 1843 *Orthoceras elongato-cinctum* Portlock, p. 372, fig. 2b (not 2a).
v* 1843 *Orthoceras tenui-cinctum* Portlock, p. 371.
? 1852 *Orthoceras tenuicinctum* (Portlk.), M'Coy in Sedgwick and M'Coy 1852, 317.
1854 *Orthoceras tenuicinctum,* Salter in Murchison, foss. 42.3.
? 1869 *Orthoceras elongato cinctum,* Portlock, Baily, p. 37, pl. 12, fig. 10.
v 1882 *Orthoceras elongatocinctum* Portlock, Blake, p. 119, pl. 13, figs 7, 8, 8a.
v 1891 *Orthoceras elongatocinctum* Portlock, Foord in Nicholson and Marr, p. 526.
v 1897 *Orthoceras* cf. *scabridum* (Angelin), Reed, p. 77.
v 1897 *Orthoceras* cf. *elongatocinctum* (Portlock), Reed, p. 77.
1993 *Geisonocerina elongatocinctum* (Portlock), Holland, p. 3, figs 1g, 1i.

Lectotype. GSM103561, pl. 27, fig. 26 of Portlock 1843.

Paralectotypes. GSM103558, GSM103560, GSM103562, GSM103564.

Type horizon. Killey Bridge Formation.

Type location. Locality 1.

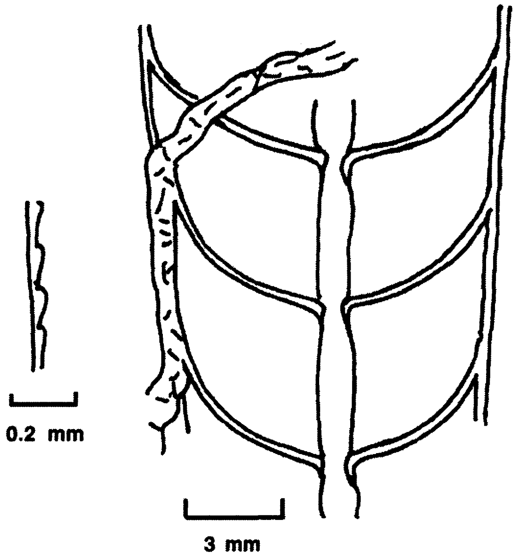


Fig. 8 — *'Orthoceras' elongatocinctum* (Portlock). Camera lucida of thin sections specimen from the Keisley Limestone. Left: TCD15882, showing detail of the shell wall. Right: TCD15883, showing the nature of the septal necks and connecting ring.

Other material. RSM1870.12.385, Desertcreat, precise locality uncertain. GSM103565, K4371–3, all from locality 1. GSM103511, syntype of *Orthoceras tenuicinctum* Portlock and holotype of *Orthoceras expansum* Blake, locality 1. NMINGF5354, probably locality 1. BELUM K24301–3, from locality 2. A12051–6 (incorporating at least 70 individuals and including the material referred to by Foord and Reed), C13524, C82984, and GSMZ63, 4, all from horizons in the Keisley Limestone at Keisley Quarry, Keisley, Cumbria. TCD15882–8 recovered from fallen blocks directly below the crags north of Keisley Quarry NGR [NY 7127 2393]. The lithology of these specimens suggests that most of the previously collected material also came from the crags north of the quarry. NMW88.30G.105–12: eight fragments from the Sholeshook Limestone. Exposure in carpark by cafe in Llanddowror NGR [SN 2555 1420], Dyfed.

Description. Type and topotype material consists of flattened and partially flattened portions of phragmocone showing a distinctive shell sculpture of transverse imbricate striae. In very few specimens transverse sutures may be seen. Best estimates of the rate of expansion of the phragmocone vary from just over 2° to just under 4°. Preserved portions of phragmocones range in mean diameter from 5mm to 13mm. All specimens show raised transverse striae with a density ranging from 4mm^{-1} to 7mm^{-1}. The striae consist of adapically imbricating laminae rising gently adorally to culminate in a sharp ridge and a rapid decline. Compression, combined with the dissolution of the shell, has resulted in striae appearing as separate raised threads; however, specimens such as GSM103562 and the Keisley material (described below) indicate the true nature of the shell sculpture. One specimen (K4373) shows sutures. These appear to be straight and transverse and indicate cameral depths which appear to conform to those of the Keisley Limestone material (see Fig. 9).

Specimens from the Keisley Limestone are very much better preserved and are used here to provide additional information on *'Orthoceras' elongatocinctum.* This material

Table 3 — Internal morphological data for two specimens of *'O.' elongatocinctum* from the Keisley Limestone. Dia = phragmocone diameter; Con = diameter of inside of connecting ring; Conw = thickness of connecting ring; SNdia = diameter of siphuncle at septal neck; SNl = length of septal neck.

	Dia	*Con*	*Conw*	*SNdia*	*SNl*
TCD15883	5.7mm	0.6mm	0.05mm	0.4mm	0.7mm
TCD15884	2.7mm	0.39mm	0.025mm	0.325mm	0.28mm

indicates that the species had a circular section with a phragmocone expanding at rates between 2° and 5°. The minimum phragmocone diameter recorded (TCD15882) is 1.3mm and maximum diameters reached are in the range of 25mm (TCD15887–8), although it is not possible to determine whether such specimens represent body-chambers. Two specimens (TCD15773–4) are thin sections and provide information about the internal morphology (see Table 3).

Both specimens show deep septa (septal depth about 40% of the phragmocone diameter). The siphuncle is narrow and tubular, being constricted at the septal necks. The septal necks are orthochoanitic and short, forming about 20% of the length of a siphonal segment. A number of specimens show the development of episeptal cameral deposits. However, their development is variable. In some adapical portions (A12052) episeptal cameral deposits are well developed, but in other specimens (TCD15882) they are absent or incipient. No specimen sectioned shows any evidence of siphonal deposits.

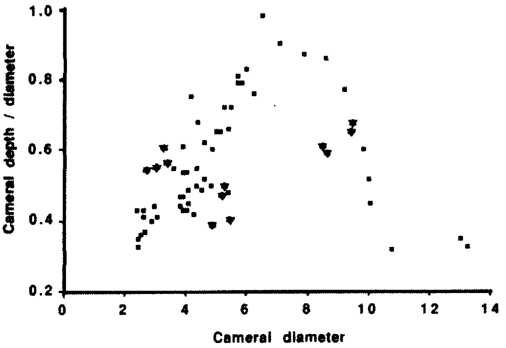


Fig. 9 — Plot of cameral diameter against cameral depth/cameral diameter for *'Orthoceras' elongatocinctum*, showing a general ontogenetic trend.

Plots of cameral depth/cameral diameter against cameral diameter (Fig. 8) suggest that an ontogenetic trend may be present wherein cameral depth increases up to a phragmocone diameter of about 6.5mm and then sharply decreases.

Many of the Kiesley Limestone specimens fail to demonstrate any shell sculpture, because the shell has either exfoliated or has been obscured by styolitic solution. In those specimens where sculpture remains, the immediate impression is that the sculpture consists of discrete raised threads. Closer study indicates that the sculpture consists of adapically imbricated lamellae with sharp culminations. This is confirmed by TCD15882 (Fig. 8), which shows a section through the phragmocone wall. The density of the striae may reach $10mm^{-1}$ in TCD15882 (1.4mm dia), decreasing to about $4mm^{-1}$ in adoral portions of phragmocone, but occasionally becoming more crowded. TCD15885 is a fragment of shell representing a conch about 20mm in diameter; the density of the striae remains at about $4mm^{-1}$.

Specimens from the Sholeshook Limestone consist predominantly of internal moulds of phragmocones ranging in diameter from 8mm to 15mm, with cameral depths of between 25% and 30%. The siphuncle is about 8% of the phragmocone diameter. NMW88.30G.111 shows a shell sculpture of imbricate transverse striae with a density of $5mm^{-1}$.

Remarks. GSM103559, listed as a syntype of *O. elongatocinctum* by Tunnicliff (1980) and figured by Portlock (1843, pl. 27, fig. 2a), came from the Bardahessaigh Formation. It is too poorly preserved to be determined as anything other than an orthoconic nautiloid.

Some justification is required for the use of the Keisley Limestone specimens in describing *'O.' elongatocinctum*, as it could be argued that the type and topotype material is too poorly preserved to be compared with any other set of specimens. I consider that the few fragments of morphological information that can be extracted from the types and topotypes (cameral depth, phragmocone expansion rate and shell sculpture) all concur with the Keisley Limestone material. Further, Orchard (1980, 13) indicated a low to mid-Cautleyan date for the conodont fauna in the north wall of Keisley Quarry. If the succession is not repeated by folding or faulting, then the material discussed above, which came from crags to the north of the north wall of the quarry, may be older, and of a similar age to that of locality 1. Price's (1973, 234) description of the lithological succession in the Llanddowror area indicates that the cephalopods came from a horizon of Cautleyan 2 age.

As body-chambers of this species are unknown and the internal morphology and shell sculpture are insufficiently different from *Orthoceras* to be certain of distinction, the term *'Orthoceras'*, as recommended by Holland (1967), is used. The constriction of the siphuncle at the septal necks appears to be more marked than in *Orthoceras regulare* (see Flower 1962, pl. 4, figs 6, 7), but this is insufficient justification for proposing a new genus.

The occurrence of cameral deposits (in some cases well developed) in the Keisley Limestone specimens may also be seen as significant. However, in the *O. regulare* material studied by Flower (1962), the smallest diameter of phragmocone was about 8.8mm, showing incipient cameral deposits. Specimens such as SMA12052 show deposits developing at a diameter of about 5mm. The presence of well-developed cameral deposits cannot safely be used to distinguish the material under study from *Orthoceras*. It should not be construed from the fact that some extreme adapical fragments do not contain cameral deposits whereas some more adoral fragments do that more than one species is present in the Keisley Limestone. The morphologies of all these individuals are otherwise very similar and it is more likely that the apparently inconsistent occurrence of cameral deposits reflects early morbidity in the population, with many individuals failing to reach a stage where cameral deposits would have developed.

The assignment of *'O'. elongatocinctum* to *Geisonocerina* by Holland (1993) depends on the nature of that genus. Foerste (1935, 22) distinguished *Geisonoceras* Hyatt from *Geisonocerina* on the grounds that the latter differed in 'being ornamented by numerous close, raised transverse lines or striae, instead of comparatively broad bands'. Both Foerste (1935) and Sweet (1964) noted the probable artificial nature of the genus. Internal structures are unknown and there is little justification for placing the genus within the Geisonoceratidae. Similarly, *'Orthoceras' elongatocinctum* should not be regarded as belonging within the Geisonoceratidae as the known internal structures indicate that siphonal annuli are not present and the nature of the siphonal deposits also differ. Assignment to *Geisonocerina* may be possible, but can only be justified after a restudy of the type and topotype material of *Orthoceras wauwatosense*, the type species of *Geisonocerina*.

Genus *Michelinoceras* Foerste 1932

Type species. Orthoceras michelini Barrande 1866. Original designation.

Michelinoceras? expansum Blake 1882. Fig. 7.10.

v* 1843 *Orthoceras tenui-cinctum*, Portlock, p. 371.

v* 1882 *Orthoceras expansum*, Blake, p. 118, pl. 16, fig. 11.

Holotype. GSM103511, holotype by monotypy. Syntype of *Orthoceras tenuicinctum*. Portlock.

Type location. Locality 1.

Description. The holotype consists of a partially flattened phragmocone 48mm long. The expansion rate cannot be calculated, but the diameter is estimated at about 12mm. Four probable sutures can be seen. These are straight and directly transverse, being 12.5mm, 11.5mm and 10.5mm apart, giving an average cameral depth of 96%. The shell sculpture consists of adapically imbricated transverse striae with a density of 4mm^{-1}. The striae are markedly oblique to the plane normal to the conch axis and, at their maximum, transect sutures at 20°. Nothing is known of the internal structure of the phragmocone or of the body-chamber.

Remarks. GSM103511 was listed as a syntype of *Orthoceras tenuicinctum* Portlock by Tunnicliff (1980) on the basis of Portlock's label. Blake (1882) was probably unaware of the status of the specimen when he designated it as *Orthoceras expansum. O. tenuicinctum* was described by Portlock but not figured. Of the material recognised as syntypes of *O. tenuicinctum* by Tunnicliff, three (K4371–3) belong to *'O.' elongatocinctum.*

Portlock's description of *O. tenuicinctum* (1843, 371–2) is vague and contradictory. The species may well be based more on preservational features than original morphology. Further, in describing the septa, Portlock first stated that 'the septa are not perceptible in any of the specimens', and second that 'they occasionally occur grouped together in great abundance'. These statements are incompatible with each other and it is probably impossible to understand Portlock's concept of the species. M'Coy's (1852, in Sedgwick and M'Coy 1851–5) description was based at least in part on GSM103555, figured by Portlock (p. 377, pl. 27, fig. 5) as *Orthoceras regulare?* (Munster). The description does not appear to relate to any of the syntypes. It seems unlikely that M'Coy's description has any validity in reference to *O. tenuicinctum.* The specimen described by Blake as *O. expansum* is quite different from *O. tenuicinctum* as described by Portlock (if the septa were crowded) insofar as the septa are set far apart. Blake described the phragmocone of *O. expansum* as rapidly expanding. The expansion rate of the holotype cannot be measured accurately, but it seems unlikely that it is as high as Blake suggested.

Michelinoceras? expansum differs from all the other orthocerids currently known from the Killey Bridge Formation in its possession of extremely deep camerae and rather strongly inclined striae. Its generic position is uncertain because it is unknown internally, but the very deep camerae suggest assignment to *Michelinoceras.*

Genus *Pleurorthoceras* Flower 1962

Type species. Orthoceras clarksvillense Foerste, 1924; original designation.

Pleurorthoceras subcostatum (Portlock). Figs 7.4, 5; 10.1, 6.

1843 *Orthoceras subcostus* Portlock, p. 371, pl. 26, fig. 6a–b.

v 1843 *Orthoceras lineatum* (Hisinger), Portlock, p. 370, pl. 27, fig. 3a, ?3b.

v 1882 *Orthoceras lineatum,* Hisinger, Blake, p. 127, pl. 7, figs 2, 11.

Neotype. The figured specimen of *Orthoceras subcostatus* Portlock (1843, pl. 26, fig. 6a–b), because of the difference in ornamentation, may represent more than one specimen. If this was the case then two syntypes may originally have existed. Neither specimen has been found in Geological Survey, Ulster Museum or Trinity College collections, the main depositories of Portlock's material. The specimen selected as neotype is TCD7933.

Additional material. GSM103510, figured as *Orthoceras lineatum* (Hisinger), Portlock, pl. 27, fig. 3a. GSM103512, figured as *Orthoceras lineatum* Hisinger, Blake, pl. 7, fig. 11. K4380, probably the specimen figured by Blake (pl. 7, fig. 2). All believed to have come from locality 1. BELUM K14204 and K24205, from locality 2.

Diagnosis. Slender orthocones. Shell sculpture consisting of 30 to 40 fine, raised longitudinal lirae. Lirae alternating between dominant and subordinate in some specimens. Lirae give way adorally to a cancellate pattern of dense longitudinal and transverse striae. Cameral depth ranging from 25% to 40% of the phragmocone diameter. Siphuncle not seen. Cameral deposits mural only.

Description. Overall dimensions of the neotype and additional material are given in Table 4. The neotype is partially crushed adorally, and adapically gives way to a koleoceras structure. Immediately adoral of the 'koleoceras' structure and partly underlying it, camerae may be observed that are partly formed by internal moulds of sediment and partly from the collapse of the sediment forming the external

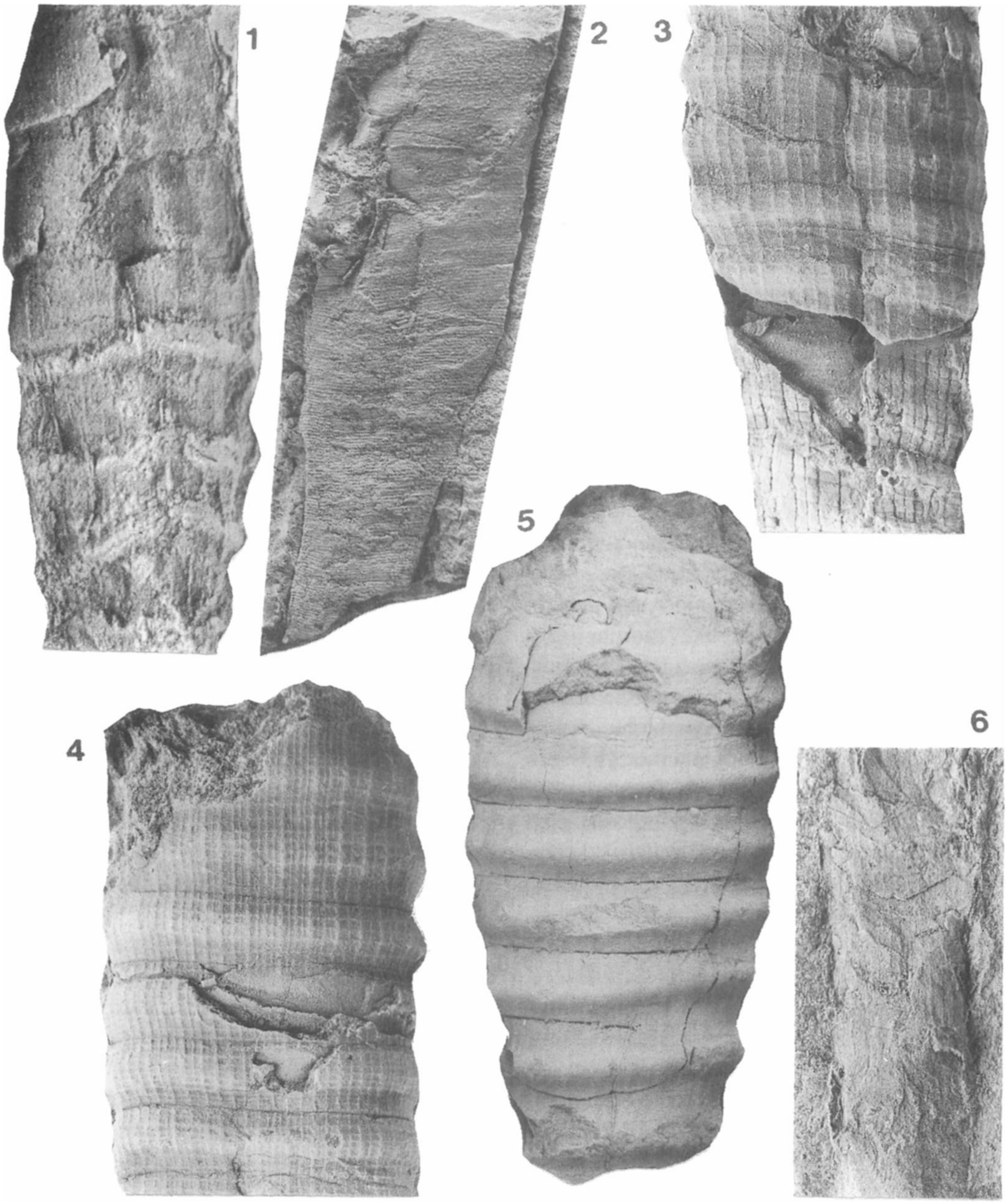


Fig. 10 — 1 and 6, *Pleurorthoceras subcostatum* (Portlock). 1, TCD7933 (x 7), showing moulds formed by the dissolution of cameral deposits with the mould of the shell wall impressed on the cameral mould. 6, BELUM K4380 (x 5). 2, *'Orthoceras' elongatocinctum* (Portlock), BELUM K24203 (x 2). 3–5, *Gorbyoceras gracile* (Portlock). 3, GSM103499 (x 2.4). 4, GSM103501 (x 2.4). 5, BELUM K20638 (x 1.5).

mould onto the internal mould. The surface produced shows the longitudinal lirae sitting on a concave impression which is more or less symmetrical over the presumed venter and deepest on the ventro-lateral flanks. These structures are interpreted as cameral deposits which developed much more strongly on the mural surface of the septum than on the episeptal surface. Development may have been stronger on either side of the venter also.

Table 4 — Morphological data for *Pleurorthoceras subcostatum.* Length = length of conch fragment; Mean dia. = mean diameter of conch; Exp. rate = estimated rate of expansion in degrees; Longit. striae = number of longitudinal striae in circumference (or density per mm); Trans. striae = density of transverse striae per mm.

Spec. no.	*Length*	*Mean dia.*	*Exp. rate*	*Longit. striae*	*Trans. striae*
TCD 7933	90mm	7mm	3°20'	40	—
GSM 103510	120mm	6mm	2°	36	—
GSM 103512	68mm	6mm	4°	34; 8mm^{-1}	8mm^{-1}
K4380	55mm	3mm	3°30'	34	—
K24204	43mm	8mm	—	34	—
K24205	70mm	7mm	3°30'	32	—

The volume surrounded by the koleoceras structure appears to consist of collapsed and broken shell. No siphuncle has been seen.

Of the other specimens, GSM103510 and K4380 both provide evidence for the presence of cameral deposits in their adapical portions, in so far as both are carbonate-filled. GSM103512 provides evidence for an ontogenetic change in shell sculpture from longitudinal lirae to a fine meshwork of cancellate striae. This specimen appears to consist of about 26mm of body-chamber. The change in shell sculpture occurs near the base of the body-chamber.

Remarks. Flower (1962, 35–6) noted that *Pleurorthoceras* was peculiar in the development of strictly mural cameral deposits. Both the then known species (*Pleurorthoceras clarkesvillense* and *P. selkirkense*) were similar to each other in their internal morphology. Foerste (1924, 220) described the surface of *P. clarkesvillense* as smooth. The surface of *P. selkirkense* does not appear to be known. Cameral depth in both species appears to be greater (40% to 70%) than in *P. subcostatum* and the conch may be much smaller in overall size. The detail of the surface of the cameral deposits in *P. subcostatum* cannot be observed in the same detail as those of the American species, but there seems no reason to doubt their nature on the basis of gross detail. Apart from the smaller proportions, the main difference seen in *P. subcostatum* appears to be the presence of a shell sculpture of longitudinal lirae. The fact that this appears to give way to a fine cancellate structure in GSM103512 suggests that more adorally preserved portions of conch might well be smooth, further reducing the distinction between these species. *P. clarkesvillense* came from either the Liberty or Waynsville Member of the Richmond according to Foerste (*ibid.*) which, on the basis of Sweet *et al.* 1959 and Ross *et al.* 1982, is Richmondian and may correlate with the Cautleyan or Rawtheyan. *P. selkirkense* came from the Selkirk Limestone of Manitoba and is late Maysvillian (= late Pusgillian) in age. The species described falls within the known range of the genus.

Superfamily Pseudorthocerataceae Flower and Caster 1935

Family Proteoceratidae Flower 1962

Genus *Gorbyoceras* Shimizu and Obata 1935

Type species. Orthoceras gorbyi Miller, 1894, p. 322; original designation.

Gorbyoceras gracile (Portlock). Figs 10.3, 4, 5; 11; 13.2, 4, 5, 6.

v* 1843 *Orthoceras gracile,* Portlock, p. 366, pl. 25, fig. 2.

v* 1843 *Orthoceras tubicinella*-(var. *subnodosum),* Portlock, p. 367, pl. 25, fig. 3a, b.

v* 1843 *Orthoceras tubicinella*-(var.) elliptic, Portlock, p. 367, pl. 25, figs 5–6.

v* 1843 *Orthoceras calamiteum,* Portlock, p. 365, pl. 25, fig. 1a, b.

v* 1882 *Orthoceras gracile,* Portlock, Blake, p. 85, pl. 3, figs 9, 9a, 9b, 9c.

Lectotype. GSM104393, figured Portlock (1843, pl. 25, fig. 2). Locality 1.

Paratype. GSM103494.

Other material. GSM103497, *Orthoceras*

Table 5 — Morphological data for *Gorbyoceras gracile*. Max. dia. = maximum diameter of the shell; Exp. rate = rate of expansion of the shell in degrees; Dist. ann. = distance between culminations in annulations in mm; Dia. = diameter at which wavelength of annulations was measured; Cam. depth = cameral depth; Dia. = diameter at which cameral depth was measured; L. lirae = number of primary longitudinal lirae present; Sub. lirae = number of subsidiary lirae present; Tran. striae = density of transverse striae.

Specimen	*Max. dia.*	*Exp. rate*	*Dist. ann.*	*Dia.*	*Cam. depth*	*Dia.*	*L. lirae*	*Sub. lirae*	*Tran. striae.*
GSM103493	—	—	5.5mm	—	5.5mm	—	4mm apart.	—	—
GSM103494	29mm	—	7mm	29mm	—	—	23 in circ.	—	5mm^{-1}
GSM103495	15.5mm	4°	4mm	—	—	—	24 in circ.	48 in circ.	2–5mm^{-1}
GSM103496	16.5mm	4°	5.0mm	16mm	—	—	26 in circ.	26 in circ.	+?
			5.5mm	17mm					
GSM103497	19mm	—	4mm	—	—	—	20 in circ.	20 in circ.	1–2mm^{-1}
GSM103498	6mm	—	2mm	6mm	—	—	0.7mm apart.	—	—
GSM103499	13mm	4.5° at 8.4mm	2.2mm	5.1mm	—	—	50	—	0.6mm^{-1}
		1.6° at 11mm	2.5mm	6.4mm					0.6mm^{-1}
			4.0mm	11.5mm					
GSM103500	29mm	—	7mm	29mm	—	—	90 in circ.	—	3mm^{-1}
GSM103501	12.4mm	1.5°	5mm	11.8mm	3.8mm	11.2mm	36 in circ.	32 in circ.	2.5mm^{-1}
			3.5mm	10.8mm					
K4362	—	—	4mm	—	—	—	1mm apart.	—	1mm^{-1}
K4364	20mm	—	6mm	—	—	—	42 in circ.	—	0.75mm^{-1}
K20635	—	—	6.5mm	—	—	—	2mm apart.	1mm apart.	—?
K20638	23mm	—	6.5mm	—	6.5mm	—	32 in circ.	—	—?
K24206	< 20mm	—	7mm	—	—	—	3mm apart.	1mm apart.	1mm^{-1}
K24207	< 13mm	—	4.5mm	—	—	—	3mm apart.	1mm apart.	—?
RSM1870.12.384a	—	—	4mm	—	—	—	1mm apart.	—	1mm^{-1}
RSM1870.12.384b	—	—	4.5mm	—	—	—	0.4mm apart.	—	15mm^{-1}
TCD7932	13mm	—	5.5mm	—	—	—	1.5mm apart.	1.5mm apart.	2.5mm^{-1}
TCD7943	3.5mm	3.8°	2.5mm	—	—	—	48 in circ.	—	2mm^{-1}
	17.2mm		5.5mm				88 in circ.		1mm^{-1}

tubicinella Sowerby (var. *sub-nodosum* Portlock), Portlock (1843, p. 367, pl. 25, fig. 3a, b); holotype of subspecies. GSM103496, *Orthoceras tubicinella* figured Portlock (1843, p. 367, pl. 25, fig. 4); figured Blake (1882, p. 85, pl. 3, fig. 9). GSM103498, *Orthoceras tubicinella.* Recognised as *Orthoceras calamiteum* by Portlock: GSM103499 (Portlock 1837, pl. 4, fig. 4), GSM103501 (Portlock 1843, pl. 25, fig. 1a, b). GSM103466 ?syntype of *Koleoceras pseudo-speciosum* Portlock. GSM103500, GSM103995, K4362, K4364. Undesignated: RSM1870.12.384a, RSM1870.12.384b. BELUM K20635a, K20638, K20634, TCD7392, TCD7843. All from locality 1. K24206–7, 4 from locality 2. TCD15889a, b; TCD15890a, b; TCD15891, from the Ladyburn Mudstone Formation of the Drummuck Group, Glenmard Wood NGR [NS 2572 0279], Quarrel Hill, Strathclyde Region.

Diagnosis. Gorbyoceras with transverse to oblique annulations and sutures. Cameral depth and annulation wavelength about 20% phragmocone diameter; sutures invariably occurring in the troughs. Annulations sharp to rounded, becoming suppressed and disappearing adorally. Conch ornament highly variable, consisting of transverse striae (sometimes absent) ranging from 0.8mm^{-1} to 15mm^{-1} in density. Longitudinal lirae present; secondary and tertiary lirae sometimes present. Twenty to ninety primary lirae in circumference; number may vary in an individual. Septal depth 25% phragmocone diameter. Siphuncle 60% across phragmocone from venter; 7% phragmocone diameter at septal neck and 17% in connecting ring. Connecting ring probably barrel-shaped. Septal necks cyrtochoanitic, equi-dimensional. Cameral deposits episeptal only. Siphonal deposits not observed.

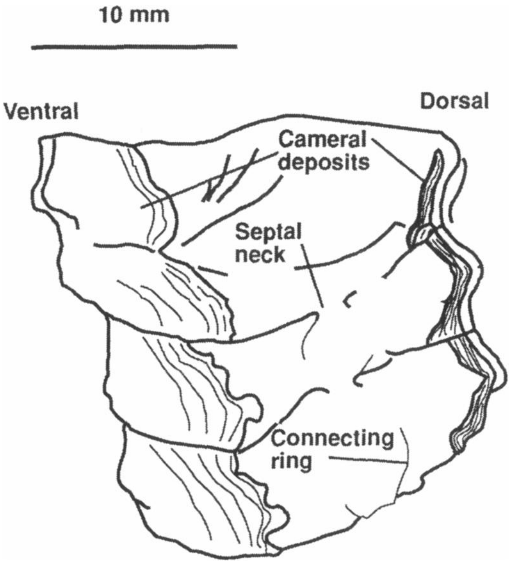


Fig. 11 — Camera lucida of dorso-ventral section of TCD15889a from the Ladyburn Mudstone, showing the nature of the siphuncle and cameral deposits.

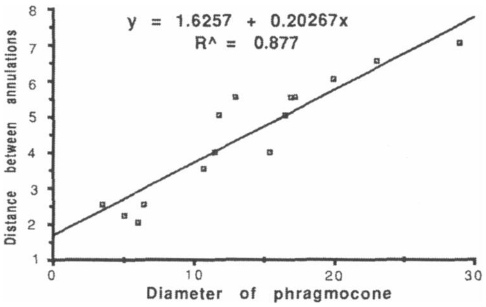


Fig. 12 — Plot of the distance between annulations against conch diameter for *Gorbyoceras gracile.*

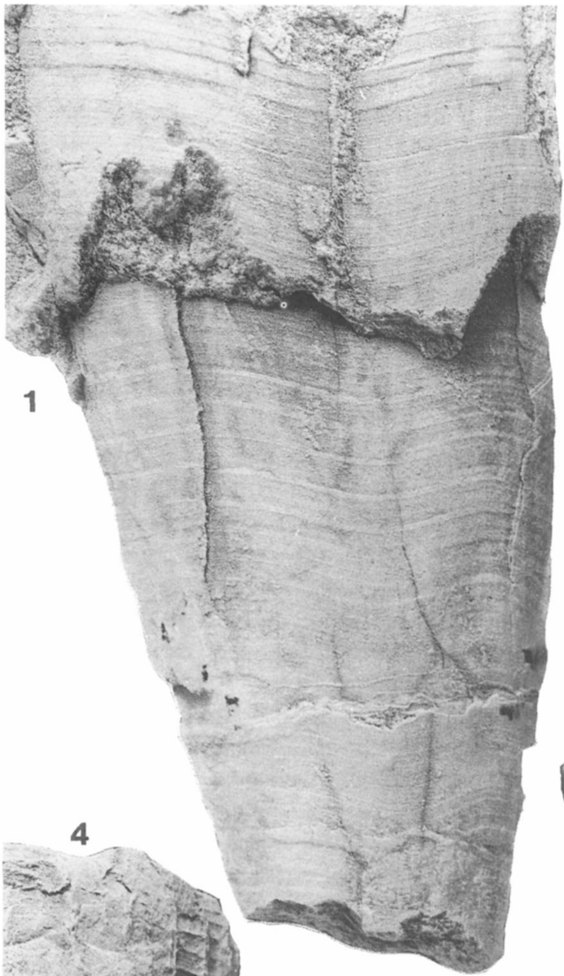
Description. The above diagnosis includes the Scottish material which provides all the information on internal morphology.

The material included consists of fragments of conch ranging from 3mm to 30mm in diameter. Annulations vary in outline from rounded to sharp. Some of this variation may have resulted from crushing; however, the high correlation of wavelength with diameter (Fig. 12) suggests that the variation is real. Conch sculpture, although consisting of longitudinal lirae and transverse striae, is in fact highly variable (Table 5). Within a single individual (TCD7943) there is an approximate doubling of the number of lirae along the length of the conch. This specimen is particularly long, but it is not possible to see where this doubling takes place. This may be because the addition of lirae is gradational. Such increases may not be indicated on other specimens simply because the fragments remaining are too short for such variation to be detected. Other individuals show regular variation in the strength of the lirae so that in GSM103494 thick primary lirae are seen, in K20635 thinner, secondary lirae alternate between the primaries, and in GSM103495 even thinner tertiary lirae occur between the secondaries and primaries. Combined with the variation in density of the transverse striae, the shell sculpture is highly variable within the species. The fragmentary and crushed nature of most of the material makes estimates of the rate of expansion of the conch uncertain. However, a number of the measurements indicate a rate of about 4°.

Cameral deposits, present in TCD15889a–b, are very strongly developed dorsally and are essentially episeptal with a thin mural development. Most of the development appears to arise from the episeptal surface of the deposit which extends both adorally and toward the axis of the camerae. The surface of the deposit appears to become mammilate at a late stage.

Remarks. Portlock's original recognition of three species was based on the presence of alternately strong and fine ribs in *Orthoceras calamiteum,* more distant annulations with no intermediate ribs and traces only of transverse ribs in *O. gracile,* and oblique and sharp annulations in *O. tubicinella.* The high correlation between the wavelength of the annulations and the conch diameter (Fig. 12) indicates that the increase in distance between annulations and probably also the reduction in amplitude may be functions of age. This high correlation tends to unite this material. Shell sculpture is regarded here as extremely plastic within the species.

Material from the Ladyburn Mudstone Formation (younger than the Killey Bridge Formation) is included on the grounds that the small number of specimens available fall



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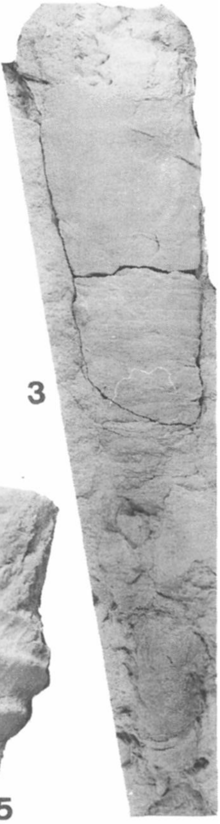

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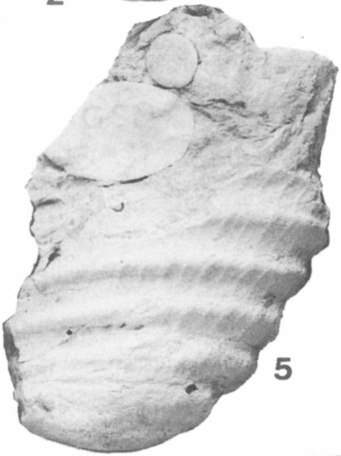

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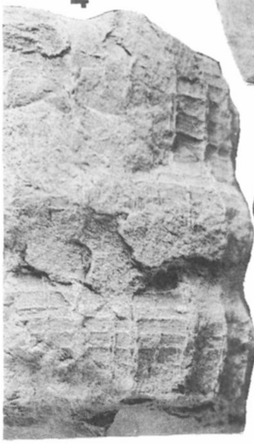

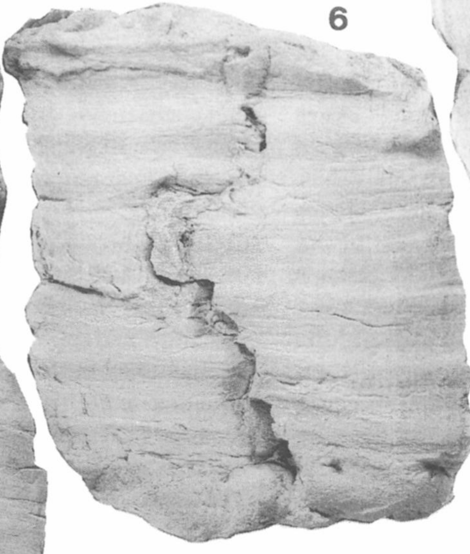

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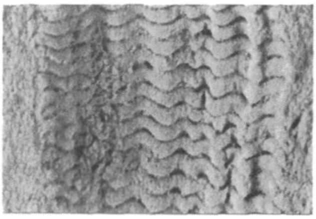

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within the range of variation seen in the Killey Bridge Formation material. However, it may be objected that cameral deposits have not been observed in Killey Bridge Formation material. This may be because pieces of phragmocone containing cameral deposits were differentially transported, or that such sections, being filled with carbonate, had no chance of sediment infill and the development of moulds and consequently disappeared through dissolution. Figure 12, showing a lack of small diameter phragmocones, suggests that some separation has taken place and may indicate that the lack of evidence for cameral deposits does not mean that they did not exist.

Portlock and possibly Blake included material from the Bardahessaigh Formation within their concepts of the species. These are excluded here on the grounds of the different age of the Bardahessaigh Formation and because of differences in the gross morphology (Evans, in prep.).

Gorbyoceras species of a broadly similar age have been reported from North America and the Baltic region. Flower (1946) described several species of *Gorbyoceras,* including the type mostly from the Whitewater Formation (= late Rawtheyan – early Hirnantian (Ross *et al.* 1982)) of Indiana, but also from farther afield. Although there seems to be a similar range of variation amongst this material, it is not possible, without seeing the relevant specimens, to determine how many species may be present. Only *G. duncanae* appears to differ strongly from the rest in the much deeper septa. The other species (including the type) appear to be distinct on the basis of both their very shallow septa and generally narrower camerae, while the siphonal segment may be more expanded. Wilson (1960, 37, 38, pl. 10) named two new species from the Maysvillian of Ottawa. *G.? latiannulatum* has sutures intersecting the annuli and might fall into the definition of *Metaspyroceras. G. perovale* shows some similarity with the material described above, both in the expansion rate and in the distribution of the annulations. However, apart from the position of the siphuncle, nothing appears to be known of the internal morphology. Wilson noted that the siphuncle was ventrad of the centre, but it is not clear how the dorsum and venter could have been distinguished in this specimen.

A number of species from the English Head and Vaureal Formations of Anticosti Island and the White Head Formation of the Gaspe Peninsula (Foerste 1928a; 1928b; 1936) were referred to *'Gorbyoceras'* or *Gorbyoceras* by Flower (1946). All differ from the present material. In the Baltic region, Dzik (1984) figured material which he ascribed to *Gorbyoceras textumaraneum* (Roemer), *Spyroceras senckenbergi* Teichert., and *Gorbyoceras* sp. All came from erratic boulders and only the first two species are undoubtedly from the Ashgill Series, having been recorded from the Lyckholm Formation (Teichert 1930). There are similarities between all three and the material described above. It may be that if sufficient material was known a broad variation in morphology might be detected. It is believed here that *G. gracile* is more similar to the Baltic species than any others.

Superfamily Lituidaceae Dzik 1984 [Nom Transl. Herein]

Family Sinoceratidae Shimizu and Obata, 1935

Sinoceras was placed in the Michelinoceratinae by Sweet (1964) and considered as doubtfully distinct from *Michelinoceras. Sinoceras* has a relatively rapid rate of expansion and exhibits cameral deposits which are continuous with the siphonal deposits, while connecting rings are often broken. Similar features are seen in other lituitids. The presence of well-developed cameral deposits

Fig. 13 — 1, *Tyrioceras subundulatum* (Portlock), BELUM K24028 (x 2.3). 2, 4–6 and 8, *Gorbyoceras gracile* (Portlock). 2, GSM103502 (x 1.5). 4, TCD15891 (x 2.5), Ladyburn Mudstone. 5, GSM103497 (x 2). 6, GSM103494 (x 1.5). 8, GSM103493 (x 2). 3, Orthocerida family and genus indet. *pseudospeciosum* (Portlock), GSM103464 (x 0.5). 7, Orthocerida family and genus indet. *pomeroense* (Portlock), GSM103428 (x 0.5). 9, *Piersaloceras* sp., BELUM K24210 (x 5).

and the general morphology (excluding coiling) of the conch suggests that the lituitids are orthoceratids. *Sinoceras, Rhynchorthoceras* and *Tyrioceras* form a distinct group of lituitids.

Genus *Tyrioceras* Strand, 1934

Type species. Tyrioceras kjerulfi Strand; original designation.

[? = *Imbricatoceras* Holland 1992]

Tyrioceras? subundulatum (Portlock). Figs 7.8; 13.1.

v* 1843 *Orthoceras sub-undulatum,* Portlock, p. 373, pl. 28, fig. 2.

v* 1882 *Orthoceras subundulatum,* Portlock, Blake, p. 133 (?pl. 11, figs 8, 9, 10?).

v* 1992 *Imbricatoceras subundulatum* (Portlock), Holland, p. 123.

Holotype. GSM54308. Holotype by monotypy. Figured; Portlock 1843, pl. 28, fig. 2. Possibly from locality 1.

Other material. BELUM K24028. Locality 2.

Description. The holotype consists of 24mm of partially flattened conch expanding from 10.8mm to 12.5mm in 13.0mm, giving an expansion rate of about 10°. There is no evidence of sutures, or of internal structures. The shell sculpture consists of adapically imbricated lamellae developed at several scales. These are a primary set with a density of 1–2mm^{-1}, a secondary set at 2–4mm^{-1}, and a tertiary set at +6mm^{-1}. These striae exhibit a slight sinus 0.5mm deep and 5mm wide.

K24208 is a partially flattened fragment of phragmocone and possibly a body-chamber 55mm long. The expansion rate is estimated as being about 9°. The maximum and minimum diameters are about 22mm and 8mm respectively. No internal structures are evident. Two sutures are present. These are straight and transverse, 10mm apart, and present at 13mm and 16mm diameter, giving a cameral depth 70% of that of the phragmocone diameter. The adoral 35mm of the conch is thought to represent body-chamber because of the lack of septation and the possible presence of an aperture. Shell sculpture again consists of adorally imbricate lamellae with a primary set usually 2.0mm to 2.5mm apart, and rarely up to 4mm. A secondary set is present, usually consisting of five striae, their separation dependent upon the separation of the primary set. A tertiary set may be present, but cannot be distinguished with certainty. The striae form a distinct undulatory pattern circumscribing the conch. The undulations consist of three sinuses, each about 2.5mm deep, where the diameter is 20mm. The axes of the sinuses are about 11mm apart, and if the central one is considered to be ventral in position then the remaining two are ventro-lateral in position.

Remarks. As the bulk of the information is derived from K24208, it is necessary to outline the reasons for assuming that the two specimens represent the same species. These are the similarity in the expansion rates of the two specimens and in the shell sculpture. In the latter case similarity is strong in that a set of differing orders of striae are present, but rather weaker insofar as the undulatory nature of the striae are concerned. Although the pattern of sculpture is clear in K24208, this pattern is only hinted at in the holotype. This may be because the holotype represents a juvenile portion of the conch where the later pattern has not yet been fully established, or the two specimens may represent different taxa. It is emphasised that because of this uncertainty, the remarks below certainly apertain to K24208 and probably also to the holotype.

Orthoceras subundulatum shows three characters: a high expansion rate, deep camerae, and ventral and lateral or ventro-lateral sinuses. The latter are not strongly pronounced. These characters are also known in the lituitid *Tyrioceras* Strand. Strand's description of the type species *T. kjerulfi* (1934, 49–50, pl. 6) is of a body-chamber with a slightly compressed section laterally. The shell sculpture indicates the presence of ventral and lateral sinuses as well as a possible broader dorsal sinus. The bands forming the sculpture were described as bands overlapping each other adorally. This and Strand's figure indicate that the conch sculpture consisted of adorally imbricated bands. The conch is far larger than K24208 at 103mm diameter dorso-ventrally. In a second specimen attributed to *Tyrioceras?* sp. the nature of the shell sculpture could not be fully ascertained, but was thought to be similar. Maximum cameral depth in this specimen appears to have been about 55% of the phragmocone diameter adapically and may have been about 30% in more adoral camerae. This specimen is also much larger than the specimens under discussion.

Frye (1982) described a new species, *Tyrioceras warburgae,* from the Boda Limestone. This species appears to confirm the presence of a dorsal sinus in the genus. It differs in its greater expansion rate and deeper sinuses. K24206 is much smaller than any of the Scandinavian specimens. Cameral depth is greater, and it is uncertain whether a dorsal sinus is present. The increased cameral depth may be because the specimen represents a relatively juvenile stage. There is some evidence from *Tyrioceras kjerulfi* that cameral depth may increase adapically. Similarly, there was some uncertainty as to the presence of a dorsal sinus in the type species.

Orthocerida family and genus indet. *pomeroense* (Portlock)

Figs 13.7; 14.1

v* 1843 *Orthoceras Pomeroense,* Portlock, p. 370, pl. 26, figs 4, 5.

v* 1843 *Orthoceras complanaro-septum,* Portlock, p. 374, pl. 28b, fig. 1.

1843 *Orthoceras pomeroense* Portlock, Blake, p. 123.

Material. GSM103480, syntype, figured Portlock, pl. 26, fig. 4. GSM103481, syntype, figured Portlock, pl. 26, fig. 5. GSM, possible syntype. GSM103483, syntype of *Orthoceras complanato-septum,* figured Portlock, pl. 28b, fig. 5. K4388, syntype of *Orthoceras complanato-septum,* and counterpart of GSM103483. All from locality 1. Questionably assigned. TCD15892 from the Ladyburn Mudstone Formation of the Drummuck Group, Glenmard Wood NGR [NS 2572 0279], Quarrel Hill, Strathclyde Region, Scotland.

Description. GSM103480 consists of two large fragments of shell probably belonging to the same conch. With an estimated circumference of 260mm the diameter of the conch was probably 80mm. At the base of the smaller fragment there appears to be a flattened septum. This specimen might represent part of a body-chamber. The conch surface consists of fine imbricate striae with a density of 4–5mm^{-1}. These appear to be separated by gaps 2–3mm apart and larger ones 5–6mm apart. The curvature of the sculpture seen in this specimen is probably due to mild deformation.

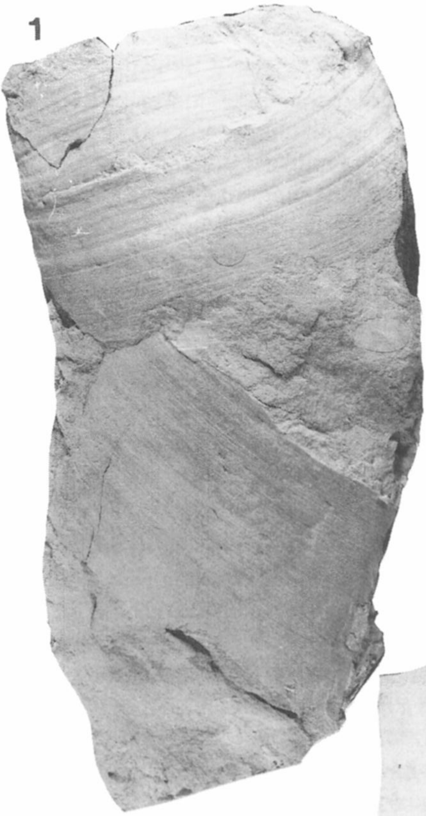
GSM103481 is 205mm long and expands in its estimated diameter from 65mm to 73mm in 115mm, giving a rate of increase of about 4°. Sutures are present. These are straight and were probably transverse. Cameral depth is estimated at 22% where the diameter is 73mm and 16% at a diameter of 65mm. Shell sculpture is largely obscured but appears to consist of imbricate striae between 1.5mm and 2mm apart and much finer striae with a density of 4–6mm^{-1}.

GSM103482 is a fragment 60mm long and originally about 50mm in diameter. The sutures are straight and transverse, indicating a cameral depth of about 17%. Shell sculpture consists of major imbricate striae 1–2mm apart and minor striae with a density of 4–5mm^{-1}.

GSM103483 and K4388 represent a vertically embedded portion of phragmocone showing a septal surface. This is partially compressed and elliptical to ovoid in transverse section, 60mm along the long axis and 53mm along the short axis. The septal foramen is situated 32mm from the margin and is about 7mm in diameter. There is no clue as to the nature of the septal necks. The distance between the sutures is 5mm. This low value probably results from the compression the specimen has undergone.

TCD15892 is a short piece of phragmocone about 20mm long and 35mm in diameter. Cameral depth is about 25% and septal depth about 33%. The siphuncle is slightly eccentric and is 20mm from the margin. The septal foramen is 6.5mm in diameter. Sectioning of the specimen revealed orthochoanitic septal necks 5mm long, approaching half the depth of the camerae. The shell appears to be smooth.

Remarks. The specimen figured by Blake (1882, pl. 11, fig. 1) is GSM103486, labelled by Portlock as *Orthoceras irregulare?* Munster. It originated from the Llandovery Series, Lime Hill Beds. This specimen is not regarded here as belonging to the species.



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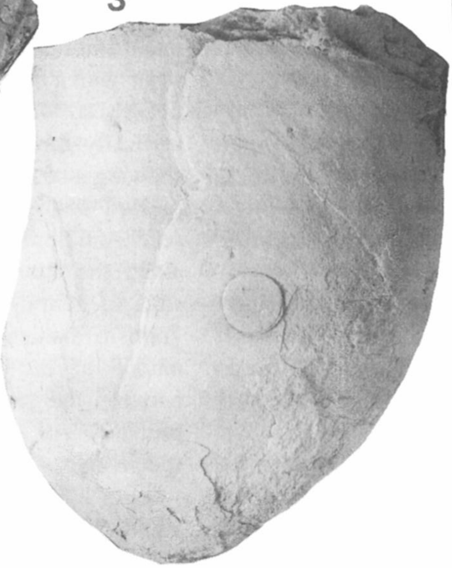

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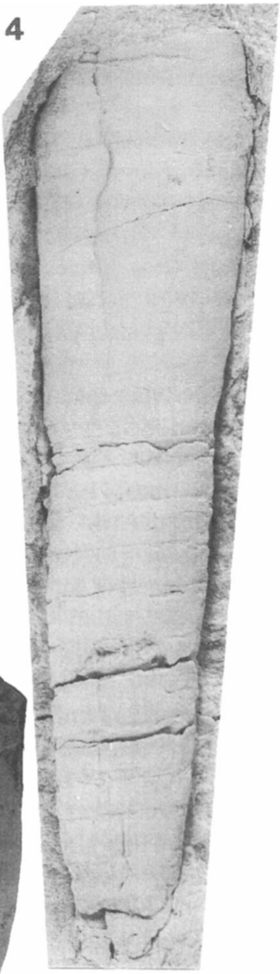

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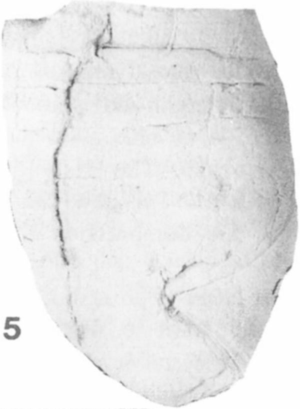

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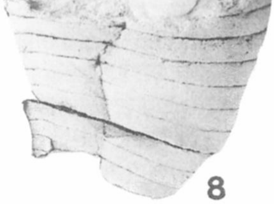

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Blake placed *Orthoceras regulare,* Munster, Portlock and *Orthoceras tumidum* Portlock in his synonymy. The syntypes of *Orthoceras tumidum* are too poorly preserved to be compared with other material. GSM104194, *O. regulare?* (figured, Portlock, pl. 27, fig. 4), may be a body-chamber about 30mm in diameter. The surface is smooth and there seems little reason to associate it with *O. pomeroense.*

Apart from the fact that *O. pomeroense* is an orthocerid, reasonable assignment is not possible. The species was an orthocone, which may have reached 80mm in diameter and a length of at least one metre. Camerae were shallow and the siphuncle slightly eccentric, possibly with rather long orthochoanitic septal necks.

Orthocerida family and genus indet. *pseudospeciosum* (Portlock)

Figs 13.3; 14.4

v* *Koleoceras pseudospeciosum* Portlock, p. 380, pl. 26, fig. 3 (part only).

Material. GSM103464, syntype, *Koleoceras pseudospeciosum,* figured, Portlock, pl. 26, fig. 3. K4368. Both specimens from locality 1.

Description. GSM103464 consists of an incomplete phragmocone about 130mm long and a body-chamber about 50mm long. The adoral diameter is 30mm and the rate of expansion of the conch 8°. The sutures are straight and transverse and cameral depth is 30% of the diameter of the siphuncle. A shell sculpture consisting of very fine transverse striae 1.5–2mm apart is present on the body-chamber. K4368 is a much smaller specimen, consisting of a body-chamber 30mm long and an incomplete phragmocone 40mm long. The adoral diameter is about 14mm and the rate of expansion is 7°. Cameral depth is 30% of the phragmocone diameter.

Remarks. Although of different sizes, the overall proportions of the two specimens are similar and the discrepancy in the length of body-chambers may be attributable to breakage in GSM103464. There is no hint of internal structures in either specimen. On the basis of the external form it is possible that the specimen could be a proteoceratid such as *Isorthoceras.*

Order Ascocerida Kuhn 1949
Family Ascoceratidae Barrande 1867
Subfamily Ascoceratinae Barrande 1867
Genus *Billingsites* Hyatt 1884

Type species. Ascoceras Canadense Billings, 1857, p. 310; original designation.

Billingsites sp. Fig. 14.5.

Material. TCD7830, labelled *Poterioceras approximatum* M'Coy, Tirnaskea, Pomeroy, Co. Tyrone. The precise locality is uncertain, but it could be locality 1. On the basis of the lithology, the specimen certainly originated from the Killey Bridge Formation.

Description. The specimen is flattened, about 34mm long, and if originally circular in section would have had a maximum diameter of about 15mm and about 13mm at the aperture. Only one surface is exposed and this provides a flattened latero-dorsal view of the shell. Four sutures representing ascoceroid septa are present and about 3mm apart across the dorsum, the most adoral septum being about 3mm behind the aperture. The aperture appears to be intact. The sutures are deflected adapically on the lateral surfaces where they fuse together while being deflected dorsally and adapically. The suture is then deflected sharply ventrally and appears to form the septum of truncation.

Remarks. Although poorly preserved, the pattern formed by the sutures indicates that referral to *Billingsites* is appropriate. Despite the apparent rarity of individuals, the three main Ordovician ascoceroid genera contain a large number of species (e.g. Flower 1963; Foerste 1928a; Kesling 1961; Miller 1932). Distinctions between species have been made

Fig. 14 — 1, Orthocerida family and genus indet. *pomeroense* (Portlock), GSM103480 (x 0.5). 2, 3, *Probillingsites?* sp., GSM103472; 2, right lateral view, and 3, ventral view (x 1.5). 4, Orthocerida family and genus indet. *pseudospeciosum* (Portlock), BELUM K4368 (x 1.5). 5, *Billingsites* sp., TCD7830, ventro-lateral view (x 1.5). 6, *Beloitoceras* sp., BELUM K24028 (x 1). 7, *Piersaloceras* sp., BELUM K24210 (x 2). 8, *Diestoceras breviconum* (Portlock), BELUM K4386–7 (x 1). 9, *Diestoceras?* sp., GSM103457 (x 1.5).

both on the number and shape of ascoceroid septa and subtle differences in the shape of the conch. Several species may occur in roughly coeval horizons (e.g. Flower 1963, 75, 82), albeit at geographically distant locations in some cases. It seems possible that the group as a whole may be heavily oversplit at species level. Until revision of the species contained within the Ordovician ascocerid genera takes place it will be difficult to assign the specimen described above at specific level. This specimen does seem unusual, however, in possessing four ascoceroid septa, and in this may be related to species such as *B. landerensis* Foerste and *B. multicameratus* Miller, although there are differences in the traces of the ascoceroid septa.

Subfamily Probillingsitinae Flower 1941

Genus *Probillingsites* Foerste 1928c

Type species. Probillingsites welleri; original designation.

Probillingsites? sp. Fig. 14.2,3.

v* 1843 *Phragmoceras arcuatum?* (Murchison), Portlock, p. 382, pl. 28a, fig. 5a–b.

v* 1882 *Cyrtoceras inaequiseptum* (Portlock), Blake, p. 170 (*pars*).

Material. GSM103472. Locality 1.

Description. A partially flattened phragmocone and body-chamber 40mm long. While distorted, the specimen retains an exogastric curvature. If originally circular in section, the maximum diameter would have been 30mm. The septum of truncation appears to be subtriangular in shape with what was probably a rather flat venter. A number of fractures are present which interfere with the sutures, making interpretation difficult. As far as can be ascertained, four sutures are present. The most adapical of these certainly represents a normal transverse septum. The next suture adorally also appears to represent a transverse septum, but the distance between these two sutures is very small on the venter. A third suture is present on the dorsum 3mm in front of the most adoral transverse septum. This suture fuses with the transverse suture laterally. The most adoral suture is strongly sinusoidal, extending forward on the dorsum about 8mm in front of the most adoral transverse suture and fusing with this suture in what appears to be a subventral position. The two most adoral sutures represent ascoceroid septa.

Remarks. Similar difficulties as to species assignment arise as with *Billingsites* sp. (above). The uncertainty in referral to *Probillingsites* stems from the nature of the ascoceroid septa, the sutures of which are seen to fuse with those of the normal or transverse sutures. This specimen is assigned to *Probillingsites* on the grounds that more than one normal septum is present — precluding an assignment to *Schuchertoceras*. There are, nevertheless, two ascoceroid septa present and these fuse ventrally. This condition is typical of *Schuchertoceras* and *Billingsites*. This specimen is seen here as intermediate between *Probillingsites* and *Schuchertoceras*.

Ascocerida indet.

Material. GSM7772 (*Phragmoceras?,* Portlock 1843, p. 283, pl. 28b, fig. 4a–b); locality 1. GSM103470; locality 1. BELUM K24209, locality 2.

Description. All three specimens represent short cyrtoconic body-chambers, probably with an exogastric curvature. GSM7772 and K24209 both show two or more sutures traversing the venter. A single suture may be present in GSM103470.

Remarks. The overall shape of these specimens and the presence of sutures adapically makes assignment to the Ascoceratida reasonable. As an insufficient portion of the conch can be seen, assignment to *Schuchertoceras* or *Billingsites* seems equally possible.

Order Oncocerida Flower in Flower and Kummel, 1950

Family Graciloceratidae Flower in Flower and Kummel 1950

Genus *Piersaloceras* Teichert, 1930

Type species. Piersaloceras gageli; original designation.

Piersaloceras sp. Figs 13.10; 14.7.

Material. BELUM K24210; locality 2.

Description. An external mould of a cyrtocone 17mm long along its axis and rotating through 30°, giving a radius of curvature of about

32mm. Adapically, the minimum possible diameter is 7mm and adorally 8.5mm. At the adapical end of the specimen a rough surface may represent a septum. The shell sculpture consists of columns of chevron-shaped flanges. The distances between the adorally directed angles of the chevrons varies from 0.5mm to 1mm and the flanges themselves have a density of $2mm^{-1}$. The stacks of chevrons show distinct ridges along their length, suggesting that the conch may originally have been fluted.

Remarks. The specimen is tentatively interpreted as a body-chamber. *Zitteloceras costatum* Teichert was recorded (Teichert 1940) from the Starfish Beds of the South Threave Formation (Upper Drummuck Group) of Girvan, and shows marked similarities in the shell sculpture. However, the specimen described above appears to have a much lower rate of expansion than *Zitteloceras* and if, as interpreted here, the specimen represents a body-chamber, then it is more slender than that of *Zitteloceras.* While the position of the siphuncle is not known, both the features discussed above are seen in *Piersaloceras gageli* Teichert (1930, p. 282, pl. 6, figs 9, 10) from the Lyckholm Beds of Estonia. Apart from the apparent smaller size of the conch, there appears to be little basis for distinguishing between the material described above and the type species.

Family Oncoceratidae Hyatt, 1884

Genus *Beloitoceras* Foerste, 1924

Type species. Oncoceras pandion Hall, 1861, p. 45; original designation.

Beloitoceras? sp. indet. Fig. 14.6.

Material. Single specimen. BELUM K24211a–b, part and counterpart. Locality 2.

Description. A flattened individual approximately 60mm long, of which about 18mm consists of body-chamber. If originally circular in section, the diameter at the aperture would have been 13.5mm and 4mm at the most adapically preserved part of the phragmocone. On the same basis cameral depth at the base of the body-chamber would have been about 14%. As far as can be seen, the suture takes the form of a broad and shallow lateral lobe, suggesting that the section may have been compressed. The adoral part of the conch is only weakly inflated and appears to involve the body-chamber almost entirely. The shell surface appears to be smooth.

Remarks. Although flattened, the overall shape of this cyrtocone appears typical of forms generally referred to *Oncoceras* and *Beloitoceras.* The nature of the adoral inflation suggests *Beloitoceras* rather than *Oncoceras.* The only feature worthy of note is that the body-chamber appears to be relatively long.

Family Deistoceratidae Foerste, 1926

Genus *Diestoceras* Foerste, 1924

Type species. Gomphoceras indianense Miller and Faber, 1894, p. 37; original designation.

Remarks. Diestoceras has been recorded from the Whiterock to Richmond Stages in North America. Flower (1946) noted the presence of forty species in North America and discussed the criteria used for discrimination between species. These were largely on the basis of size and the extent and position of the gibbosity of the shell. Given the diversity of the rest of the Killey Bridge Formation cephalopod fauna, the number of species of *Diestoceras* described below seems very large. It seems likely that *Diestoceras* and its allied genera are in need of substantial revision as the result of using the above criteria with the material under study may be resulting in taxonomic oversplitting.

Diestoceras breviconum (Portlock)

Figs 14.8; 15.7

v* 1843 *Orthoceras breviconum* Portlock, p. 372, pl. 28, fig. 8a,b.

Material. GSM103476. Holotype by monotypy. Locality 1. K4386–7. Probably locality 1.

Description. The holotype consists of a fragment of breviconic conch about 41mm long. If circular in cross-section then the diameter at the base of the body-chamber would have been 33mm, decreasing to 18mm at 22mm adapically. This gives an expansion rate of around 38°. As far as can be ascertained, the conch continues to expand to the orad of the base of the body-chamber. A section at the adapical end of the preserved portion of the phragmocone represents a


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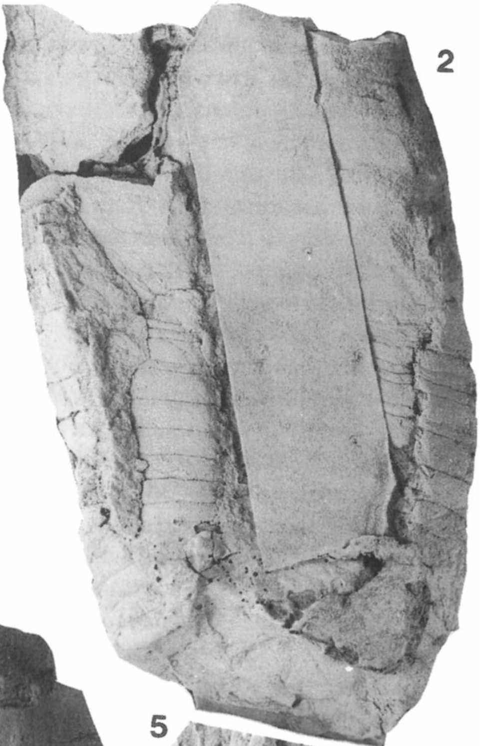
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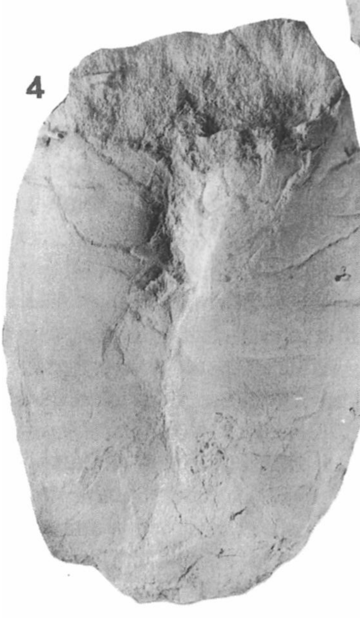
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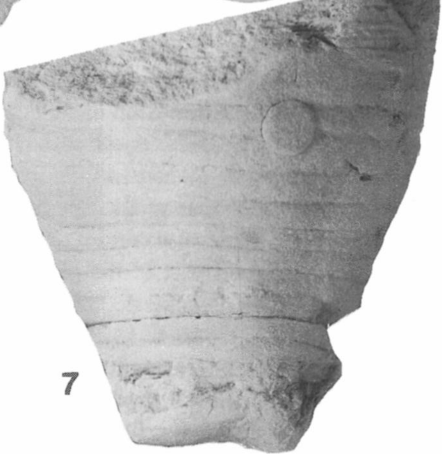
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cracked septal surface. The section is ovoid and depressed, with a dorso-ventral diameter of 15.5mm and a lateral diameter of 13mm. Cameral depth is estimated at about 10% of the phragmocone diameter. The difference in the distances between sutures along their circumferences suggests that the conch was cyrtoconic and possibly rather inflated on the convex side. A few traces of shell sculpture remain on the body-chamber. These consist of transverse wrinkles about 1mm apart. No trace of a hyponomic sinus has been seen.

K4386–7 is a similar but more crushed specimen. The diameter at the base of the body-chamber is 25.5mm and 20mm at 12mm further in an adapical direction. Despite being crushed, this specimen demonstrates rather more clearly the existence of a curvature. A shell sculpture is partly preserved and is similar to that seen in the holotype, but is seen to be strongly downturned where the distance between sutures is greatest. If this downturn in the sculpture represents the hyponomic suture, it suggests that the conch was exogastrically curved.

Remarks. Despite the difference in expansion rate between the two specimens, it seems likely that they belong to the same species. It should be noted that the diameter of K4386–7 at the base of the body-chamber is less than that of the holotype. This specimen probably represents a more juvenile shell and the difference in expansion rate probably results from the lack of development of the more inflated adoral region of the phragmocone. As a species, *D. breviconum* may be related to *Diestoceras acuminatum* Strand (from the Gastropod Limestone of The Asker district of the Oslo Region) in combining a high expansion rate, probably with maximum inflation in the body-chamber.

***Diestoceras? inaequiseptum* (Portlock)**

Fig. 15.1, 2

v* 1843 *Phragmoceras inaequiseptum,* Portlock, p. 382, pl. 28a, fig. 4a–b.

v* 1857 *Cyrtoceras inaequiseptum,* Salter in Murchison, Foss. gr. 43, fig. 1.

v* 1882 *Cyrtoceras inaequiseptum,* Portlock, Blake, p. 170, pl. 20, figs 5, 5a, 8.

Material. GSM103468. Holotype by monotypy. Locality 1. Tunnicliff (1980, 65) considered this specimen as the only certain syntype, as the label on a second specimen (GSM103470) is too incomplete to be certain of the indication. As this specimen is most probably an ascocerid (see above), it is considered here that GSM103468 was the only specimen originally assigned to the species.

Description. The specimen consists of a partially crushed conch about 65mm long, of which 25mm may represent a complete body-chamber. Assuming a circular section, the diameter 20mm orad of the base of the body-chamber is 29mm, at the base of the body-chamber 32mm, and 27mm apicad of the base of the body-chamber the diameter is 24mm. This indicates an expansion rate of about 19° in the preserved part of the phragmocone. Maximum diameter is probably near the base of the body-chamber. The phragmocone shows sutures which appear to have been transverse and indicate a cameral depth of about 10%. The six most adoral septa are strongly approximated. Measurement of the distance between sutures on either side of the conch indicates that it was curved.

The body-chamber shows traces of sculpture and weak annulations. The sculpture consists of low ridges about 1mm apart. The annulations consist of two smooth grooves set 3.5mm apart. These might be pathological in origin. Both annulations and ornament are deflected to form a sinus about 13mm wide and 5mm deep. The sinus is deepest where the distance between sutures is greatest. The structure is taken to be the hyponomic sinus and indicates an exogastric curvature for the shell.

Remarks. Diestoceras inaequiseptum differs from *D. breviconum* in its lower expansion

Fig. 15 — 1, 2, *Diestoceras inaequiseptum* (Portlock), GSM103468; 1, probable ventral view; 2, dorsal? view (both x 1.5). 3–5, *Diestoceras* sp. 1. 3 and 4, GSM103572 (x 1). 5, GSM103528 (x 1). 6, Discosorida? indet., BELUM K4374 (x 1). 7, *Diestoceras breviconum* (Portlock), GSM103476 (x 1.5).

rate, while it appears to be a smaller and more slender form than *D.* sp. 1.

***Diestoceras* sp. 1**

Fig. 15.3, 4, 5

v* 1843 *Gomphoceras sub-pyriforme,* Munster, Portlock, pl. 28a, fig. 1a, b, p. xxvii.
1882 *Poterioceras(?) intortum* Blake, Blake, p. 187.

Material. GSM103527. Locality 1. Figured: Portlock 1843, pl. 28a, fig. 1a, b. Mentioned: Blake 1882, 187. GSM103528. Locality 1. Mentioned: Blake 1882, 187. NMINGF14762. Probably locality 1.

Description. GSM103527 is a shell 70mm long with the adapical portion missing. The most adoral 30mm consists of body-chamber. Assuming an originally circular section, the diameter is 33mm at the adoral end of the body-chamber, 37mm at the base of the body-chamber, and 30mm at a distance 20mm adapical of the base of the body-chamber. Maximum expansion of the conch appears to be at or near the base of the body-chamber. It is possible that the walls of the body-chamber contract more strongly at the aperture, but given the preservation of the specimen this cannot be demonstrated with certainty. Cameral depth is about 10% of the phragmocone diameter in the portion seen. The distance between sutures of a single camera appears to vary consistently along the circumference, suggesting that the conch was probably weakly cyrtoconic. Faint traces of buttresses may be seen running the length of the phragmocone and onto the body-chamber. No trace of shell sculpture is evident.

GSM103528 is a smaller specimen. It is 45mm long, of which 25mm consists of body-chamber. The conch has an estimated diameter of 26mm at the base of the body-chamber. It is unclear whether the body-chamber contracts towards the aperture. Differences in the distances between septa on either side of the phragmocone suggest that the shell was cyrtoconic. Cameral depth is about 11% of the phragmocone diameter. No evidence of shell sculpture can be seen.

NMINGF14762 consists of a phragmocone 18mm long with a body-chamber 27mm long. If circular in section, the diameter at the base of the body-chamber would be 32mm. The specimen appears to be crushed in a lateral plane and it is difficult to determine whether the body-chamber is expanding or not. A septal surface has been preserved which shows a septal foramen 5mm in diameter with its centre 4mm from the phragmocone wall. The nature of the scar on the foramen suggests that the septal neck may have been cyrtochoanitic, possibly with a wide, recumbent brim.

Remarks. The difference in size between the three specimens throws doubt on the impression that they belong to the same taxon. It is not possible to tell whether the body-chamber in the smaller specimens is contracting or expanding. If the latter, then the smaller specimens are likely to belong to the same taxon, as there are otherwise no discernible differences. Given the preservation of the material, it could be assigned to either *Diestoceras* or *Danoceras.* The conchs appear to expand more rapidly than those of *Danoceras* and are considered best assigned to *Diestoceras.* Comparison with other species of *Diestoceras* is difficult, partly because of the preservation of the current material and also because of the large number of species (partly as a result of splitting) which have been recorded. The present forms belong with the less inflated, more slowly expanding forms such as *D. kirki* Foerste 1935 (Lander Sandstone of Wyoming) and *D. vagum* Foerste 1928a (English Head Formation of Anticosti Island). In both these species, maximum expansion is slightly adoral of the base of the body-chamber, as appears to be the case with the above material. *Poterioceras (?) intortum* Blake appears to expand more rapidly than these specimens and in any case is older, probably coming from the Ardwell Group. Both species described by Teichert (1940) (*D. lamonti* and *D. scoticum*) from the Starfish Beds of the Girvan area are much smaller when mature and *D. scoticum,* at least, expands too rapidly.

***Diestoceras?* sp. 2**

Fig. 14.9

1843 *Orthoceras subarcuatum* Portlock, p. 374 (part).

Material. GSM103475, paralectotype of *Orthoceras subarcuatum* Portlock. Locality 1.

Description. Nearly flattened conch 20mm long, including about 5mm of a fractured body-chamber. If originally circular then the diameter at the base of the body-chamber is estimated to have been about 15mm and 6mm at 14mm further adorally, giving an expansion rate of about 35°. Sutures appear to be straight and transverse, ranging from 2mm to 1.5mm apart, giving a cameral depth of about 13%. No shell sculpture is seen. The body-chamber is still expanding at the break.

Remarks. It is possible that this specimen may represent a juvenile of one of the forms described above. In its small size and rapid rate of expansion it bears a strong resemblance to *Diestoceras lamonti* from the Starfish Beds of the Drummuck Group. *D. lamonti* is younger than the specimen discussed here.

Order Discosorida Flower in Flower and Kummel, 1950

Family Westonoceratidae Teichert, 1933

Genus *Faberoceras* Flower, 1946

Type species. Faberoceras multicinctum; original designation.

Faberoceras? subarcuatum (Portlock). Fig. 16.1.

1843 *Orthoceras subarcuatum* Portlock, p. 374, pl. 28, fig. 9.

1957 *Faberoceras? subarcuatum* (Portlock), Flower and Teichert, p. 92.

Material. Lectotype: GSM103474, figured, Portlock 1843, pl. 28, fig. 9. Paralectotype: GSM103475. Here regarded as probably referrable to *Diestoceras.* Both from locality 1.

Description. The lectotype is a fragment of conch about 35mm long, consisting of approximately 22mm of body-chamber. The conch has a compressed oval section which appears to be an original feature. The dimensions of the section adorally are 27mm laterally and 44mm dorso-ventrally. The venter is more narrowly rounded than the dorsum. The rate of expansion of the conch is about 26° in the dorso-ventral plane. This could be exaggerated as the shell may have been vertically embedded, the apical angle rate being artificially increased through the shortening of the conch axis. Sutures are nearly transverse with weak lateral lobes. Sutures are between 3mm and 4mm apart, giving a cameral depth of about 10% of the dorso-ventral phragmocone diameter. Shell sculpture takes the form of weak transverse costae about 2mm apart. These form a deep and relatively narrow sinus over the convex side of the conch. This is interpreted as a hyponomic sinus and therefore indicates that the curvature is exogastric.

Remarks. Flower and Teichert (1957, 92) considered that the known features of the species strongly suggested *Faberoceras,* but noted also that it was not similar to any other Ordovician genus. The species shows a superficial resemblance to *Strandoceras* and *Lyckholmoceras,* but is distinct from both in that they are endogastrically curved. If belonging to *Faberoceras,* the species does not conform well with other upper Ordovician species from North America. Most, if not all, of these species have strongly costate to weakly annulate conchs (e.g. *F. multicinctum* and *F. percostatum*). This species is more reminiscent of earlier, Middle Ordovician forms. On the basis of data in Flower and Teichert 1957, the later annulate and costate forms of *Faberoceras* range through the Maysvillian into the Richmondian (Pusgillian to Rawtheyan). Thus this Cautleyan species with its relatively smooth shell appears to be somewhat anomalous.

Discosorida? indet.

Fig. 15.6

Material. K4374. Probably from locality 1.

Description. Fragment of incomplete internal mould about 50mm long, probably representing a rather slender and compressed phragmocone with a dorso-ventral diameter of about 30mm. Sutures are straight and about 5mm apart, becoming more distant on the right-hand side indicating that the shell was curved. There are strongly marked buttresses running the length of the phragmocone.

Remarks. Although indeterminate, this fragment is reminiscent of *Lyckholmoceras* Teichert.

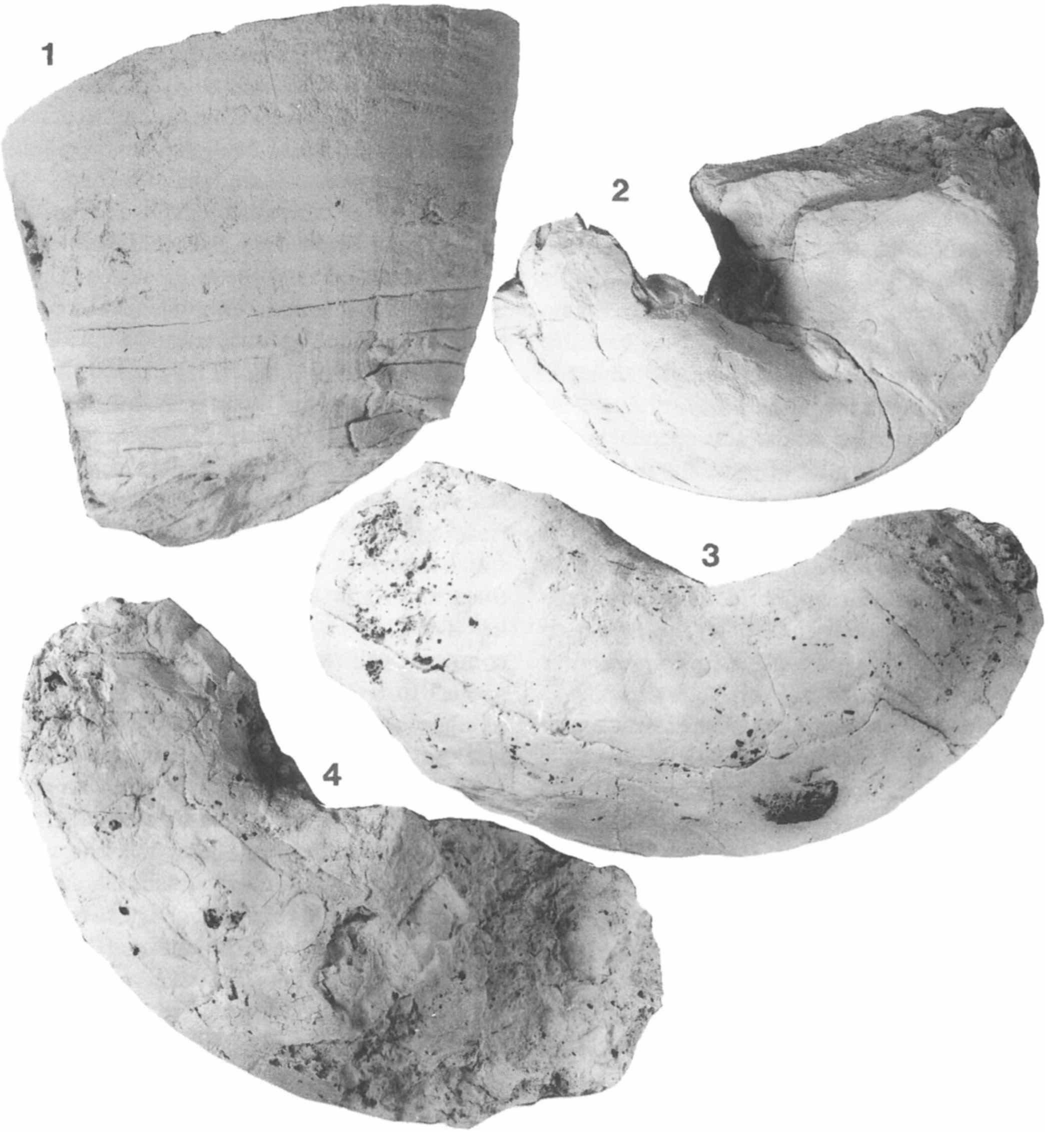

Fig. 16 — 1, *Faberoceras? subarcuatum* (Portlock), GSM103474, venter? on right (x 1.5). 2–4, *Characteroceras cinereum* (Blake). 2, Lateral view of torted body-chamber and adoral camerae, GSM103524 (x 0.5). 3 and 4, Two ventro-lateral views of GSM103522, a body-chamber showing costae. The most adoral camerae remaining (x 0.5).

Order Tarphycerida Flower in Flower and Kummel, 1950

Family Apsidoceratidae Hyatt, 1884

Remarks. The placement of the Apsidoceratidae in the Tarphycerida follows from Flower's (1984) discussion of the Barrandeocerida and recommendation for the suppression of the order.

Genus *Charactoceras* Foerste, 1924

Type species. Trochoceras baeri Meek and Worthen, 1865, p. 263.

Characteroceras? cinereum (Blake). Fig. 16.2, 3, 4.

1843 *Phragmoceras compressum?* Murchison, Portlock, p. 382, pl. 28b, fig. 2.

1882 *Trochoceras(?) cinereum* Blake, p. 216, pl. 20, fig. 2.

1957 *Faberoceras? cinereum* (Blake), Flower and Teichert, p. 91.

Material. Holotype. GSM103522, figured; Blake 1882, pl. 20, fig. 2. GSM103524, figured; Portlock 1843, pl. 28b, fig. 2. GSM103523, GSM103525. All from locality 1. K20624, locality uncertain.

Description. The holotype consists of the body-chamber and the three most adoral camerae. It is about 200mm long and partially crushed. If circular its diameter would have been about 60mm at mid-length. Cameral depth was approximately 15% of the phragmocone diameter. Sutures appear to be transverse and essentially straight, although a weak and broad lobe may be present on the venter. The surface of the shell shows very shallow annulations on the lateral surfaces with a distance of about 10mm between culminations. These may die out adapically. Shell ornament consists of costae with a density of about 1mm^{-1}. The costae form a deep sinus on the venter, which from the lateral surfaces is 90mm wide and 40mm deep. Costae curve over the dorsum, forming a shallow and gently curved adorally projected culmination.

The other specimens are essentially similar to the holotype. GSM103525 shows crushed septal surfaces which, assuming a circular section in the phragmocone, would indicate a septal depth of approximately 25%. None of the specimens appears to show an impressed zone on the dorsum, and where crushing has occurred, one of the main fractures is on the venter.

Remarks. The genus *Charactocerina* was diagnosed by Foerste (1935) as differing from *Characteroceras* in the presence of costae on the dorso-lateral surfaces of the conch. These have been described as shallow annulations here following Frye (1982), who recommended the suppression of *Charactocerina* (*ibid.*, p. 1285), mainly on the basis of the close coincidence of the stratigraphic ranges of the two genera and the apparent continuum between smooth and annulate forms. This material is questionably assigned to *Charactoceras* on the basis of the apparent high rate of whorl expansion. It differs from *Charactoceras* in a number of features. The pattern produced by the sutures suggests that the impressed zone on the dorsum was either very weak or was not present. *Charactoceras* is an involute genus and an impressed zone ought to be present in this material. It is possible, though, that since all the specimens appear to represent body-chambers the impressed zone may have been lost on the divergence of the body-chamber. If so, this may indicate early divergence of the body-chamber. Species such as *C. suecicum* (Frye 1982) from the Boda Limestone of the Siljan District of Sweden do appear to show a rapid divergence of the body-chamber and may be related in that the density of the annulations is also relatively low. The weak sutural lobe on the venter suggests that the venter may have been slightly flattened, although the crack present in most specimens in a mid-ventral position would suggest that the venter was probably still rounded in section.

Acknowledgements

I thank Dr A. J. Jeram of the Ulster Museum for arranging loans of material and for showing me the recent exposures of the Killey Bridge Formation; the British Geological Survey for the loan of material; and Dr J. D. Johnston for discussion of the structural aspects of the preservation of this fauna.

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