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Relative dating of the fossil hominids of Europe

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Contents

Synopsis

The application of analysis of skeletal materials for fluorine, 'uranium' and nitrogen contents is described as a method of relative dating, with particular reference to Pleistocene and early Post-Pleistocene hominids and associated Mammalia in Europe. Tables of analyses are presented.

Introduction

When there is doubt as to whether a bone[1] or tooth is contemporaneous with other skeletal remains in a particular deposit, techniques are now available which in favourable circumstances can solve the problem. The fluorine and 'uranium' contents of the mineral matter of buried bones and teeth increase with the passage of time, whereas the organic (protein) content measured as nitrogen decreases. Thus, comparison of the fluorine, 'uranium' and nitrogen contents of a bone or tooth of questionable age with the ranges of these elements present in other bones or teeth of known age and in similar matrix at the same site may indicate clearly the relative antiquity of the specimen in question.

Whether the comparison of fluorine content, of 'uranium' content or of nitrogen content is the more likely to solve a particular bone or tooth dating problem, or whether the use of two of these methods or of all three in combination is necessary or preferable, will depend on the local circumstances. These methods are essentially empirical. As they are methods of relative and not

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[1] In reading this Introduction it should be understood that the relative dating methods applicable to 'bone' are equally applicable to 'antler'. Strictly speaking therefore any reference to bone should be read as 'bone or antler'.

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absolute dating, it is essential to have local controls. It would be impossible to date a bone or tooth relatively by fluorine, 'uranium' or nitrogen analysis if it had been found at a site which had yielded no skeletal material of known age for analytical comparison, although if both the 'uranium' and the fluorine content of an isolated bone or tooth were high and the nitrogen low one might infer that the specimen was 'fossil' rather than Recent.

History of the fluorine dating method

At the beginning of the nineteenth century the Italian chemist Morichini (1805) detected fluorine (in the form of 'fluate of lime') in the enamel of a fossil elephant tooth found near Rome. Gay-Lussac (1806), commenting on this result, said that it was a discovery which might have important consequences. However, he thought that the 'fluoric acid' had been absorbed by the animal during its life. Two other French chemists, Fourcroy & Vauquelin (1806*a*, *b*), reported that they had failed to find fluorine in a new ivory or enamel, whereas they confirmed its presence in fossil ivories. 'This singular circumstance' they said 'seems to indicate that fluoric acid exists in the earth; . . . that during the long continuance of these substances [ivories] in the earth they combine with the fluoric acid'.

With refinements in methods of analysis it became clear that new ivory or dentine and bone contain minute traces of fluorine but that after fossilization they contain considerably more, having adsorbed it from percolating water or the soil in which they have been embedded. An English chemist, James Middleton (1844), was the first to recognize this fact clearly, and he read a paper to the Geological Society of London, showing that fossil bones contained fluoride in proportion to their antiquity. He compared the fluorine content of various fossil bones with that of a Greek human skeleton 2 000 years old. He estimated on this basis that fossil mammal bones from the Siwalik beds of India had an antiquity of 7 700 years, and one from the Eocene beds in France, of 24 000 years. Middleton's brave attempt at geochronology was not taken seriously, and his discovery appears to have been forgotten for a century or so, but the principle was reaffirmed fifty years later by a French mineralogist, Adolphe Carnot (1892*a*, 1893). He analysed a number of fossil bones obtained from different localities, representing geological horizons ranging from Ordovician to Recent. By averaging the results he showed conclusively that the concentration of fluorine in fossil bones varies almost uniformly with time. Carnot expressed the fluorine content of the analysed bones as the proportion relative to that in fluorapatite taken as unity. If we assume the maximum fluorine content of fluorapatite is 3·8 %, his figures can be converted into average percentages of fluorine in bones of successive geological epochs as follows:

Recent	<0·3
Pleistocene	1·5
Tertiary	2·3
Mesozoic	3·4
Palaeozoic	3·7

By considering Carnot's individual analyses it is evident that the averaging process has obscured the important fact that there is a wide variation in the concentration of fluorine in bones of the same geological age but from different localities. So many variables are involved that it would be impossible to ascertain accurately the geological age of any isolated fossil by determining how much fluorine it contained; still less would it be possible to calculate the absolute age of a vertebrate specimen from its fluorine content. At one locality fluorine may be abundant in the ground-water, at another it may be only present as a trace. The rate at which fluorine is accumulated in skeletal material also depends on climatic factors and on the permeability of the matrix. For all these reasons, Carnot's work was generally regarded as interesting but as having no practical outcome, and like Middleton's paper entered the scientific limbo.

It is difficult to account for the importance of Carnot's discoveries being overlooked, particularly as another paper by him (Carnot 1892*b*) contained the essence of the method of relative dating by fluorine which was revived with considerable success in the present century. He showed that by analysing the fluorine content of a human bone found in a Pleistocene gravel pit at Billancourt (Seine) and comparing it with the fluorine content of fossil bones from the same site, the human bone evidently represented an intrusive burial of Post-Pleistocene age. The following figures illustrate the striking difference between the degree of fluorination in the Pleistocene and in the Post-Pleistocene material at Billancourt:

Human tibia	Pleistocene mammal bones
0·17% F	1·43% F
	1·84% F

Only a few of Carnot's contemporaries realized the potentialities of his results, but one was Thomas Wilson, Curator of Prehistoric Archeology in the U.S. National Museum, who had the 'fluorine test' applied to the pelvic bone of the Natchez human skeleton in Mississippi, thereby proving that it has the same antiquity as the associated bone of the Pleistocene ground-sloth *Mylodon* (Wilson 1902, Stewart 1951).

During World War II, while I was working with the Geological Survey of Great Britain, research into phosphate resources and the geological aspects of dental fluorosis (Bromehead 1943; Oakley 1943) focussed our attention on Carnot's forgotten papers. It became evident that if one were interested in separating bones of different ages which happened to have been mixed together in a single deposit, either through artificial interment or through natural rearrangement such as by stream action, widely different concentrations of fluorine in the bones could be most revealing. This is the theoretical basis of the fluorine-dating method.

In 1947 Dr H. J. Walls, then in the Home Office Forensic Science Laboratory at Bristol, undertook to determine the fluorine content of a series of selected bone and tooth samples which I obtained, with the cooperation of the late Dr L. S. B. Leakey, from various deposits in the region of the Kavirondo Gulf on the Kenya side of Lake Victoria. Working with samples weighing 20–40 mg, Walls used the method of determining fluorine described by Milton, Lidell & Chivers (1947). It was hoped that the results might settle the questions regarding the antiquity of the fossil human bones from Kanam and Kanjera (Boswell 1935). In fact they showed clearly that the method was not applicable in regions where fluorine is excessively abundant in the ground-water, as it is in most volcanic areas with tropical weathering, where fluorination of vertebrate materials occurs rapidly and sometimes in a random fashion. The analyses of the East African material reported by Walls may be summarized as follows:

Fossil bones from Kavirondo Gulf	Fluorine content
Upper Pleistocene and Holocene bones (5)	1·2–4·9%
Middle Pleistocene bones (6)	0·5–3·4%
Lower Pleistocene bones (2)	1·7–3·4%

These results appeared to contradict Carnot's rule, but if a larger number of fossil bones and teeth from the same sites had been analysed this might not have been the case. However, the fact remains that in pyroclastic sediments, such as those abounding in East Africa, volcanic ashes rich in fluorine sometimes contribute to the formation of layers overlying deposits in which the fluorine content is much lower. This would account for the fact that the average fluorine content of bone samples from Bed IV in Olduvai Gorge, Tanzania, is higher than that of bone samples from the underlying Bed III (Day & Molleson 1976 : 456).

It is remarkable that some Upper Pleistocene bones in the Kavirondo Gulf series (notably from Kuguta) contained over 5% fluorine, greatly in excess of the theoretical maximum for fluorapatite (3·8%). Under exceptional geochemical conditions the isomorphously related sodium fluorapatite ($Ca_6Na_4(PO_3F)_6O_2$; Mehta & Simpson 1975) may be formed and in this the fluorine content could theoretically be as high as 12% (*fide* Duncan McConnell, Emeritus Professor, The Ohio State University, *in lit.* Oct. 27, 1976). However, it should be noted that according to Glover & Phillips (1965 : 574) in some of the oldest bone samples analysed in the BM(NH) programme, where a greater proportion of fluorine was found than that required in fluorapatite, X-ray diffraction evidence suggested that some fluorine may be present as calcium fluoride in the bone matrix. Mineralogical investigation of the fluorine-rich bones collected by Leakey from Kuguta near Homa Mountain, Kenya is clearly desirable.

The fluorine content of the controversial Kanam mandible ranged from 1·4% to 2·2%, but strangely enough its fluorine/phosphate ratio (as defined on p. 5) was at one point 30, which is higher than that recorded in any other fossil bone analysed in our programme of work. Although this jaw was presumed when discovered (Leakey 1932 : 722) to have been contemporaneous with the Lower Pleistocene deposit in which it appeared to lie, comparative analyses eventually indicated that it was probably in an intrusive calcrete block, and no older than Middle Pleistocene (Oakley 1975).

There seemed a much better chance that the method of fluorine dating would yield more useful results in regions of temperate weathering, where one might reasonably expect the increase of fluorine in fossil bones and teeth to be gradual. In 1948 the then Department of the Government Chemist in London agreed to cooperate with the British Museum (Natural History) in exploring more fully the possible applications of this method. The initial aim was to confirm or disprove the alleged antiquity of the Galley Hill skeleton (for results of this enquiry see p. 17). At the same time the antiquity of bones of the Swanscombe skull was confirmed by this method (see p. 26).

With the aid of grants from the Wenner-Gren Foundation, the Subdepartment of Anthropology of the BM(NH) has had about a thousand vertebrate specimens selectively analysed. The results have been used in preparing this Introduction. Early in the investigations the analyses for fluorine content of the vertebrate samples were made in the Department of the Government Chemist by R. H. Settle, E. C. W. Maycock and C. R. Hoskins, using a method similar to that described by Willard & Winter (1933). Later when the fluorine dating method was applied to the Piltdown bones and teeth the analytical work was carried out by Hoskins & Fryd (1955). They worked with 20–100 mg samples when available, but in exceptional cases they made determinations of fluorine in samples weighing considerably less than 20 mg. Continuation of analytical work on fossil bones and teeth was carried out by Glover & Phillips (1965).

At this stage it seems appropriate to sum up the principles of the fluorine dating method. As Middleton found, buried bones and teeth adsorb fluorine from ground-water or from moist sedimentary matrices, and by a process of irreversible ionic interchange the element is fixed in their mineral substance. Consequently when bones or teeth of different ages occur at the same site, comparison of their fluorine contents provides a useful method of estimating their relative antiquity. The main mineral constituent of bones and teeth, hydroxyapatite $Ca_{10}(PO_4)_6.(OH)_2$, has a strong affinity for fluorine which in the form of fluorides occurs as a trace in the ground-water of sedimentary formation and soils, usually in the proportion of about one part in a million. When fluoride ions come into contact with this mineral matter they are adsorbed and locked into its structure, in fact displacing the hydroxyl ions in the crystal lattice of the hydroxyapatite, which is thus converted particle by particle into fluorapatite $Ca_{10}(PO_4)_6.F_2$. This form of apatite is more stable and is not readily dissolved, so that unless conditions in the soil or rock formation become so acid that the whole vertebrate specimen is destroyed the fluoride ions which have entered its structure are not removed. Owing to both the ease with which fluoride ions diffuse and the porosity of bony material, the fixation of the fluorine is not confined to the surface of the specimen but takes place relatively uniformly throughout its substance, at any rate under temperate conditions of weathering; see analyses of the fossil deer antler from Swanscombe quoted below. All types of bone, antler, and dentine are nearly equal in their capacity for adsorbing fluorine, but the enamel of teeth is more resistant to the penetration of fluoride ions, especially in the early stage of fossilization. The theoretical maximum fluorine content of fossil bones or teeth is 3·8%.

In uniformly porous dentine, bone and antler there is very little evidence of zonation of the adsorbed fluorine. Apparent differences in fluorine content between the outside and the inside of a bone, tooth or antler occur sometimes because the interior tissue is more cancellar (spongy) and consequently often contains grains of infiltrated mineral matter. Thus, the degree of fluorination of a bone or other vertebrate specimen is more usefully expressed by the fluorine/phosphate ratio than by the percentage of fluorine, as the following example illustrates; cross-section of a Pleistocene cervid antler, BM(NH) E.600:

	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$
Outer zone, compact tissue	1·2	26·0	4·6
Inner zone, spongy tissue (with infiltrated clay)	0·2	5·0	4·0

If comparison is made between the fluorine/phosphate ratio rather than between the fluorine content of the samples the complicating factor of any contamination by adventitious mineral matter is eliminated. Although the ratio is usually written out as

$$\frac{F\%}{P_2O_5\%} \times 100$$

for convenience it can be stated as $100F/P_2O_5$. This practice was followed by Oakley, Campbell & Molleson (1971 : ix).

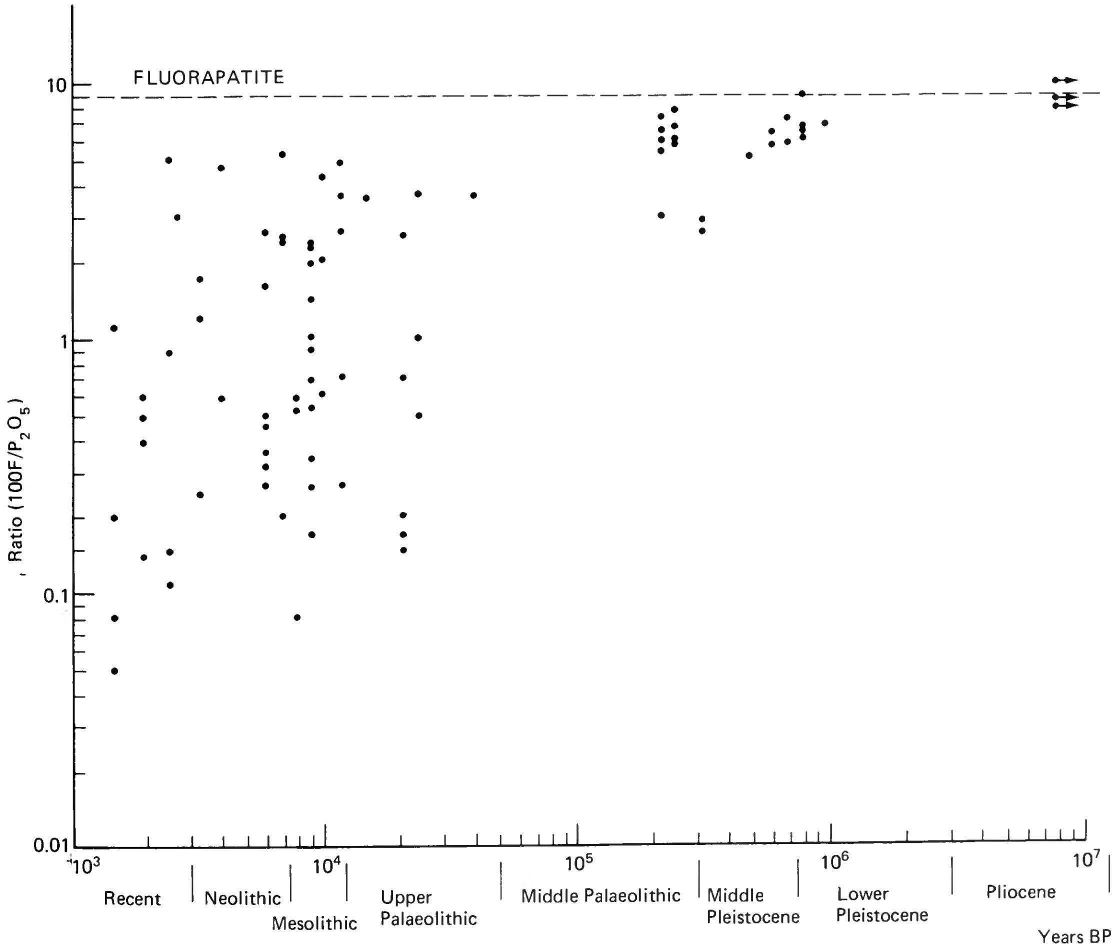

Fig. 1 Fluorine/phosphate ratios in fossil skeletal samples from the British Isles (including Ireland but excluding Channel Islands), plotted against their stratigraphical ages. Note the trend with increasing age towards the theoretical limit: complete transformation of apatite into fluorapatite. Redrawn by G. F. Phillips to combine data presented by Glover & Phillips (1965 : 575) with further results obtained by colleagues at the Laboratory of the Government Chemist.

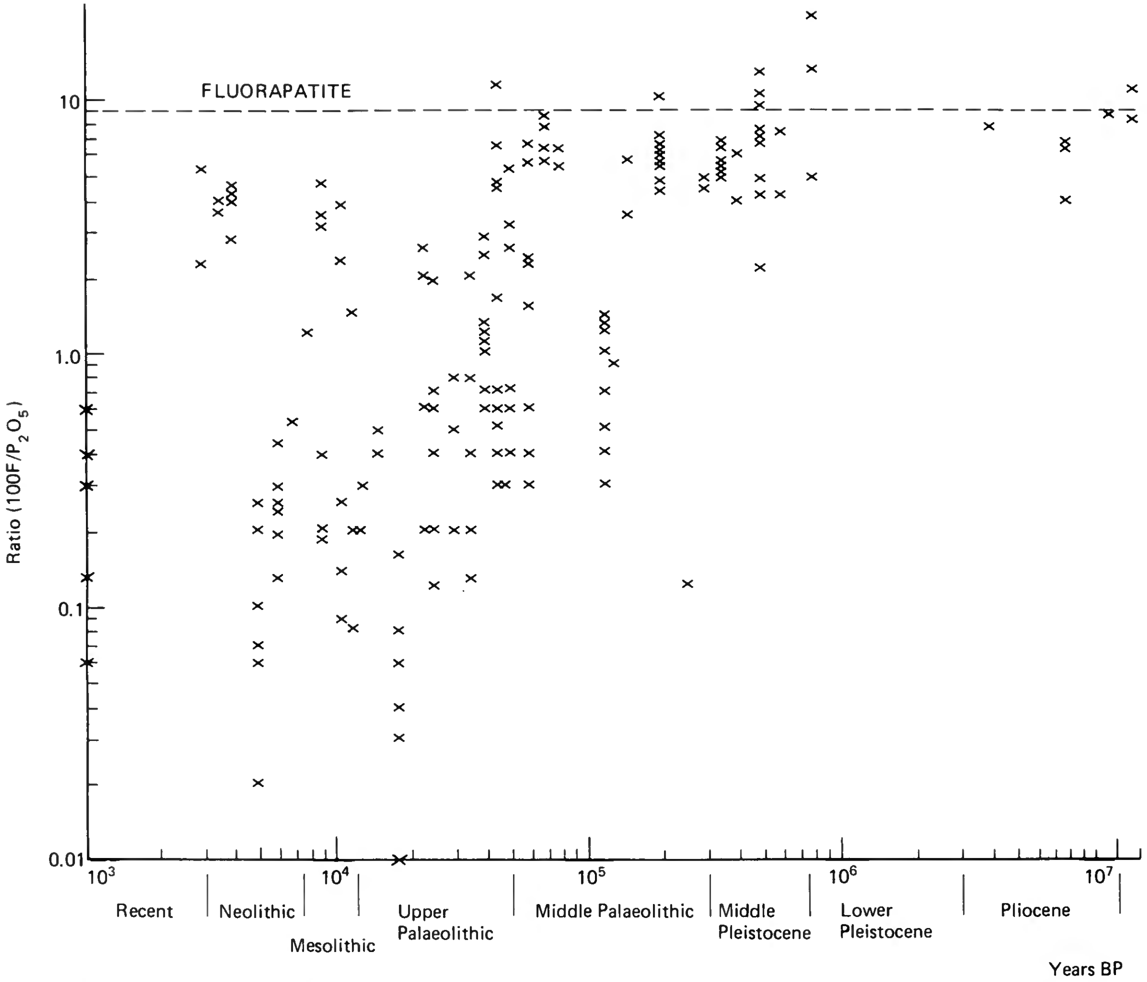

Fig. 2 Fluorine/phosphate ratios in fossil skeletal samples from Europe other than the British Isles, plotted against their stratigraphical ages. Compare with Fig. 1. Redrawn by G. F. Phillips to combine data presented by Glover & Phillips (1965 : 575) with further results obtained by colleagues at the Laboratory of the Government Chemist.

Analyses of a cross-section of a cervid antler from the Lower Gravel, Barnfield Pit, Swanscombe gave the following results:

		F%	$100F/P_2O_5$
Outer Zone	0–3 mm	2·5	7·0
Underlying layer	3–6 mm	2·3	6·3
Central cancellar tissue	6–15 mm	2·2	6·3

Glover & Phillips (1965 : 575) illustrated the relationship between the geological age and the fluorine/phosphate ratio for 345 samples of vertebrate fossils which were analysed for the BM(NH) at the Laboratory of the Government Chemist between 1955 and 1965. G. F. Phillips here re-presents the European data, with the addition of subsequent results obtained by his colleagues, as Figs 1 and 2, in which fluorine/phosphate ratio is related to stratigraphic age for material respectively from the British Isles and from mainland Europe. Although there is an upward trend in fluorine/phosphate ratio from Holocene (Recent) to Miocene, the broad spread

Table 1 Estimation of fluorine in material from Lagow, Texas (after Oakley & Howells 1961: 545). X-ray diffraction data: difference in mm between $2\theta_{(004)}$ and $2\theta_{(140)}$ for copper-Kα radiation in 19-cm diameter powder-camera.

Human rib, Lagow	3·13
Human tibia, Lagow	3·12
Mammoth ischium, Lagow	2·65
Camelops bone, Lagow	2·73
Bone from Lower Schuler Sands, condition friable	2.80
Bone from Lower Schuler Sands, condition hard	2·75
Equus bone, Hill Gravel	2·75
Bison vertebra, Upper Schuler Clay	2·71
Compare:	
Recent animal bone	3·34 (F = 0·03%)
Fossil human skull from Midland, Texas	3·13 (F = 0·70%)
Fossil human skeleton from Tepexpan, Mexico	2·67 (F = 1·50%)

of the figures indicates the danger of trying to employ the ratio as an index for geological age without taking into account local factors which in so many cases affect the degree of fluorination of vertebrate fossils.

When a long series of fossil skeletal materials from a given site require to be analysed for their fluorine content, microchemical analysis of the samples can be replaced in large measure by employing the X-ray powder diffraction technique which was introduced by Niggli, Overweel & van der Vlerk (1953). In this method the distance between a suitable pair of lines on an X-ray powder photograph of the bone apatite varies with the fluorine content. In order to indicate the corresponding fluorine percentage in the materials under investigation, the tabulated results should include measurements which have been made on two or three samples analysed chemically. As an illustration of an application of this technique I reproduce here (Table 1) a summary of the results obtained when the age of a fragmentary human skeleton from the Lagow Sand Pit, Texas was investigated. The X-ray diffraction data of the samples were obtained by G. F. Claringbull and the late R. J. Davis in the Department of Mineralogy, BM(NH).

The fossil animal bones from Lagow, which date from a temperate stage prior to the Last Glacial event of the Pleistocene, gave highly homogeneous results for fluorine content clustering between measurements of 2·65 and 2·80 mm for six samples of bone, while the two human bones gave readings which are clearly out of this range. But the human bones were evidently not modern, for their fluorine content indicates a slight degree of mineralization, apparently comparable with that of the Midland skull from Texas. On the other hand they appear to be much later than the fossil fauna characteristic of the formation, and tentatively they can be interpreted as probably intrusive burials dating from early Post-Pleistocene times.

When Carnot's fluorine dating method was first used, and when it was reintroduced (Oakley 1948, 1951, Oakley & Montagu 1949, Oakley & Hoskins 1950), no use was made of nitrogen analysis and uranium analysis for relative dating. When the laboratory investigations of the Piltdown fossils were undertaken (Weiner, Oakley & Le Gros Clark 1953, Oakley *in* Weiner *et al.* 1955 : 247–253 & 254–261) it was found that the most effective method of relative dating of fossil bones preserved under temperate conditions was to analyse the skeletal material for fluorine, 'uranium' and nitrogen. It is relevant to mention here that the Lagow investigation (Oakley & Howells 1961) utilized the combined techniques of fluorine, 'uranium' and nitrogen dating, but only the fluorine results are quoted here.

A few of the factors which limit the usefulness of fluorine dating should be mentioned. As already indicated (p. 3), it is unreliable in tropical regions and or where the soils are rich in volcanic minerals. Since the adsorbtion of fluorine by buried bones depends on the percolation of fluorine-bearing ground-water, the fluorine dating method also gives unreliable results in exceptionally arid regions (e.g. Transvaal cave deposits) and in calcareous cave deposits where layers or seams of calcite commonly prevent the free circulation of the ground-water.

The question of what time-interval is adequate to permit differentiation by fluorine analysis can best be answered in the light of experience at a particular locality. The amount of fluorine that has accumulated in the bones or teeth during Post-Pleistocene periods in Britain, at any rate, is usually quite inadequate for differentiating them very clearly. Thus the range of fluorine content in a series of Neolithic bones would overlap that of Bronze Age bones excavated in the same region. On the other hand Pleistocene bones, and bones buried at the same locality only a century or so ago, would in both cases be clearly separable from Neolithic or Bronze Age groups by fluorine analysis. From the point of view of the present paper it is worth quoting figures obtained when two groups of Upper Pleistocene bones were analysed from a site in Austria (Kulna cave, specimens collected by K. Velloch):

	$100F/P_2O_5$
Bones (3) from Magdalenian layer	0·4–0·5
Bones (9) from Mousterian layer	0·3–1·4

From these results it is evident, as would be expected, that on average there is a greater concentration of fluorine in the Mousterian bones. However, as the ranges of fluorine for the Magdalenian bones falls within that of the Mousterian, it would not be possible to use fluorine-dating to decide whether a bone of uncertain horizon in this cave, with a ratio of say 0·4, had been derived from the Magdalenian deposits or from the Mousterian deposits at this site. Even at such a site it would nevertheless be valuable to determine the fluorine content (or better the ratio $100F/P_2O_5$) in a specimen of uncertain horizon because the results of the analysis would indicate the degree of probability that the specimen had been derived from the younger or from the older layer.

At a given level of fluorination within a bone-bearing deposit, the fluorine content of a specimen may prove to vary with the texture or the type of vertebrate tissue that was sampled. It is therefore essential in fluorine dating (as in all methods of relative dating by analysis) to compare like with like as far as possible. Fluorine is adsorbed almost uniformly throughout the thickness of compact bone, compact antler or dentine (e.g. elephant tusk or root of tooth), and at about the same rate in all these materials; but it is adsorbed at slightly higher rates in spongy bone or antler, while enamel is a law unto itself and is better excluded from comparative series when other dental material is available. Cancellar or spongy tissue is liable to be contaminated by silt or other mineral matter, but if comparison is made between fluorine/phosphate ratios rather than between the actual fluorine contents of the samples this complicating factor is eliminated.

References. Publications on fluorine in fossil bones and teeth, including applications of the 'fluorine test' for relative antiquity of fossil vertebrate remains: Bergman & Karsten 1952, Bromehead 1943, Carnot 1892*a*, *b*, 1893, Cook 1960, Day & Molleson 1976, Földvari-Vogl & Kretzoi 1961, Glover & Phillips 1965, Hoskins & Fryd 1955, Mehta & Simpson 1975, Middleton 1844, Milton, Lidell & Chivers 1947, Oakley 1948, 1950, 1951, 1954*a*, *b*, 1955*b*, *c*, 1963*c*, 1969, 1974, Oakley & Gardiner 1964, Oakley & Hoskins 1950, 1951, Olsen 1950, Stewart 1951, Van der Vlerk 1957, Vayson de Pradenne 1932, Wilson 1902.

Relative dating by uranium

Uranium is adsorbed from ground-water by the apatite of bones and teeth, which accumulate this element in course of time, and thus provides a useful alternative to fluorine as an indicator of the relative ages (or of the sources) of buried skeletal remains, particularly in sands and gravels. The rate at which the uranium is accumulated in bone or tooth depends largely on the abundance of this element in the environment, but also to a considerable extent on the hydrological conditions prevailing at the site and on the nature of the mineral matrix. In clays and limestones the circulation of uranium is considerably inhibited, but in sands and gravels the accumulation of uranium and its daughter elements in skeletal material provides a most useful means of distinguishing between indigenous and intrusive specimens. 'Intruders' may of course be younger or older than the indigenous series.

The 'uranium' content of a specimen (and by 'uranium' in this context we mean all elements of the uranium family) can be conveniently assessed by a physical method: the so-called radiometric assay, which takes the form of exposing a sample of the bone, antler or tooth to a Geiger counter screened in a lead chamber, and counting its β-radiations per minute, with due allowance for any background radiation. The counts per minute due to the skeletal sample are expressed as equivalent to so many units of uranium oxide per million (*e* U_3O_8 ppm).

Radiometric assays are of little or no use for the relative dating of bones from post-Glacial deposits owing to the initially slow build-up of uranium, but as the adsorbed uranium generates a series of unstable daughter elements, there is a steep rise in the radioactivity of buried bones in the course of tens of millennia, so that radiometric assays usually distinguish quite clearly between fossil and recently-intruded bones in Pleistocene gravels and sands.

Radiometric assays of the 'Piltdown assemblage' showed (as fluorine had done) that it was not uniform in geological age or origin. The radiometric assay went further than fluorine analysis, for it revealed that some of the specimens (fragments of molar tooth or teeth of *Elephas* cf. *planifrons*) were more radioactive than any Pleistocene fossils known in Britain and had probably been derived from a foreign source (see p. 13).

The radiometric assay has an advantage over fluorine analysis for relative dating, since it can be made without any destruction of material if the bone or tooth can be placed in a space measuring 4 × 3 × 2 cm. Its surface can then be assayed directly. In the case of larger specimens the assay can be made on about a gram of bone or dentine powder drilled out by means of a dental burr.

It should be noted that the weak radioactivity due to carbon-14 (^{14}C) atoms in the residual organic matter or protein of bone or dentine is never confused in practice with the much stronger radioactivity of the adsorbed uranium in the apatite of fossil bone, dentine or enamel. This is evident enough from the fact that fresh bone with maximum content of ^{14}C shows a *nil* count rate on a radiometric assay devised for measuring the uranium content of the specimen.

References. Publications on uranium in fossil bones and teeth and on uses of the radiometric assay in determining the relative antiquity of vertebrate specimens: Bowie & Davidson 1954, 1955, Davidson 1953, Fleischer, Price & Walker 1965, Howell *et al.* 1972, Molleson & Oakley 1966, Oakley 1961, Oakley & Rixon 1958.

Relative dating by nitrogen

The nitrogen content of bones and teeth is due to the protein collagen which forms the organic matrix on which the phosphatic mineral matter has been deposited in the course of formation within the body.

Electron microscopy has made it possible to study the fibrous structure of collagen. In 1955 J. T. Randall and A. V. W. Martin prepared an electron micrograph of the decalcified residue of a sample of the Piltdown mandibular bone, revealing well-preserved collagen fibrils with characteristic banding at intervals of 640Å (Oakley 1955*c*: pl. 30, fig. 11). Residue of a decalcified sample of the Lloyd's site woolly rhinoceros bone, although about 30 000 years old, proved to contain intact collagen fibrils, but they were partly denatured and showed only vague shadows of the original banding (Fig. 5, p. 21). The only fossils in which collagen fibrils had been found previously were samples of mammoth ivory from frozen ground (Figs 3, 4; see also Randall *et al.* 1952).

It is noteworthy that when Randall & Martin (*in* Oakley 1955*c* : 255) undertook to examine the collagen in samples of the teeth in the Piltdown mandible, the first results were inconclusive for in drilling the samples frictional heat had denatured the collagen; this takes place at 70–100°C.

On chemical analysis fresh bone or dentine usually proves to contain 4–5% nitrogen derived from the collagen matrix. After burial the collagen in the bones and teeth is gradually lost but at a relatively slow, sometimes almost uniformly declining, rate. The rate of the regression of nitrogen in buried bone and dentine depends on the physical, chemical and bacteriological conditions of the immediate environment. Nitrogen is lost most rapidly under oxidizing conditions. Under

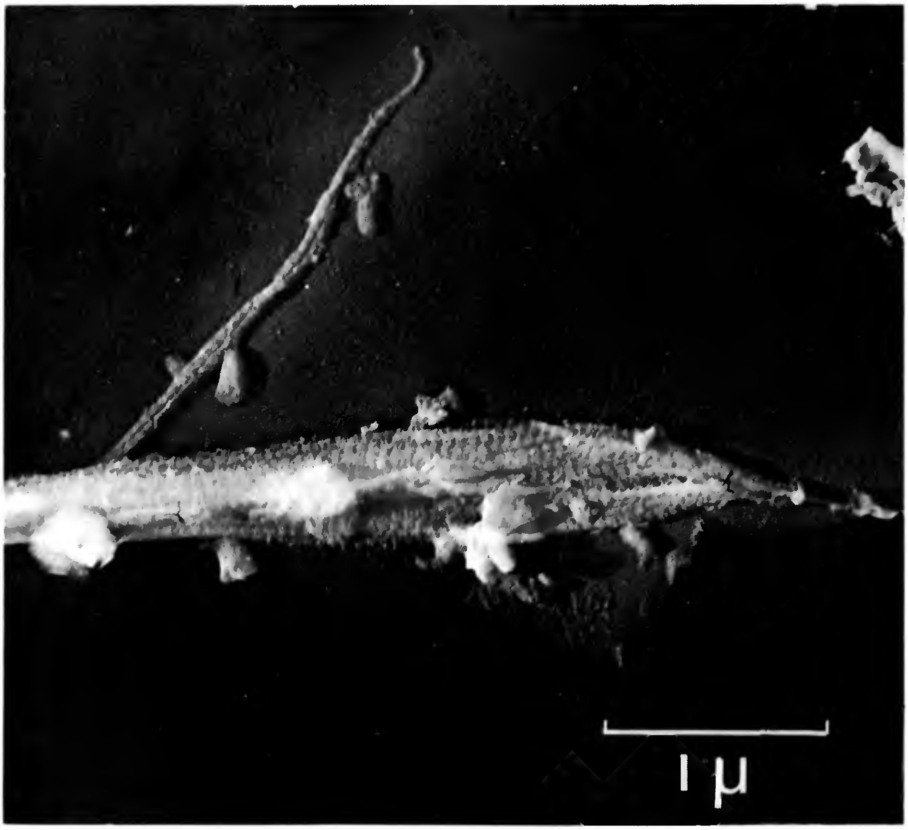

Fig. 3 Electron micrograph of decalcified residue of mammoth ivory from permafrost, Alaska, showing banded collagen fibrils. Shadowed with palladium and gold. × 30 000 (approx.) Photo: C. G. Ogden.

some circumstances the extent to which the nitrogen content has regressed provides a most useful guide to the antiquity of a bone or tooth. Nitrogen analysis is notably useful for the relative dating of bones and teeth when they are of several different geological ages but preserved together under identical conditions. Relative dating by nitrogen content is particularly useful in cases where the bones or teeth are too recent to be within range of the fluorine or uranium dating methods. As with fluorine, it may be unreliable in limestone cave deposits where the vertebrate items have been sealed by films of calcite, but it gives good results in permeable deposits on open sites. It is always important that the control series should include a sufficient number of samples to indicate the range of variation of nitrogen content at a given horizon, and also that allowance should be made for variation in the type of material tested (e.g. outer layer of compact bone, spongy bone, dentine, enamel). The principle that like must be compared with like is particularly important in relative dating by nitrogen content. The nitrogen test is perhaps most valuable as a means of cross-checking the results of uranium or fluorine analysis of bone believed to be of Pleistocene age on open sites.

Nitrogen analysis of *unburnt* bones from archaeological sites is now frequently used as an indirect, but very convenient guide as to whether a specimen contains enough residual protein for ^{14}C dating and if so, what quantity of material will be required. The carbon/nitrogen ratio in bone has been given as 3 : 1 (Orr & Berger 1965), but in practice I have found it approximates more closely to 2·5 : 1. Thus, if a bone has had its collagen content reduced in course of natural weathering to the level of 1 % N, about 100 grams of this bone would be needed to yield 2·5 grams of carbon.

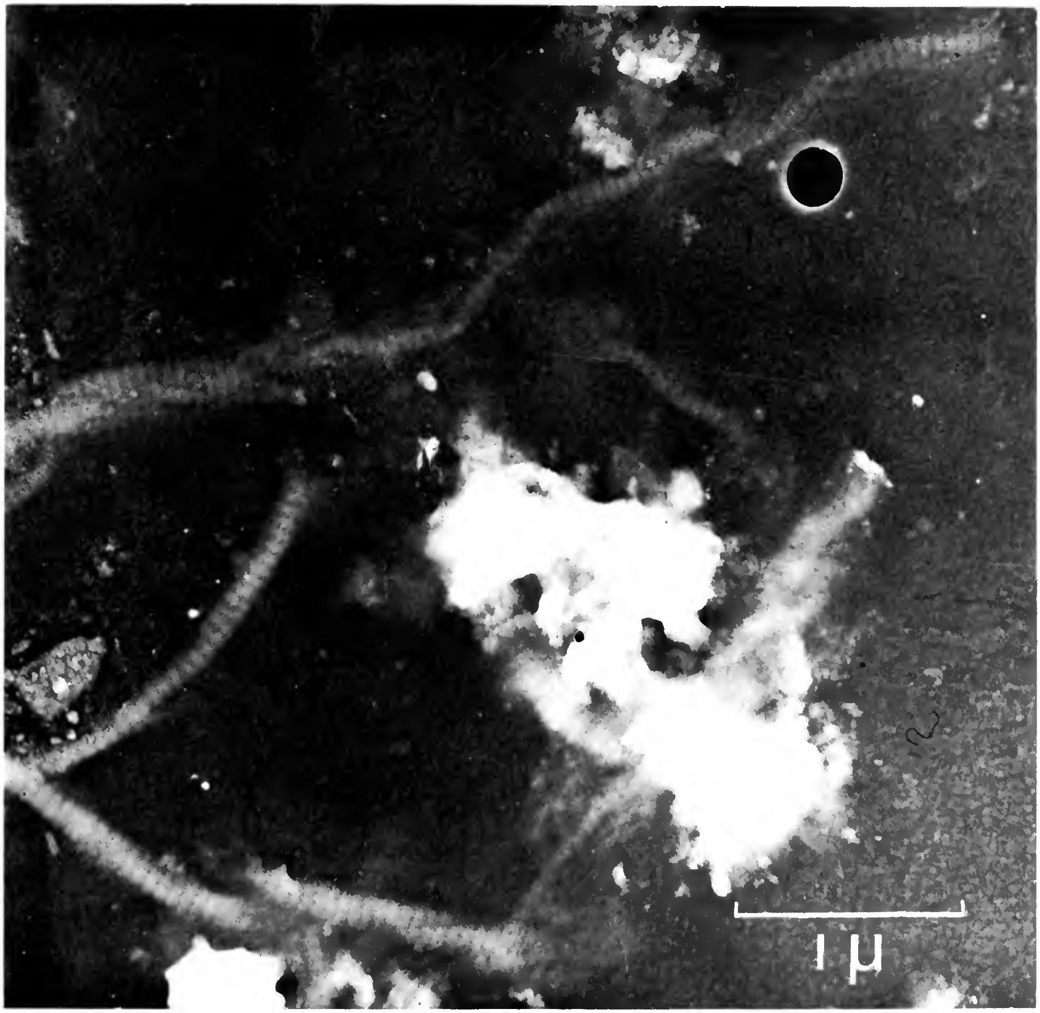

Fig. 4 Electron micrograph of decalcified residue of mammoth ivory showing banded collagen fibrils. Shadowed with palladium and gold. × 30 000 (approx.). Photo: C. G. Ogden.

Nitrogen in bone, antler, dentine or enamel was at one time usually determined by the chemical micro-Kjeldahl method, but this is only applicable with accuracy to samples weighing more than 10 mg. Most of the nitrogen determinations reported in this paper were made by a method of microcombustion (*fide* F. B. Strauss). The amino-acid or protein content of skeletal materials can be measured by chromatography (p. 20). It is of course essential to be certain that samples sent for analysis in 'nitrogen dating' are free from contamination by any nitrogenous hardening agent, adhesive or moulding medium (e.g. size, celluloid, glue or gelatin). Whenever possible only *untreated* bone or dentine should be submitted. If there is any doubt about this, as there often is when the specimens are from an old museum collection, the analyst should be warned so that he can, as a precaution, wash the ground or drilled samples in warm water (< 70° C) and in acetone or other solvents capable of removing nitrogenous contaminants but leaving any original collagen intact. All the samples in a comparative series should receive the same treatment.

As bone protein or collagen decays in the course of fossilization it is broken down into the various component amino-acids, which are leached out or retained for varying lengths of time depending on the local conditions (Abelson 1956). Some amino-acids were found surviving even in the bones of fishes embedded in hard shale at least 350 million years old in the Devonian of

Ohio. To assess the degree of degradation of collagen in fossil bone a sample is first dissolved in a suitable acid, and the amino-acids present in the resulting hydrolysate are then determined by means of chromatography. A paper-chromatogram (Fig. 6, p. 21) prepared from a sample of the ulna of a woolly rhinoceros preserved in Upper Pleistocene clay at the Lloyd's site, London, showed strongly the main amino-acids composing collagen. In marked contrast the Galley Hill skeleton (p. 17), although only dating from the Bronze Age but preserved in a gravelly matrix, gave a chromatogram which showed only a few of these amino-acids and those in reduced strength. It is impossible to use the residual amino-acids in fossil bones determined by chromatography as a method of relative dating, but as they are subject to a process of change known as racemization[2] they do provide a method of chronometric dating (Bada & Protsch 1973, Bada *et al.* 1974, Fleming 1976 : 193–200).

The concentration of nitrogen does not decrease with absolute uniformity in time because it is influenced by the variety of factors listed above. Many more observations are required before we shall know the extent to which climatic factors govern the rate of decline in the nitrogen content of fossil bones; work along these lines has already been published (Buczko & Vas 1977, Buczko 1978, Vonach 1976). Measurements on buried bones on the Hungarian Plain indicated that the minima in nitrogen content coincide fairly closely with the climatic maxima during the last 9 000 years. The effect of temperature on protein decay in bone has been studied experimentally (Ortner, von Endt & Robinson 1972). Further light might be thrown on this problem by analysing pieces of bone buried under various microclimates and determining their nitrogen contents after the lapse of various short periods of time.

References. Publications on the collagen, nitrogen and amino-acid contents of fossil bones and teeth: Abelson 1956, Ascenzi 1955, 1969, Bada & Protsch 1973, Bada *et al.* 1974, Buczko & Vas 1977, Cook 1960, Cook & Heizer 1947, Ezra & Cook 1957, Fleming 1976 (esp. 193–200), Garlick 1969, Isaacs, Little, Curry & Tarlo 1963, King & Bada 1979, Oakley 1954*a*, 1955*c*, 1963*b*, Orr & Berger 1965, Randall *et al.* 1952, Vonach 1976, Weiner, Oakley & Le Gros Clark 1953 (esp. 143–144).

Uses of combined techniques

Fluorine, uranium and nitrogen analyses have been used in combination mainly for relative dating of fossil bones and teeth (Day & Molleson 1973 : 146, 148, Molleson & Oakley 1966, Oakley 1955*a*, *b*, *c*, 1963*c*, 1969). In addition to many applications to fossil remains in Europe, the combined techniques have been applied to remains from hominid sites in Asia (Day & Molleson 1973, Oakley 1969 : 44–45), Africa (Oakley 1957, 1958*c*) and U.S.A. (Oakley & Howells 1961).

Analyses of vertebrate specimens for fluorine, uranium and nitrogen have sometimes proved valuable in helping to establish the origins of specimens of doubtful provenance. A notable example is a molar tooth of *Hippopotamus major*, BM(NH) 18304, in MacEnery's collection from Kent's Cavern, a specimen which a number of workers suspected had really originated in Villafranchian deposits of the Mediterranean region. On analysis of this tooth the fluorine/phosphate ratio proved to be 5·7, compared with 5·3 in a tooth from the Val d'Arno, Italy, whereas the fluorine/phosphate ratio in teeth from Kent's Cavern has not been recorded as exceeding 0·6 (Oakley 1964*b*). These results strongly suggest that it *had* been imported from the Villafranchian deposits of southern Europe and accidently incorporated in the Kent's Cavern collection. Other instances where analyses of fluorine and uranium in fossil bones have proved useful in indicating the provenance of the specimens are worth quoting here.

The 'Piltdown I assemblage' included a molar tooth of *Anancus* cf. *arvernensis*. On analysis its enamel showed *e* U_3O_8 97 ppm and the fluorine/phosphate ratio proved to be 6·4. The enamel

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[2] There are two distinct molecular forms of amino-acids, known as optical isomers, and these are distinguished as L or D forms according to whether they rotate the plane of polarization of polarized light to the left (laevorotatory) or to the right (dextrorotatory). In living tissue proteins are composed almost entirely of L amino-acids, but after death the amino-acids slowly racemize, that is to say L forms are converted into D forms, the proportions of the two tending to become equal. Fossil bones are thus found to contain both D and L forms and the ratio of D to L increases with the advancing age of the specimen. The relative amounts can easily be measured by an optical method. Aspartic acid and iso-leucine are the amino-acids most commonly used in this method.

of a typical tooth of *Anancus arvernensis* from the Red Crag of Suffolk showed *e* U_3O_8 38 ppm and a fluorine/phosphate ratio of 7·0. Since *e* U_3O_8 is recorded as ranging from 13 to 174 ppm in teeth from the Red Crag of Suffolk, the disparity between the uranium content of the enamel of the *Anancus* tooth used for comparison and the one in the 'Piltdown' group is insignificant. However, the enamel of another 'Piltdown' tooth, of obviously extraneous origin and identified as *Elephas* cf. *planifrons*, contained *e* U_3O_8 520 ppm and the cementum of the same tooth *e* U_3O_8 610 ppm[3].

When the latter radiometric assays were compared with those of teeth of the *Elephas planifrons* group from numerous localities in Europe, Asia and Africa the only ones which were closely comparable were from Ichkeul in Tunisia. The dentine of a typical molar tooth from there showed *e* U_3O_8 580 ppm and the enamel *e* U_3O_8 480 ppm. But the fact that Ichkeul was unknown as a source of Lower Pleistocene fossils until 1949 greatly reduces the likelihood that the 'Piltdown' elephant molar fragments originated there. Dr Vincent Maglio has informed me, however, that specimens of *Elephas* cf. *planifrons* (now *Archidiskodon africanavus*) have also been found at six other north African sites (a second site in Tunisia, three in Chad and two in Morocco). He agreed that 'the most likely source for the Piltdown fragments is north Africa'. It is surely significant that uranium fields occur in Morocco and in Tunisia.

A hominid femur, OH34, was excavated in 1962 from Olduvai Gorge Bed III at site JK2. On account of its strange preservation it was thought wise to analyse samples of this specimen in an attempt to confirm its contemporaneity with other fossils undoubtedly from Olduvai Bed III. The level of 'uranium' proved to fall within the range recorded in other bones from Bed III, and the fluorine content was consistent with its recovery from this deposit (Day & Molleson 1976).

The usefulness of the combined techniques is also illustrated by the results obtained through applying them to the problem of the age and origin of the remains of sabre-tooth cats reported from British cave deposits. In 1876 a canine tooth of *Homotherium* ['*Machairodus*'] was found in an Upper Palaeolithic layer in Robin Hood's cave, Creswell Crags, Derbyshire (Dawkins 1876). Some authorities doubted whether this was a genuine find, suspecting that it had been fraudently placed at the site, and it had really originated in alluvial deposits of Early Pleistocene age in France or Italy, where specimens of this genus are not uncommon. Comparison of the fluorine, 'uranium' and nitrogen contents of the Creswell tooth with Villafranchian specimens from the main Continental localities dispels this suggestion (Table 2), but other possibilities have to be considered. Was the Creswell canine derived from a Lower Pleistocene deposit in Derbyshire and brought into the Robin Hood's cave by prehistoric man? There are many instances of fossils having been treasured by stone age man and transported to a considerable distance from their natural source. *Homotherium* canines, but specifically different from the Creswell specimen, have been found in association with Lower Pleistocene fossils in a fissure deposit at Doveholes, also in Derbyshire. Yet in their lack of nitrogen, high fluorine content and high 'uranium' content they contrast sharply with the Creswell specimens whose composition on the other hand agrees closely with that of local Upper Pleistocene cave mammal remains.

Table 2 Fluorine, nitrogen and uranium content of *Homotherium* teeth from Creswell Crags and other European sites.

Source of *Homotherium* dentine tested	Nitrogen %	Fluorine %	$100F/P_2O_5$	Uranium *e* U_3O_8 ppm
Val d'Arno, Italy	0·2	1·6	5·3	35
Mt Perrier, France	nil	1·9	6·3	30
Doveholes, Derbyshire	nil	2·5	8·6	68
Creswell, Derbyshire	2·1	0·2	0·8	<1
Kent's Cavern, Devon	1·2	<0·01	<0·1	5

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[3] Fluorimetric determination of uranium in this tooth indicated U_3O_8 = 1000 ppm.

Table 3 Fluorine and nitrogen content of mammalian teeth from Kent's Cavern.

Specimens of dentine	Nitrogen %	$100F/P_2O_5$
Homotherium canine, BM(NH) 14954, from cave-earth	1·2[4]	<0·1
Mammuthus molar from cave-earth	0·8	<0·1
Ursus molar from hard breccia	0·2	<0·1

If it were still to be maintained that the Creswell specimen had been fraudulently planted, its composition could only be accounted for by supposing that it had been obtained from some other similar limestone *cave* deposit elsewhere. For in my experience it is only in limestone cave deposits that Pleistocene vertebrate specimens are so deficient in fluorine as this one. Teeth of *Homotherium* have in fact been reported from Upper Pleistocene cave-earth in Kent's Cavern, Torquay. It has been widely assumed by vertebrate palaeontologists that these specimens were residues from some much older deposits in the Torquay Cave system. The composition of one of the Kent's Cavern canines was therefore tested. The fluorine content of the dentine proved to be negligible and the 'uranium' content to be very low. The failure of these two elements to circulate in calcareous cave deposits is recognized, but if these specimens were derivatives considerably older than the Upper Pleistocene mammoth tooth that apparently occurred in the same cave-earth, they should contain substantially less nitrogen. In fact they proved to contain just as much (Table 3). Thus it can be inferred provisionally that sabre-tooth cats (*Homotherium*) survived as rarities in Britain during Upper Pleistocene times, and that the last examples were contemporary with Middle Palaeolithic (Mousterian) and possibly with the earliest Upper Palaeolithic men. The survival of *Homotherium* on the Continent into late Middle Pleistocene times is already well established (Adam 1961).

References: Adam 1961, Dawkins 1876, Day & Molleson 1973, 1976, Molleson & Oakley 1966, Oakley 1955*a*, *b*, *c*, 1957, 1958*a*, *c*, 1963*c*, 1964*b*, 1969, Oakley & Howells 1961.

European fossil hominids to which analytical methods of relative dating have been applied

Note on the Tables

The tables show significant analyses of fossil hominids of Europe compared with similar analyses of associated mammalian faunas. No authentic fossil hominid has been reported from Lower Pleistocene deposits in Europe. Table 4 (p. 25) shows the composition of mammalian teeth identified as derived from the Lower Pleistocene (Red Crag) of Suffolk but which were used to form part of the fraudulent faunal assemblage placed in association with the forged hominids Piltdown I and II, Sussex. The fluorine/phosphate ratios and the uranium contents of these Lower Pleistocene fossils range to higher levels than in Middle Pleistocene material from southern Britain. (See Table 5, p. 27).

Between 1948–75, fluorine, phosphate, iron and carbonate determinations (and occasionally uranium, manganese, sodium, potassium and chloride) were made in the Laboratory of the Government Chemist, London, by R. H. Settle and E.C.W. Maycock (1948–49), Dr C. R. Hoskins (1949–53), C. F. M. Fryd (1953–57), P. J. Hardwick (1953–63), A. D. Baynes-Cope (1954–58), Dr J. R. Cooke (1958–59), A. A. Christie (1959), G. F. Phillips (1960–66), M. J. Glover (1963–65), J. Roburn (1966–67), E. C. Hunt (1968–70) and N. M. Soutar (1971–75). A few of the nitrogen determinations were made in the same Laboratory by E. I. Johnson (1957–61), P. J. Cooper (1965) and N. M. Soutar (1971–72), but the majority were made by Dr G. Weiler (from 1953) and Dr F. B. Strauss (1953–77) in the Microanalytical Laboratory, Oxford. The calcium carbonate was estimated in the Laboratory of the Government Chemist on the basis of determination of CO_2. The uranium determinations expressed as U parts per million were made by Dr R. L. Fleischer in the General Electric Research Laboratory, Schenectady, New York, using the fission-track method; the larger number expressed as *e* U_3O_8 were made on the basis of radioactivity measurements by

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[4] Washing the sample in warm water and then in acetone to remove any possible traces of nitrogenous preservative effected no reduction in the nitrogen content.

S. H. U. Bowie and Dr C. F. Davidson, Atomic Energy Division, Institute of Geological Sciences (1953–54) and by twelve members of staff of the Department of Palaeontology (including the Subdepartment of Anthropology), BM(NH), 1955–75.

The majority of the tables plot the percentages of the following components: F, P_2O_5, $CaCO_3$, N (w = after washing) and the uranium content expressed as U or *e* U_3O_8 in parts per million (ppm). The ratio $100F/P_2O_5$ is also indicated. Radiocarbon (^{14}C) dates are designated by bc or bp (before present); calendar dates, derived by correction of the radiocarbon dates (Clark 1975) are designated by BP or BC. In Tables 6 and 17 some radiocarbon ages (bp) of hominid bones are given, and in Tables 6, 9 and 17 the radiocarbon ages (bp) of associated mammalian remains are shown. References to the radiocarbon reports are given at the end of the descriptions of the sites. CFH No. – Catalogue of Fossil Hominids **2** (Oakley, Campbell & Molleson 1971).

British Isles

AVELINE'S HOLE (Somerset). Skeletal remains of *Homo sapiens* generally attributed to the final stage of the British Upper Palaeolithic have been recovered from Aveline's Hole, a blocked cave on the east side of Burrington Combe in the Mendip Hills. They include an adult male calvaria encrusted with stalagmite, discovered by W. Buckland in 1823 (Aveline's Hole 1), a mandible excavated by R. Bright before 1840 (Aveline's Hole 2) and a cranium with mandible obtained during excavation by the Bristol Speleological Research Society in 1914 (Aveline's Hole 9).

Aveline's Hole 1: F = 0·47%, $100F/P_2O_5$ = 1·98, *e* U_3O_8 = 2 ppm, N = 3·8% (w)
Aveline's Hole 2: F = 0·29%, $100F/P_2O_5$ = 1·04, *e* U_3O_8 = nil, N = 1·8% (w)
Aveline's Hole 9: F = 0·48%, $100F/P_2O_5$ = 2·28, N = 3·47%.
Human metacarpal, Aveline's Hole 1914 unnumbered: F = 0·20%, $100F/P_2O_5$ = 0·92, N = 3·49%
Mammalian bones from cave-earth, Aveline's Hole: F = 0·07%, $100F/P_2O_5$ = 0·26; F = 0·20%, $100F/P_2O_5$ = 0·67; N = 1·4–3·0%
See Table 6, p. 28.

The ^{14}C dating of residual collagen in a human femur (1914 unnumbered) from Aveline's Hole was determined in the British Museum Research Laboratory as 9114 ± 110 bp (BM-471). This result compares significantly with the ^{14}C dating of stalagmite filling the Aveline's Hole 1 skull: 8100 ± 150 bp (GrN-5393), a determination kindly made by Dr J. C. Lerman in the Groningen Radiocarbon Laboratory (information *in lit.*, 1968). Some of the Aveline's Hole skeletal material is therefore as late as Lower Flandrian, but the total amount (including fragments of *c.* 50 skeletons found in 1797 and subsequently lost) is sufficient to make it probable that occupation or use of the cave began in Devensian times.

References: Barker, Burleigh & Meeks 1971 : 179–180; Campbell 1977 : 163, Table 4; Molleson 1977 : 88, 90; Oakley 1971*a* : 17–19; Tratman 1977.

BADGER HOLE (Somerset). A child's mandible (Badger Hole 1) and pieces of an adult cranium (Badger Hole 3) were found in hard cave-breccia at this site by H. E. Balch in 1939 and 1945.

Badger Hole 1: N = 1·58%
Badger Hole 3: N = 0·93%
Associated *Crocuta* bone N = 2·5%
See Table 6, p. 28.

The ^{14}C dating of charred bone fragments from layer 1 (Proto-Solutrean): > 18 000 bp (BM-497). It is inferred that the Badger Hole skeletal material is stratigraphically Middle Devensian.

References: Barker, Burleigh & Meeks 1971 : 168, Campbell 1977 : 51, 88, Molleson 1977 : 87, 88, Oakley 1971*a* : 19–20.

BAKER'S HOLE (Kent). In 1903 G. White described the finding in the previous year of a human skull in brickearth at Baker's Hole, Ebbsfleet. Analyses have shown that this skull was a Post-Pleistocene intrusion.

Homo skull, Baker's Hole: F = 0·06%, $100F/P_2O_5$ = 0·2, *e* U_3O_8 = nil, N = 2·04% (w)
Mammuthus, Baker's Hole: F = 1·2%, $100F/P_2O_5$ = 4·3, *e* U_3O_8 = 15 ppm, N = 0·32% (w)
See Table 6, p. 28.

Reference: Oakley 1971*a* : 20.

BURY ST EDMUNDS (Suffolk): see under Westley (p. 26)

CRESWELL CRAGS (Derbyshire). Human teeth and bones from late Upper Palaeolithic (Creswellian) occupation layers in three caves in the Creswell Crags have been analysed, and compared with associated Late Glacial mammalian bones and teeth.

Mother Grundy's Parlour 1, cranium of child discovered 1876; dentine of molar: N = 0·95% (w)
Probably Mother Grundy's Parlour, *Meles* molar dentine: N = 1·20% (w)
Pin Hole Cave 1, skeleton of child from upper red cave-earth; ilium bone: F = 0·06%, $100F/P_2O_5$ = 0·27, *e* U_3O_8 = nil, N = 3·41%
Pin Hole Cave, mammalian bone: F = 0·54%, $100F/P_2O_5$ = 2·5, *e* U_3O_8 = nil, N = 1·94%
See Table 6, pp. 29–30, under Mother Grundy's Parlour, Pin Hole Cave and Robin Hood's Cave; also Table 2, p. 13

The composition of the ilium of Pin Hole Cave 1 compares unfavourably with that of the mammalian bone representing the Late Glacial fauna of the cave, but a longer series of comparative analyses would be needed before the antiquity of this skeleton could seriously be called in question.

In July 1969, J. B. Campbell made excavations in Robin Hood's Cave, and found a human frontal bone at a depth of 196 cm below the surface, associated with Creswellian shouldered points. Layer OB, in which the frontal bone was found, was identified by Campbell as 'undisturbed Late Glacial thermoclastic scree'. A sample of metacarpal bone of *Equus przewalskii* bulked with a sample of *Megaloceros* antler from the same layer was submitted to the British Museum Research Laboratory, where radiocarbon dating of the residual collagen gave a date of 10 390 ± 90 bp (BM-603). Pollen recovered from cavities in the *Equus* bone indicated a Late Glacial flora. On the basis of this evidence the human frontal bone (Robin Hood's Cave 1) has been accepted as dating stratigraphically from the Late Devensian. The unexpectedly high nitrogen content of this bone (3·89%) raises a slight doubt as to whether the bone was introduced into layer OB during post-glacial disturbance. It is to be regretted that samples of the *Equus* metacarpal and of the *Megaloceros* antler were not submitted for nitrogen analysis. There is a lesson to be learnt here, because clearly if these two items of Late Glacial fauna were known to be as high in nitrogen as the human frontal, all suspicion that this bone might be intrusive would vanish. There are well-authenticated Late Pleistocene bones from limestone cave deposits with equally high nitrogen content, and Robin Hood's Cave 1 is only suspect because a recently-discovered fossil human bone from the same cave proved to contain much less nitrogen (see below). During his 1969 excavations, Campbell recovered a number of other human bones from his layer E, consisting of tip-heap material from nineteenth century excavations. After a detailed study of these bones, Miss Rosemary Powers came to the conclusion that they were all parts of the skull of a single individual, the same as that represented by the frontal from layer OB (Powers & Campbell 1977, Campbell 1977 : fig. 175). All of the human bones from layer E so far analysed prove to be high in nitrogen (e.g. one of the maxillae: N = 3·81%).

R. D. S. Jenkinson, Curator at the Creswell Crags Visitor Centre, has kindly informed me about a fossil human mandible which was extracted from cave-earth in Robin Hood's Cave in 1974 by two schoolboys. It was situated *c.* 1 m below the travertine floor. In view of the importance of this discovery, the mandible was sent to the BM(NH) for reconstruction by R. J. Parsons. It was satisfactory to find that the nitrogen content (1·11%) was low enough to be consistent with the inference that the specimen was contemporaneous with the Devensian cave-earth.

References: Burleigh, Hewson & Meeks 1976 : 22 (Robin Hood's Cave); Campbell 1977 : 62–64 (Mother Grundy's Parlour), 47–48 (Pin Hole Cave), 64–69 (Robin Hood's Cave); Molleson 1977 : 87–89 (Mother Grundy's Parlour), 89, 91 (Pin Hole Cave), 89, 91 (Robin Hood's Cave); Oakley 1971*a* : 32 (Mother

Grundy's Parlour), 35–36 (Pin Hole Cave), 36–37 (Robin Hood's Cave); Powers & Campbell 1977 : 218–220 (Robin Hood's Cave).

FLINT JACK'S CAVE (Somerset). In 1893 or earlier R. Pavey recovered two human skulls from this rock-shelter in the Cheddar Gorge. Late Upper Palaeolithic (Cheddarian) artifacts were in presumed association. No fossil mammalian material has been reported from this site. The results of analysing these skulls gave figures consistent with their being of Late Devensian age.

Flint Jack's Cave 1: F = 0·052%, $100F/P_2O_5$ = 0·17, N = 1·36%(w)
Flint Jack's Cave 2: F = 0·122%, $100F/P_2O_5$ = 0·4, N = 1·25%(w)
See Table 6, p. 28.

References: Campbell 1977 : 158, Molleson 1977 : 88, 91, Oakley 1958*b*.

GALLEY HILL (Kent). In 1888 R. Elliott reported that workmen had found a skeleton of *Homo sapiens* at a depth of 8 ft (2·4 m) in the 100-ft terrace Acheulian gravel in a pit adjoining Galley Hill School in Swanscombe, Kent. In 1884 a similar discovery had been made in the same pit. For a number of years these two Galley Hill skeletons were regarded by Sir Arthur Keith as proof that *Homo sapiens* already existed in the earlier part of the Pleistocene period, but there remained doubt about their antiquity.

The more complete skeleton found in 1888 (Galley Hill 1) was acquired by Frank Corner, whose collection was offered for sale by his widow Mrs D. H. Pearson in 1948. The skeleton in question was eventually bought by Dr C. T. Trechmann, who presented it to the Subdepartment of Anthropology, BM(NH), where it has been registered under EM 249–262.

Application of the fluorine-dating method to Galley Hill 1 in 1948 indicated that it was an intrusive burial in the Acheulian gravels and dated from end-Pleistocene or early Holocene times. This was confirmed by measurement of the nitrogen-content of the skeleton in comparison with fossil bones contemporaneous with the gravel and from later deposits.

Galley Hill 1 femur: F = 0·56%, $100F/P_2O_5$ = 2·0, N = 1·61% (w)
Galley Hill 1 humerus: N = 2·04% (w), *e* U_3O_8 = nil
Mammal bones from Middle Pleistocene gravels, Swanscombe: F = 1·6–2·4%, $100F/P_2O_5$ = 5·7–7·4, N = <0·01 to 0·2%
Mammal bones from Upper Pleistocene deposits, Swanscombe: F = 1·0–1·3%, $100F/P_2O_5$ = 2·8–4·6, N = 0·2–0·5%
Holocene (Anglo-Saxon) bone: F = 0·05%, $100F/P_2O_5$ = 0·2, N = 2·5%
See Table 5, p. 27 (Swanscombe).

A prepared sample of the humeri of Galley Hill 1 was later submitted to the Research Laboratory of the British Museum for radiocarbon dating (BM-86). The sample was decalcified in cold dilute hydrochloric acid. The resulting granular gel represented the residual collagen of the bone. After combustion, its ^{14}C content was measured and indicated a date of 3310 ± 150 yrs bp, or *c.* 3409 bp using the new half-life of radiocarbon. By reference to the bristlecone pine calibration curve (Clark 1975) this gives a calendar date of *c.* 3600 BP (*c.* 1650 BC), suggesting burial in late Neolithic or early Bronze Age times.

References: Barker & Mackey 1961 : 41, Clark 1975, Keith 1912 : 517, Montagu & Oakley 1949, Newton 1895, Oakley & Montagu 1949.

GOUGH'S CAVE (Somerset). The most important series of hominid skeletal remains of the British Upper Palaeolithic – Early Mesolithic are those found at various levels in Gough's Cave on the east side of the Cheddar Gorge, Somerset. These include the complete skeleton of 'Cheddar Man' discovered by R. C. Gough in December 1903 (Gough's Cave 1), and regarded as a burial pene-contemporaneous with the Upper Cave-earth; fragmentary skulls and other bones excavated by R. F. Parry in 1927-8, comprising the two[5] crania Gough's Cave 2 and 3 from layers 10–13, and unnumbered post-cranial fragments from layers 6–7; an adult mandible (Gough's Cave 8) found

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[5] When this paper was originally drafted two other crania found by R. F. Parry in 1927–8, Gough's Cave 4 and 5, were included in the list, but according to the late Professor E. K. Tratman the precise provenance of these specimens is uncertain; Gough's Cave 4 has the appearance of being late Holocene, while the whereabouts of Gough's Cave 5 is unknown.

by R. F. Parry in 1928–9, and an adult parietal bone (Gough's Cave 7) excavated from layer 14 by a workman in 1950. Most of this material is preserved in Gough's Cave Museum, Cheddar, but the whereabouts of Gough's Cave 2 is unknown.

Analyses of Hominids from Gough's Cave:
Gough's Cave 1, talus: F = 0·25%, $100F/P_2O_5$ = 2·4, *e* U_3O_8 = nil, N = 1·83% (w), $CaCO_3$ = 55%, organic C = 3·7%
Gough's Cave 1, tibia: N = 1·74–3·95% (21 samples)
Gough's Cave 1, dentine (M_1): N = 2·7%
Gough's Cave 3, cranium: N = 2·9%
Gough's Cave 6, mandible: F = 0·47%, $100F/P_2O_5$ = 2·16, *e* U_3O_8 = 6 ppm, N = 3·02%, $CaCO_3$ = 14·07%
Gough's Cave 7, parietal: F = 0·09%, $100F/P_2O_5$ = 1·37, *e* U_3O_8 = nil, N = 0·71%, $CaCO_3$ = 63·4%

Mammalian bones from the cave-earths:
Rangifer bone, above Gough's Cave 1: F = 0·14%, $100F/P_2O_5$ = 0·9, *e* U_3O_8 = nil, N = 1·5%, $CaCO_3$ = 28·2%
Ursus bone, layer 11: N = 3·0%
Equus bone, layer 18: F = 0·29%, $100F/P_2O_5$ = 1·42, *e* U_3O_8 = 4 ppm, N = 2·1%, $CaCO_3$ = 21·4%
See Table 6, p. 29.

Radiocarbon dating of the residual collagen in the left tibia of Gough's Cave 1 was undertaken by the Research Laboratory of the British Museum and the result was published as 9080 ± 150 bp (Barker, Burleigh & Meeks 1971 : 180). If the result had been calculated using the new half-life of radiocarbon it would be *c.* 9350 bp. It should not be assumed that the actual time of burial was very close to this date (= *c.* 7400 bc), because a nearly correct calendar date could only be obtained after allowing for the natural radiocarbon variations that occurred over the period of time involved. Seven or eight thousand years is beyond the present backward limit of the bristlecone pine calibration. On the basis of extrapolation from the existing calibration curve, the dating of 'Cheddar Man' is approximately 700 years too young. Assuming he was buried around 8100 BC he still postdated the Younger Dryas stage, the upper limit of which (8300 BC) has been generally adopted in Europe as the Pleistocene/Holocene boundary. Thus on the available evidence 'Cheddar Man' is of Flandrian age, but only just. He may reasonably be regarded as not differing from a typical member of the Upper Palaeolithic population of SW Britain. He was probably buried after Gough's Cave had ceased to be actively occupied (Molleson 1977). It should be remembered that the main period of occupation of this cave was during the Late Devensian, when it was used by hunting people with Creswellian culture which persisted with scarcely appreciable change into earliest Flandrian times.

From the point of view of using nitrogen-content in the relative dating of skeletal material, it is worth noting that the distribution of the collagenous residue containing this element evidently varies widely in fossilized long bones (see %N in left tibia of 'Cheddar Man', Table 6, p. 29). Even so, the ratio of the extremes of the range of nitrogen in a given specimen is rarely more than two.

References: Barker, Burleigh & Meeks 1971 : 180, Campbell 1977 : 4, 166, Cooper 1931, Davies 1904, Donovan 1955 : 76–104, Gray 1904, Molleson 1977 : 88, 91, Oakley 1971*a* : 22–25, Parry 1928, 1929, Seligman & Parsons 1914, Tratman 1975 : 7–24.

HALLING (Kent). A contracted burial was found by workmen in 1921 at a depth of about 6 ft (173–190 cm) in brickearth containing flint implements on an occupation floor regarded by the first investigator (W. H. Cook 1914) as Aurignacian. The skull was identified by A. Keith as belonging to T. H. Huxley's 'river-bed' type.

The application of relative dating tests to the skeleton of Halling Man did not give conclusive results, but very few specimens had been available for comparison. If the comparative series had been longer it is probable that the Halling skeleton would have been seen to fall well within the early Holocene range of composition.

Holocene bones:
Bos longifrons: F = 0·09%, $100F/P_2O_5$ = 0·32, *e* U_3O_8 = nil, N = 1·71%
Caprid ('large sheep'): F = 0·41%, $100F/P_2O_5$ = 1·6, *e* U_3O_8 = 2 ppm, N = 2·93% (w)

Pleistocene bones:
Equus: F = 0·75%, $100F/P_2O_5$ = 2·6, *e* U_3O_8 = 6 ppm, N = 1·23%
Mammuthus: F = 1·30%, $100F/P_2O_5$ = 3·9, *e* U_3O_8 = 4 ppm, N = 0·62%
Halling Man, ulna: F = 0·9%, $100F/P_2O_5$ = 3·0, N = 0·9% (w)
Halling Man, femur: *e* U_3O_8 = 5 ppm.

A sample of the Halling femora was submitted to the Research Laboratory of the British Museum, where ^{14}C measurements on the residual collagen indicated a radiocarbon age of 4180 ± 190 bp (BM-249), or *c.* 4305 bp if the calculation is made using the new half-life of ^{14}C, that is *c.* 2355 bc. If one attempts correction of this date by reference to the bristlecone pine calibration curve, the probable calendar antiquity of the Halling skeleton appears to be very close to 3000 BC. This dating is in conformity with the results of re-examining the flint implements from the 'floor' overlying the skeleton, for it was found that they could fit into either a Late Mesolithic or a Neolithic context (G. de G. Sieveking *in lit.* 1967).

References: Barker, Burleigh & Meeks 1969 : 289, Cook 1914, Oakley 1963*a*, Oakley, Barker & Sieveking 1968.

KENT'S CAVERN (Devonshire). A few fragments of hominid skeletons have been found with Late Upper Palaeolithic (cf. Magdalenian) industry in the cave-earths of this cave. They include a left humerus (= Kent's Cavern 2) found probably in the first-foot level below the upper or granular stalagmite in Underhay's Gallery when W. Pengelly was digging in November 1878 on behalf of the British Association. A hominid ulna from Pengelly's excavations (specimen 16769) was not numbered in the *Catalogue of Fossil Hominids* (Oakley, Campbell & Molleson 1971). The level from which it came is unrecorded, but it is embedded in a matrix of cave-earth. Both specimens have been analysed.

Kent's Cavern 2, humerus: F = 0·1%, $100F/P_2O_5$ = 0·3, *e* U_3O_8 = nil, N = 1·38%
Kent's Cavern unnumbered, ulna: F = 0·01%, $100F/P_2O_5$ = 0·03, *e* U_3O_8 = nil, N = 2·11%
See Table 2, p. 13, Table 3, p. 14 and Table 6, p. 29.

The fairly high nitrogen content of the ulna cannot be considered to throw doubt on its Upper Palaeolithic antiquity, because analyses of Pleistocene fauna from Kent's Cavern showed nitrogen content ranging up to 3·53%.

References: Campbell 1977 : 37–42, Campbell & Brazier *in* Campbell 1977 : 203–207, Molleson 1977 : 88–90, Oakley 1971*a* : 26–28.

KILGREANY (County Waterford, Republic of Ireland). Two human skeletons were found in a discontinuous layer of stalagmite in Kilgreany Cave during excavations in 1928 under the leadership of E. K. Tratman. The stalagmite contained remains of a Late Glacial fauna, and at first it was suggested that the human remains were contemporaneous. Further excavations in 1934 showed that the deposits were in a confused state. The Late Glacial faunal material was intermingled with bones of domesticated animals and sherds of Windmill Hill (Neolithic) pottery.

Kilgreany A, *Homo* post-cranial bone: F = 0·11%, $100F/P_2O_5$ = 0·36, *e* U_3O_8 = nil, N = 1·07% (w)
Megaloceras phalange: F = 0·14%, $100F/P_2O_5$ = 0·48, *e* U_3O_8 <1 ppm, N = 1·54% (w)
Kilgreany B, *Homo* post-cranial bone: N = 0·85% (w)

Radiocarbon dating of residual collagen in a sample of the post-cranial bones of skeleton A gave 4580 ± 150 bp (BM-135), indicating that it was probably Neolithic, presumably a burial. Radiocarbon dating of collagenous residue in a sample of post-cranial bone of skeleton B at first proved unreliable owing to the impregnation of the skeleton with a waxy preservative. It is intended that, after more thorough pretreatment, a second attempt will be made to date this material.

References: Barker & Mackey 1968 : 4, Oakley 1971*a* : 28–29, Molleson & Vogel in prep.

LANGWITH CAVE (Derbyshire). In 1909 E. H. Mullins, while excavating this cave on the north side of Poulter Valley, Langwith Basset, found a human cranium together with vertebrae and phalanges representing a burial. The cave-earth in which the bones were discovered contained hearths and an Upper Palaeolithic (Creswellian) industry.

Cranium, Langwith Cave 1: N = 2·7%
See Table 6, p. 29.

The high nitrogen content of this Upper Palaeolithic skull is an illustration of the unreliability of collagenous residues for relative dating of bones in limestone cave deposits. If the bone became sealed off from percolating water by calcitic films, the decay of collagen and the leaching out of amino-acids would have been arrested at that point. Another bone of the same age in a situation where percolation of water had been unimpeded would show substantially less nitrogen representing residual collagen.

References: Campbell 1977 : 158, Molleson 1977 : 89, Oakley 1971 : 29–30.

LLOYD'S SITE (City of London). As reported by Warren R. Dawson in October 1925, workmen collected a human calvaria from redeposited London Clay 42·6 ft (*c.* 13 m) below the surface in excavations for the Lloyd's Building in Leadenhall Street. Assuming that the containing deposit formed the base of the Upper Flood-plain Terrace of the Thames, many authorities assumed that this London skull was of Upper Pleistocene age, and since it clearly belonged to *Homo sapiens* it was regarded as possibly of considerable importance. Analytical dating techniques when applied to the skull in comparison with fossil mammalian bones from the same site showed that it was probably intrusive. The chemical composition of the London skull agrees more closely with that of skulls of the Thames 'river-bed' series of Post-Pleistocene age.

Homo skull, Lloyd's site: F = 0·07%, $100F/P_2O_5$ = 0·23, N = 1·52%
Coelodonta ulna (M 12575), clay at *c.* 13m, Lloyd's site: F = 1·1%, $100F/P_2O_5$ = 4·2, N = 3·42%
Mammuthus femur, sand at *c.* 7m, Lloyd's site: F = 1·3%, $100F/P_2O_5$ = 4·8, N = 0·1%
Mammal bone, Holocene silts, London Docks: F = 0·2%, $100F/P_2O_5$ = 0·8.
Homo skull, 'river-bed' series, Mortlake: F = 0·32%, $100F/P_2O_5$ = 1·3, N = 5·25%
Homo skull, 'river-bed' series, Mortlake: N = 2·7%

A sample of the ulna of woolly rhinoceros (*Coelodonta*) from the Lloyd's site was submitted to the Groningen Radiocarbon Laboratory, where J. C. Vogel obtained a radiocarbon date on the residual collagen: 29 450 ± 350 bp (GrN-4630).

The reason for the preservation of so much of the protein in the Lloyd's rhinoceros bone is that it was embedded in an unoxidized clay—an environment in which collagen decays very much more slowly than in sand or gravel through which water percolates carrying with it soluble nitrogenous breakdown products of the protein. Thus, in marked contrast, a portion of mammoth femur found at the same site but in a layer of sand had lost most of its collagen and therefore showed only a small percentage of nitrogen. It is worth noting that the fluorine content of fossil bone may increase at about the same rate in sand as in clay. The fluorine content of the rhinoceros bone is almost the same as that of the mammoth bone.

As the collagen of the Lloyd's rhinoceros bone is almost undiminished in spite of its considerable antiquity we considered that it would be interesting to have a chromatogram prepared from an acid hydrolysate of the bone (Fig. 6). G. C. Ross of the Department of Zoology, BM(NH), who undertook this was able to distinguish the amino-acids alanine, arginine, beta-phenylalanine, cystine, glycine, hydroxyproline, leucine/iso-leucine, lysine, ornithine and proline. An EM-photograph of a decalcified sample of this bone showed that collagen fibres were preserved, but they had lost their characteristic banding, so were in a denatured condition (Fig. 5).

References: Oakley 1969 : 40, 1971*a* : 30, Smith 1925, Young 1938.

PAVILAND (West Glamorgan). W. Buckland was mainly responsible for the discovery in December 1822–January 1823 of the skeleton of *Homo sapiens* ceremonially buried in red ochre in the Paviland Cave (Goat's Hole) on the coast of the Gower Peninsula. This fossil skeleton (Paviland 1)

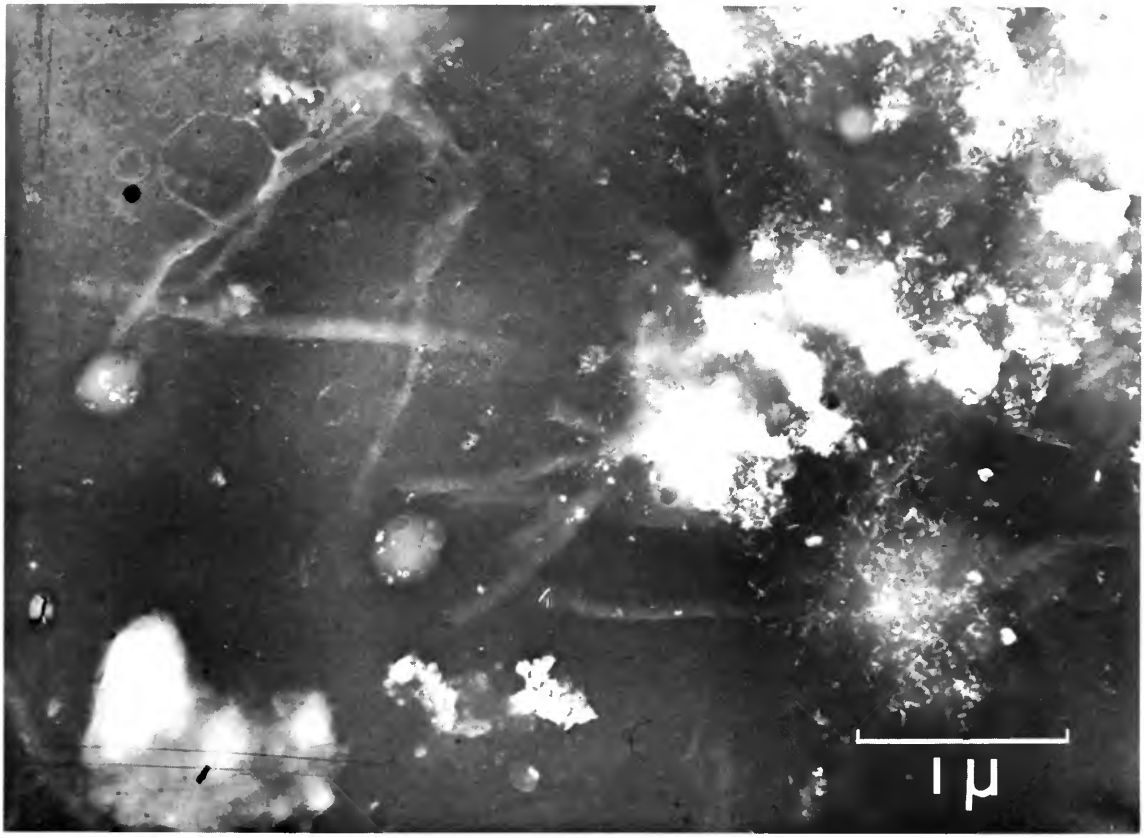

Fig. 5 Electron micrograph of decalcified residue of an ulna of rhinoceros (*Coelodonta antiquitatis*) from Upper Pleistocene clay, Lloyd's site, City of London, showing slightly denatured collagen fibrils. Shadowed with palladium and gold. × 28 500 (approx.). Original specimen in Department of Palaeontology (reg. no. M12575). Photo: C. G. Ogden.

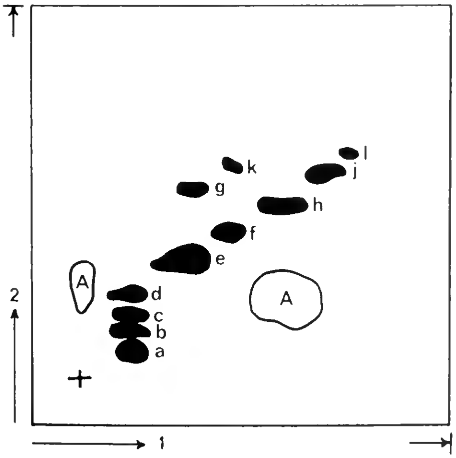

Fig. 6 Two-dimensional chromatogram, on thin-layer Silica Gel G, of amino-acids in electrolytically desalted acid hydrolysate of rhinoceros ulna from Lloyd's site, City of London, developed in methanol : chloroform : ammonia :: 16: 16: 7 (1) and phenol (2). a, ornithine; b, cystine; c, lysine; d, arginine; e, glycine; f, alanine; g, hydroxyproline; h, valine; j, leucine/isoleucine; k, proline; l, β phenylalanine; A, artefact. Prepared by G. C. Ross; redrawn from tracing of chromatogram.

is that of a male aged about 25, but it became known as the 'Red Lady'. The associated fauna undoubtedly included *Mammuthus primigenius*. The skull and tusk of a mammoth had evidently been buried ceremonially with the human skeleton. Other grave-goods included an ivory bracelet, a pendant made from pulpstone extracted from the mammoth tusk, 40–50 polished ivory rods and 'two handsfull' of *Littorina* shells.

In preparation of a full entry on Paviland for the second part of the *Catalogue of Fossil Hominids* (Oakley, Campbell & Molleson 1971) relative dating tests were carried out on samples of material available for analysis.

Homo (Paviland 1), tibia: $F = 0{\cdot}06\%$, $100F/P_2O_5 = 0{\cdot}20$, $e\ U_3O_8 =$ nil, $N = 1{\cdot}31\%$
Homo (Paviland 1), humerus: $F = 0{\cdot}17\%$, $100F/P_2O_5 = 0{\cdot}69$, $N = 2{\cdot}65\%$ (w)
Ursus bone: $F = 0{\cdot}048\%$, $100F/P_2O_5 = 0{\cdot}15$, $e\ U_3O_8 =$ nil, $N = 0{\cdot}93\%$ (w)
Mammuthus dentine (ivory rod): $F = 0{\cdot}064\%$, $100F/P_2O_5 = 0{\cdot}17$, $N = 0{\cdot}13\%$ (w)
See Table 6, p. 30.

Without a longer series of samples for analysis it was not possible to infer that the human skeleton was appreciably later than the mammalian faunal material.

The cave and remaining contents of Goat's Hole were excavated by Sollas (1913), who found nearly 800 flint and chert artefacts, and remains of a characteristic Upper Pleistocene fauna, including *Rangifer*, which indicated cold dry climatic conditions. As there was no clear stratification, the time-span during which the cave was occupied by man can only be inferred from the typology of the stone tools. Mousterian, Lower, Middle and Upper Aurignacian, Proto-Solutrean and Creswellian tool-types were represented (Garrod 1926).

As there seemed to be no archaeological means of deciding to which of these human cultures the Paviland skeleton might belong, I requested that samples of the lower limb-bones should be drilled from the sides of their medullary cavities and submitted for radiocarbon dating at the Research Laboratory of the British Museum. The Curator of the Geological Collections at the University Museum, Oxford, (where the Paviland skeleton is preserved) agreed to the necessary procedures being carried out in the Subdepartment of Anthropology, BM(NH), and in turn the Research Laboratory of the British Museum accepted the sample for radiocarbon dating. The resulting date of 18 460 ± 340 bp was obtained from residual collagen separated from bulked samples of the tibiae and left femur of the skeleton (BM-374; Barker, Burleigh & Meeks 1969 : 289, Oakley 1968). This dating pointed to the burial having taken place around the time of the Last Glacial maximum, when according to the geological evidence (Bowen 1970) glacier-ice was only about 6 km north of Paviland.

Molleson (1976) has argued that the date of the Paviland burial may not have been the date when the cave was actively occupied by the Palaeolithic hunters whose débris accumulated there. In an attempt to verify this she obtained a humerus of *Bos primigenius* from Goat's Hole, Paviland, in the Sollas collection in the National Museum of Wales, and submitted it to the Research Laboratory of the British Museum for radiocarbon dating. The result obtained using collagen separated from this bone was 27 600 ± 1 300 bp (BM-1367, Molleson & Burleigh 1978). This date compares closely with that of the earlier Upper Palaeolithic from Kent's Cavern (Davidson 1974) and can be seen as remarkably consistent with that part of the Paviland artefact collection which has been compared with the industry from Illsen Höhle near Leipzig, dated by palaeobotanical evidence to about 30 000 bp (McBurney 1965).

References: Barker, Burleigh & Meeks 1969 : 289, Bowen 1970, Buckland 1823 : 82–98, Davidson 1974, Garrod 1926 : 49–64, McBurney 1965, Molleson 1976 : 112–6, Molleson & Burleigh 1978, Oakley 1968, Sollas 1913.

PILTDOWN (Sussex). In 1950 it was shown by the fluorine method of relative dating that the Piltdown mandible and cranial bones were considerably younger geologically than the Lower and Middle Pleistocene fossils said to have been found at the same site. Assuming that they were genuine finds, the hominoid remains therefore could not be older than Upper Pleistocene, but it was noted that drill-holes into the teeth revealed that they were 'apparently no more altered than the dentine of recent teeth from the soil' (Oakley & Hoskins 1950 : 381). In 1953, J. S. Weiner, after reviewing this evidence in the light of anatomical considerations, suggested that the mandible was that of a recent ape which had been broken and stained to resemble a fossil, and the teeth artificially abraded to suggest wear through the human type of mastication. According to this hypothesis, the fraudulent jaw-bone had been placed in the Piltdown gravel pit so as to appear associated with fragments of a thick human cranium of presumed great antiquity.

Determination of the organic content and redetermination of the fluorine content of these specimens, together with evidence obtained from a detailed anatomical analysis of the teeth, confirmed this hypothesis (Weiner, Oakley & Le Gros Clark 1953).

	Fluorine % (1950)	Fluorine % (1953)	Nitrogen %	Carbon %
Piltdown mandible	0·2 ± 0·2	<0·03	3·9	14·5
Piltdown cranium	0·2 ± 0·1	0·10 ± 0·01	1·4	5·3
Modern bone		0·03 ± 0·01	4·0	14·0

The mandible had the composition of modern bone, whereas the cranial fragments appeared 'slightly fossilized'.

In 1953–55, the possibility of dating the Piltdown bones by the radiocarbon method was not seriously considered because it would have involved total destruction of the specimens to provide the minimum quantity of carbon (2 gm) then demanded by radiocarbon laboratories for a single determination. By 1959 improvement of technique made it possible to attempt ^{14}C dating on the basis of much smaller quantities. Powder samples of the Piltdown mandible and right parietal bone were then submitted to the late Professor H. de Vries of Groningen, after repeated washing in acetone and then in warm water (at 70°C), which was carried out under rigorous conditions in the Department of the Government Chemist, London. The nitrogen content of the samples proved to be the same before and after submission to this treatment, proving their freedom from nitrogenous contaminants, such as glue, gelatine and celluloid. Their nitrogen content represents the bone protein (collagen), which is not removable by acetone or warm water. This is the material which provided the carbon whose radioactivity was then measured in the Groningen Laboratory.

Professor de Vries reported that the sample of Piltdown mandible was burnt without further pre-treatment. The sample of the Piltdown cranium was dissolved in hydrochloric acid; the fraction which was not precipitated by alkali was dated. Both samples gave a very small amount of carbon dioxide, corresponding to about 0·1 gm of carbon. The radiocarbon dates obtained were as follows:

Piltdown mandible (GrN-2204) 500 ± 100 years bp (= AD 1450)
Piltdown skull (GrN-2203) 620 ± 100 years bp (= AD 1330)

These results show that both the mandible and the cranium are of Holocene age, conclusions not inconsistent with the relative dating published in 1955 when it was reported that 'the low fluorine content of the skull indicates that it is more probably Post-Pleistocene than Pleistocene in age' (Oakley 1955*c* : 257). The indication that the mandible was several centuries old raised the question of its origin. When Sir Wilfrid Le Gros Clark established that it was the jaw-bone of an orang-utan (and therefore came from Borneo or Sumatra), it was assumed to be a zoological collectors' piece. It seemed very unlikely that an orang-utan jaw-bone falling into the hands of a collector would prove to be several centuries old, but not impossible because the Dyaks of Borneo are known to keep orang-utan skulls as trophies in their long-houses for generations, although the chance of a dealer obtaining such a highly treasured object directly from the living Dyaks is negligible. However, Tom Harrison pointed out to me that a number of sub-recent bones of orang-utan, obtained in Sarawak in various circumstances, were brought back to Britain in 1875 by A. H. Everett. Some were obtained from caves whose contents were washed by Chinese gold-workers. A large part of Everett's collection (including one specimen No. 55 which appears to have been a trophy skull) was presented to the Department of Zoology of the BM(NH). All the orang-utan skulls and jaws listed as received by the Museum in 1879 can be accounted for, but Harrison believed that Everett brought back much more material to Britain, and what became of it is unknown.

Comparison of the Piltdown jaw-bone with one of the 'sub-recent' orang-utan jaw-bones in the Everett Collection (No. 100 in Everett's list, recorded as 'doubtfully from a cave in Sarawak', registered as ZD.84.10.30.2) has brought out a number of points of resemblance. Not only is the nitrogen content of the 'antique' Sarawak specimen (4·6%) undiminished in comparison with modern bone (4·0 to 5·3% in one series), but also the surface of the bone is in the same finely crackled condition. Attempts to reproduce the appearance of the Piltdown mandible by artificial treatment of modern bones failed in just this respect (Weiner *et al.* 1955 : pl. 27). The banded condition of the collagen fibrils in the Piltdown mandible, as revealed by the electron microscope (Weiner *et al.* 1955 : pl. 30, fig. 11), indicates that it was not boiled by the forger.

According to the radiocarbon dating of a sample of the right parietal bone, the Piltdown cranium appears to be only marginally older than the mandible. This is surprising in so far as in 1953 it was proved that all the cranial fragments had been artificially stained to match the gravel, so it became clear that like the mandible they were fraudulent introductions at the site.

Evidence was found by G. F. Claringbull & M. H. Hey (1955) that the Piltdown cranial bones had received very severe chemical treatment in an attempt to make them appear fossilized. The calcium phosphate in the bones had been partially altered to calcium sulphate (gypsum). Such alteration is unknown under natural conditions, but does occur when bones are artificially stained by an acid iron sulphate solution. Experiments showed that this alteration only occurs if the bone has the porosity due to partial loss of the organic matrix. Thus the Piltdown cranial bones are evidently of moderate antiquity. Presumably they were parts of a skull selected for the hoax on account of its exceptional thickness from amongst a series obtained in the excavation of some early burial ground. The fluorine content of the unaltered portion of the bone substance of the cranium also indicates moderate antiquity, but unless one knows the source of a bone precise relative dating by fluorine content is impossible. However, in many British and foreign cemeteries bones less than a thousand years old can be found with the same fluorine content (0·1%).

Although the difference in the radiocarbon ages of the cranial bone and the mandible is less than might have been expected in view of their contrasting states of preservation, it should be borne in mind that whereas a bone that has been buried in the ground for a few centuries may have become porous and 'sub-fossil' (with some absorbed fluorine), a bone of equal antiquity that has been preserved in air, for example on the floor of a dry cave, in a building or in a reliquary, may have retained the composition of recent bone.

References: Baynes-Cope 1955, Claringbull & Hey 1955, de Vries & Oakley 1959, Everett 1879 : 149, Oakley 1955*b*, *c*, Oakley & Hoskins 1950, Weiner, Oakley & Le Gros Clark 1953, Weiner *et al.* 1955.

STRUMPSHAW (Norfolk). A cranium regarded as representing one of the River Valley people of the Téviec Group was recorded from Strumpshaw by Wells (1961). Analysis suggests that the skull is of early Holocene age.

Strumpshaw skull: F = 0·17%, $100F/P_2O_5$ = 0·74, N = 2·94% (w)
Skull of *Bos*, Early Iron Age, Stiffkey, Norfolk: F = 0·03%, $100F/P_2O_5$ = 0·1, N = 1·21% (w)

References: Oakley 1971*a* : 39, Wells 1961.

SUN HOLE (Somerset). In 1926–28 excavations by the Bristol University Speleological Society in Sun Hole, a cave on the north side of Cheddar Gorge, Mendip Hills, produced a human radius bone (Sun Hole 2) at a depth of 5 ft (1·5 m) in soliflucted scree overlying red cave-earth.

Sun Hole 2: F = 1·09%, $100F/P_2O_5$ = 4·86, N = 1·65%
Rangifer bone at same level: F = 0·64%, $100F/P_2O_5$ = 2·64, N = 3·16%
See Table 6, p. 30.

^{14}C dating of residual collagen in a bone of *Ursus arctos* from the B2 complex of soliflucted screes in Sun Hole gave a date of 12 378 ± 150 bp (BM-524).

References: Barker, Burleigh & Meeks 1971 : 168, Campbell 1977 : 51–55, Molleson 1977 : 89, 91, Oakley 1971*a* : 39.

Table 4 Analyses, British Isles, Lower Pleistocene. Piltdown I and II.

BM(NH) Lab. No.	Locus and Description	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$	N%	*e* U_3O_8 ppm	U ppm	BM(NH) Register No.
'Piltdown I' collection, specimens inferred to be from Red Crag, Suffolk:								
P. 6	*Anancus* cf. *arvernensis* molar enamel	1·9	23·0	8·3	—	11	24	E.595
P. 25	*Anancus* cf. *arvernensis* molar enamel	2·3	36·0	6·4	nil	97	80	E.622
P. 26	*Dicerorhinus* cf. *etruscus* premolar enamel	2·0	24·0	8·3	nil	68	—	E.623
P. 48*a*	*Dicerorhinus* cf. *etruscus* molar dentine	2·07	30·3	6·8	—	40	—	E.624
P. 48*b*	*Dicerorhinus* cf. *etruscus* molar dentine	—	—	—	—	11	—	E.624
'Piltdown II' collection included one specimen inferred to be from Red Crag, Suffolk:								
P. 47*a*	*Dicerorhinus* cf. *etruscus* molar dentine	2·65	27·9	9·5	—	18	—	E.649
P. 47*b*	*Dicerorhinus* cf. *etruscus* molar enamel	—	—	—	—	<1	—	E.649

SWANSCOMBE (Kent). The Swanscombe skull, now referred to *Homo sapiens steinheimensis*, was discovered by A. T. Marston in 1935 and 1936, at a depth of 24 ft (7·3 m) below the surface in Barnfield gravel-pit, about ½ mile (0·8 km) NW of Swanscombe Church. It lay near the base of the Upper Middle Gravels of the 100-ft terrace of the river Thames. The occipital bone was found on 29th June 1935 and the left parietal on 15th March 1936. The right parietal was found by A. Gibson on 30th July 1955.

The sandy gravel in which the skull bones were embedded contains a mammalian fauna including *Palaeoloxodon antiquus*, and has been accepted as belonging to the Hoxnian (= Holsteinian) interglacial.

Swanscombe, occipital: F = 1·7%, 100F/P_2O_5 = 6·1, *e* U_3O_8 = 27 ppm, N = 0·18%
Swanscombe, l. parietal: F = 1·4%, 100F/P_2O_5 = 5·9; F = 1·5%, 1·8% (mean 1·6%); *e* U_3O_8 = 11 ppm.
Swanscombe, r. parietal: F = 1·9%, 100F/P_2O_5 = 6·7, *e* U_3O_8 = 40 ppm, N = 0·09%
Associated mammalian bones: F = 1·7–2·3%, 100F/P_2O_5 = 5·7–6·8, *e* U_3O_8 = 10–47 ppm, N = trace–0·2%, $CaCO_3$ = 6–9%

By measuring the thorium 230/uranium 234 and protactinium 231/uranium 235 activity ratios in a sample of bone collected from the Middle Gravels by Desmond Collins (sample 39), Barney J. Szabo (U.S. Geological Survey, Denver, Colorado) has obtained a provisional uranium-series dating of more than 272 000 years.

References: Molleson 1977 : 84–85, 88, Oakley 1971*a* : 40–41, Oakley & Gardiner 1964, 1968, Szabo & Collins 1975.

THATCHAM (Berkshire). Part of an adult human humerus was found on a Maglemosian (Mesolithic) site at Thatcham near Newbury in 1959. It lay in reworked algal marl of Boreal age overlying peat and containing wood which was dated by ^{14}C as 9490 ± 160 bp (Q-652).

Thatcham 1 bone: F = 0·69%, 100F/P_2O_5 = 2·5, *e* U_3O_8 = 5 ppm, N = 1·74%
Cervid antler: F = 0·7%, 100F/P_2O_5 = 2·4, *e* U_3O_8 = 7 ppm, N = 1·28%

Reference: Oakley 1971*a* : 41.

WALBROOK (City of London). An adult human frontal bone was found in a layer of gritty earth, 17 ft (5 m) below the surface, during excavation of shafts on the site of Western Union House, in the Walbrook Valley, London EC2 in 1944.

Walbrook 1 bone: F = 0·63%, 100/P_2O_5 = 2·57, *e* U_3O_8 = nil, N = 2·6%

F. E. Zeuner suggested that this bone was of Upper Pleistocene age, but an early Holocene date seems more probable in view of the moderately high nitrogen content and the lack of uranium.

Reference: Zeuner & Weiner 1947.

WESTLEY (Suffolk). The discovery at Westley near Bury St Edmunds in 1882 of a fragmentary human skull with sapient frontale, embedded in brickearth containing Acheulian hand-axes, was for long regarded as an indication that *Homo sapiens* had been in existence since Middle Pleistocene times. Application of the fluorine-dating method in 1950 left no doubt that the skull was part of an intrusive burial of Holocene age. The analyses were made by Dr C. R. Hoskins in the Department of the Government Chemist.

Westley skull: F = 0·1–0·2%, 100F/P_2O_5 = 0·5–0·9
Local Pleistocene bones: F = 0·8–2·1%, 100F/P_2O_5 = 3·3–7·2

Reference: Baden-Powell & Oakley 1953.

WHALEY (Derbyshire). Human skull fragments were reported from cave-earth in rock-shelter no. 2 at Whaley in 1947. According to A. L. Armstrong, the bones represented a ceremonial burial associated with Creswellian culture. J. B. Campbell reported (*in lit.*) that T. G. Manby was

Table 5 Analyses, British Isles, Middle Pleistocene. Swanscombe.

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3$%	N%	*e* U_3O_8 ppm	Collection & BM(NH) Register No.
Lower Gravel, Swanscombe:									
S. 1	*Dama* humerus	—	2·0	32·0	6·3	17	—	15	M.16500
S. 2	*Dama* incisor (osteodentine)	—	2·8	35	8·0	6	—	—	M.16499
S. 36	*Dama* vertebra	—	2·1	34·0	6·2	10	—	14	M.16511
S. 41*a*	*Dama* antler, compact zone	—	2·2	29·0	7·6	11	—	—	A. T. Marston Coll., BM(NH) unreg.
S. 41*d*	*Dama* antler, cancellar core	—	2·6	30·0	8·7				
S. 82	*Dama* antler	—	—	—	—	—	0.20	9	J. Wymer Coll., BM(NH) unreg.
S. 83	*Dama* antler	—	—	—	—	—	—	14	
S. 48	fragment of ungulate limb-bone	—	2·4	33·2	7·4	—	—	42	E.2707
Lower Loam, Swanscombe:									
S. 16	*Panthera* humerus	—	1·7	32·5	5·2	9	—	15	M.16501
Middle Gravels, Swanscombe:									
S. 3	*Dama* metapodial	—	2·3	34	6·8	6	—	—	M.16510
S. 37	*Bos* rib	—	2·0	30	6·7	9·4	trace	32	E.2710
S. 18	*Bos* limb-bone	—	2·0	32	6·3	—	—	21	K. P. Oakley Coll., BM(NH) unreg.
S. 19	rolled bone fragment	—	1·7	30	5·7	8	—	—	
S. 4	*Homo* occipital	Swl	1·7	27·8	6·1	9·0	0·18	27	A. T. Marston Coll., M.15709
S. 17	*Homo* left parietal	Swl	1·5	—	—	—	nil (w)	11	
S. 17	*Homo* left parietal	Swl	1·4	24	5·9	—	—	—	
S. 53	*Homo* right parietal	Swl	1·9	28·2	6·7	6·9	0·09 (w)	40	J. Wymer & A. Gibson Coll., EM.40
S. 78	nine mammal bone fragments from *Homo* skull layer, Middle Gravels, Swanscombe	—	—	—	—	—	0·20	47	BC/23 (from J. Wymer's excavations, 1955)
S. 79		—	—	—	—	—	—	21	BC/23
S. 80		—	—	—	—	—	—	17	AB/1–2
S. 81		—	—	—	—	—	—	27	CD/2–3
S. 84		—	—	—	—	—	—	29	AB/2–3
S. 85		—	—	—	—	—	—	31	BC/2–3
S. 86		—	—	—	—	—	—	22	—
S. 87		—	—	—	—	—	—	32	D1/3–4
S. 88		—	—	—	—	—	—	35	—

Table 6 Analyses, British Isles, Late Upper Pleistocene and Early Holocene.

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%}\times 100$	$CaCO_3$%	N%	*e* U_3O_8 ppm	^{14}C yrs bp	Collection & Register No.
C. 21	Aveline's Hole, *Homo* cranium	AH1	0·47	23·7	1·98	13·0	3·8 (w)	2	—	W. Buckland Coll., BM(NH) E.11.6.257
C. 19	Aveline's Hole, *Homo* mandible	AH2	0·29	27·8	1·04	20·5	1·8 (w)	nil	—	R. Bright Coll., BM(NH) E.504
C. 24	Aveline's Hole, *Homo* cranium	AH9	0·48	21·0	2·28	6·3	3·47	—	—	Wells Museum, 174
C. 25	Aveline's Hole, *Homo* metacarpal	—	0·2	21·6	0·92	8·3	3·49	nil	—	Univ. Bristol Spel. Soc., 133
—	Aveline's Hole, *Homo* femur	—	—	—	—	—	—	—	9114±110 (BM-471)	Univ. Bristol Spel. Soc., unreg.
C. 26	Aveline's Hole, mammal bone	—	0·07	27·1	0·26	6·0	2·9	nil	—	Univ. Bristol Spel. Soc., 139
C. 27	Aveline's Hole, mammal bone	—	—	—	—	—	3·0 (w)	—	—	Univ. Bristol Spel. Soc., unreg.
C. 30	Badger Hole, *Crocuta* bone	—	—	—	—	—	2·5	—	—	K. P. Oakley Coll., BM(NH) unreg.
C. 32	Badger Hole, *Homo* cranium	BH3	nil	22·2	0	8·1	0·93	nil	—	Wells Museum, 228
C. 48	Badger Hole, *Homo* mandible	BH1	—	—	—	—	1·58	—	—	Univ. Bristol Spel. Soc., 226
S. 39	Baker's Hole, *Mammuthus* limb-bone	—	1·2	28	4·3	12	0·32 (w)	15	—	F. N. Haward Coll., BM(NH) unreg.
C. 15	Flint Jack's Cave, *Homo* cranium	FJC1	0·05	30·6	0·17	8·7	1·36 (w)	—	—	R. Pavey Coll., BM(NH) M.16796
C. 16	Flint Jack's Cave, *Homo* cranium	FJC2	0·12	27·8	0·44	12·9	1·25 (w)	—	—	R. Pavey Coll., BM(NH) M.16795

Table 6, cont.

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%}\times 100$	$CaCO_3$%	N%	*e* U_3O_8 ppm	^{14}C yrs bp	Collection and Register No.
C. 3	Gough's Cave, *Homo* right talus	GC1	0·25	10·5	2·4	55	1·83 (w)	nil	—	R. C. Gough Coll., Gough's Cave Museum, 1.1/29
C. 2	Gough's Cave, *Homo* molar (M_1) dentine	GC1	—	—	—	—	2·7	—	—	R. C. Gough Coll., Gough's Cave Museum, 1.1/5 or 1.1/6
C. 78	Gough's Cave, *Homo* left tibia	GC1	—	—	—	—	1·74–3·95 (21 samples)	—	9080±150 (BM-525)	R. C. Gough Coll., Gough's Cave Museum, 1.1/35
C. 79	Gough's Cave, *Homo* right tibia	GC1	—	—	—	—	0·8, 1·5	—	—	R. C. Gough Coll., Gough's Cave Museum, 1.1/27
C. 80	Gough's Cave, *Homo* left femur	GC1	—	—	—	—	1·5, 3·9	—	—	R. C. Gough Coll., Gough's Cave Museum, 1.1/34
C. 4	Gough's Cave, *Homo* cranium	GC3	—	—	—	10·7	2·9	—	—	R. F. Parry Coll., Gough's Cave Museum, 1.1/1
C. 33	Gough's Cave, *Homo* mandible	GC6	0·47	25·78	2·16	14·07	3·02	6	—	R. F. Parry Coll., Gough's Cave Museum, 1.1/3
C. 34	Gough's Cave, *Homo* parietal	GC7	0·09	6·57	1·37	63·42	0·71	nil	—	Gough's Cave Museum, 1.1/2
C. 6	Gough's Cave, level 11, *Ursus* radius	—	0·24	27·0	0·89	10·32	3·0	nil	—	Gough's Cave Museum, 1.2/63a
C. 7	Gough's Cave, level 12, *Ursus* radius	—	—	—	—	—	2·7	—	—	Gough's Cave Museum, 1.2/63
C. 8	Gough's Cave, above[6] GC1, *Rangifer* mandible	—	0·14	16·3	0·9	28·2	1·5	nil	—	Gough's Cave Museum, 1.2/25
C. 9	Gough's Cave, above[6] GC1, *Rangifer* molar dentine	—	—	—	—	26·3	1·6	—	—	
C. 10	Gough's Cave, level 18, *Equus* talus	—	0·29	20·44	1·42	21·4	2·1	4	—	Gough's Cave Museum, 1.2/2
M. 16	Kent's Cavern, *Homo* humerus	KC2	0·1	37	0·3	—	1·38	nil	—	W. Pengelly Coll., BM(NH) M.576
M. 40	Kent's Cavern, *Homo* ulna	—	0·01	27·9	0·03	5·55	2·11	nil	—	W. Pengelly Coll., BM(NH) 16769
M. 46	Kent's Cavern, Proto-Solutrean, *Ursus* bone	—	—	—	—	—	3·53	—	—	J. B. Campbell Coll. 1562
AY	Langwith Cave, *Homo* cranium	L1	—	—	—	—	2·7	—	—	Oxford Coll. E.11.6/258, BM(NH)
M. 21	Mother Grundy's Parlour, *Homo* molar dentine	MGP1	—	—	—	—	0·95 (w)	—	—	W. B. Dawkins Coll., Manchester Museum P4410
M. 22	Probably Mother Grundy's Parlour, *Meles* molar dentine	—	—	—	—	—	1·20 (w)	—	—	W. B. Dawkins Coll., Manchester Museum P2961

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[6] According to a register of the Gough's Cave finds shown to the author in 1954 by the late Curator, Mr Gerald Robertson, the reindeer bone 1.2/25 had been found 'above' the skeleton of Cheddar Man. As it is now generally agreed that this skeleton (GC1) represents an early Post-Pleistceone burial, any overlying bones could easily have been derived from a pre-existing Pleistocene deposit through which the burial was made (Prof. D. T. Donovan *in lit.* 26 June 1975).

Table 6, cont.

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3$%	N%	*e* U_3O_8 ppm	^{14}C yrs bp	Collection and Register No.
E0	Paviland, *Homo* humerus	P1	0·17	25·1	0·69	—	2·65 (w)	nil	—	W. Buckland Coll., Oxford Univ. Museum Q1/1–1/28
K1	Paviland, *Homo* tibia	P1	0·06	29·8	0·20	7·25	1·31	nil	18 460 ± 340 (BM-374)	
PJ	Paviland, *Bos primigenius* humerus	—	—	—	—	—	1·07 (w)	—	27 600 ± 1300 (BM-1367)	W. J. Sollas Coll., Nat. Mus. Wales
EP	Paviland, *Ursus* metapodial	—	0·048	32·3	0·15	—	0·93 (w)	nil	—	F. Corner Coll. 291, BM(NH) unreg.
FA	Paviland, *Mammuthus* dentine	—	0·064	36·8	0·17	—	0·13 (w)	—	—	P. Egerton Coll., BM(NH) M.416
C. 17	Pin Hole Cave, *Homo* ilium	PHC1	0·06	21·03	0·27	16·24	3·41	nil	—	A. L. Armstrong Coll., BM(NH) EM 607
C. 18	Pin Hole Cave, carnivore phalange	—	0·54	21·5	2·51	8·39	1·94	nil	—	A. L. Armstrong Coll., BM(NH) M. 36779
P1	Robin Hood's Cave, *Homo* mandible *c.* 1 m below travertine floor	—	—	—	—	—	1·11	—	—	Creswell Crags Visitor Centre Museum (1974 coll.)
—	Robin Hood's Cave, *Equus przewalskii* metacarpal, layer OB	—	—	—	—	—	—	—	10 390 ± 90 (BM-603)	J. B. Campbell Coll. (1969), Creswell Crags Visitor Centre Museum
M. 41	Robin Hood's Cave, *Homo* frontale from layer OB	RHC1	—	—	—	—	3·89	—	—	J. B. Campbell Coll. (1969) No. 465, Creswell Crags Visitor Centre Mus.
M. 43	Robin Hood's Cave, *Homo* maxilla from layer E (tip)	—	—	—	—	—	3·81	—	—	J. B. Campbell Coll. (1969) No. 466, Creswell Crags Visitor Centre Mus.
M. 54	Robin Hood's Cave, *Homo* cervical vertebra from layer E (tip)	—	—	—	—	—	4·12	—	—	J. B. Campbell Coll. 1969, Creswell Crags Visitor Centre Mus.
M. 55	Robin Hood's Cave, *Homo* calotte from layer E (tip)	—	—	—	—	—	3·94	—	—	
C. 39	Sun Hole, 5th ft *Homo* radius	SH2	1·09	22·44	4·86	25·02	1·65	5	—	Univ. Bristol Spel. Soc. M.5.13/24
—	Sun Hole, 5th ft (B2–7 in up. thermoclastic scree), *Ursus arctos* humerus	—	—	—	—	—	—	—	12 378 ± 150 (BM-524)	J. B. Campbell Coll.
C. 40	Sun Hole, 1st ft mammal bone	—	0·65	17·39	3·74	44·08	2·71	nil	—	Univ. Bristol Spel. Soc. unreg.
C. 42	Sun Hole, 3rd ft *Rangifer* talus	—	—	—	—	—	2·0	nil	—	Univ. Bristol Spel. Soc. M.5.2/12
C. 43	Sun Hole, 4th ft mammal bone	—	—	—	—	—	2·5	nil	—	Univ. Bristol Spel. Soc. unreg.
C. 44	Sun Hole, 5th ft *Rangifer* femur	—	0·64	24·25	2·64	14·50	3·16	nil	—	Univ. Bristol Spel. Soc. M.5.2/2
C. 45	Sun Hole, 6th ft mammal bone	—	—	—	—	—	1·3	nil	—	Univ. Bristol Spel. Soc. unreg.
C. 46	Sun Hole, 7th ft *Equus* humerus	—	—	—	—	—	3·2	nil	—	Univ. Bristol Spel. Soc. M.5.2/27

'unable to recognize any Creswellian material amongst the excavated industry from this site'. Analyses indicate that the skeletal material is not older than Early Holocene.

Whaley 1: F = 0·12%, $100F/P_2O_5$ = 0·5, N = 2·29% (w)

References: Oakley 1971*a* : 42–43, Radley 1967.

France

AURIGNAC (Haute-Garonne). Human mandible of Aurignacian or Neolithic age from grotte d'Aurignac collected by Rev. W. S. King before 1871 (reg. no. EM 326): F = 0·035%, $100F/P_2O_5$ = 0·12, N = 1·33%.

In this cave 17 human skeletons representing a collective burial dating from the Neolithic period occurred on top of a cave deposit of Upper Palaeolithic age. Some detached human bones were found mixed with bones of Upper Pleistocene mammals in the substratum of the burial chamber. Chemical analyses in the last century proved that the Neolithic human bones contained no more gelatine (cf. nitrogen) than the Pleistocene mammal bones. See Table 9, p. 36.

References: Lartet 1861 : pl. 10, fig. 1; Oakley 1964*c* : 106–107.

BRUNIQUEL (Tarn et Garonne). Humerus of *Homo sapiens sapiens* from Upper Magdalenian layer in Trou des Forges, Bruniquel (reg. no. EM 546): F = 0·44%, $100F/P_2O_5$ = 1·41, *e* U_3O_8 = nil, N = 1·64%. See Table 9, p. 36.

The ^{14}C age of the collagen fraction of associated biserial antler fragments is 11 750 ± 300 bp (BM-302).

References: Barker, Burleigh & Meeks 1969 : 283, Petit-Maire *et al.* 1971 : 88–91

LA CHAPELLE-AUX-SAINTS (Corrèze). Postcranial bone of the neandertal skeleton La Chapelle-aux-Saints 1: F = 0·358%, $100F/P_2O_5$ = 2·2, *e* U_3O_8 = 12 ppm, N = 2·12% (w). See Table 9, p. 36.

The relatively high nitrogen content (representing residual collagen) is probably to be explained by the fact that the burial was covered by stony clay. Water rising through the rock floor of the grave evidently carried elements of the uranium series.

Reference: Petit-Maire *et al.* 1971 : 98–99.

CHÂTELPERRON (Allier). A human calvaria from Châtelperron is preserved in the Wellcome Historical Medical Museum, London. It was widely supposed that this had been obtained from an Aurignacian horizon in the Grotte des Fées in the Châtelperron province, 5 km east of Jaligny (Allier), which was excavated by Bailleau (1868–70). As indicated by Vallois & Movius (1953 : 105), and confirmed personally by H. Delporte (*fide* 1963), the calvaria in the Wellcome Museum did not come from the Grotte des Fées but from an open site in the same region. Although its precise antiquity is doubtful, the following comparative analyses of bones from Châtelperron and neighbourhood suggest that it is probably of Late Pleistocene age.

Châtelperron *Homo* calvaria: F = 0·15%, $100F/P_2O_5$ = 0·5, *e* U_3O_8 = 13 ppm, N = 1·64% (w)
Neolithic *Homo* cranium: F = 0·12%, $100F/P_2O_5$ = 0·5, *e* U_3O_8 = 8 ppm, N = 3·24%
Perigordian *Ursus* bone: F = 0·07%, $100F/P_2O_5$ = 0·4, *e* U_3O_8 = 7 ppm, N = 1·49%

References: Petit-Maire *et al.* 1971 : 100, Vallois & Movius 1953 : 105.

CRO-MAGNON (Dordogne). Postcranial bone of *Homo sapiens sapiens* skeleton, 'Le Vieillard' (= Cro-Magnon 1): F = 0·12%, $100F/P_2O_5$ = 0·38, *e* U_3O_8 < 1 ppm, N = 0·455% (w). See Table 9, p. 36.

The low fluorine content is typical of bones in limestone cave deposits of Late Pleistocene age. The nitrogen content (representing residual collagen) is unusually low, probably because the containing layer was in contact with gravel and well drained.

Reference: Petit-Maire *et al.* 1971 : 104–105.

LA DENISE (Haute-Loire). In 1843 or 1844 an adult hominid frontal bone was found by Adsclénard in deposits overlying the southern slopes of an ancient volcano, La Denise, 5 km from Le Puy-en-Velay, Haute-Loire. Later, other hominid bones were found by Aymard, Pichot and Gervais. Although no fossil mammalia were found in association with the hominid bones, deposits (breccias) on the eastern slopes of the volcano contain *Equus stenonis*, *Dicerorhinus etruscus* and *Archidiskodon meridionalis*, indicating their Lower Pleistocene antiquity.

The age and authenticity of the hominid remains have for long been controversial. Application of analytical methods of relative dating showed that none is contemporaneous with the Lower Pleistocene fauna.

Homo, frontal (first discovery): $F = 0{\cdot}06\%$, $100F/P_2O_5 = 0{\cdot}19$, $N = 1{\cdot}68\%$ (w), $e\ U_3O_8 =$ nil
Homo, ilium, Aymard block: $F = 0{\cdot}06\%$, $100F/P_2O_5 = 0{\cdot}25$, $N = 4{\cdot}35\%$, $e\ U_3O_8 =$ nil
Homo, ilium, Pichot block: $F = 0{\cdot}07\%$, $100F/P_2O_5 = 0{\cdot}30$, $N = 4{\cdot}21\%$, $e\ U_3O_8 =$ nil
Dicerorhinus, occipital, breccias: $F = 1{\cdot}53\%$, $100F/P_2O_5 = 4{\cdot}89$, $N = 0{\cdot}74\%$, $e\ U_3O_8 =$ nil
See Table 7, p. 34.

The high nitrogen content shown by the bones from the Aymard and Pichot blocks is comparable with that of recent (Holocene) bones. Brown earth with which the bones were covered suggests that they represent burials (M. R. Gounot, *in lit.*). The lower nitrogen content of the frontal indicates that it may be slightly more ancient than the other bones, but probably they are all of Holocene age.

References: Heintz & Oakley 1969 : 2873–2874, Petit-Maire *et al.* 1971 : 107.

LA FERRASSIE (Dordogne). Cancellous bone from foot of neandertal skeleton, La Ferrassie 1: $F = 0{\cdot}06\%$, $100F/P_2O_5 = 0{\cdot}37$, $e\ U_3O_8 =$ nil, $N = 1{\cdot}26\%$ (before washing), $N = 2{\cdot}74\%$ (after washing). See Table 9, p. 36.

The composition of this bone is typical of skeletal material from French limestone cave deposits of Upper Pleistocene age. The nitrogen content appears to form a higher proportion of the sample *after* washing, indicating that much non-nitrogenous material was removed by the process of elutriation.

Reference: Petit-Maire *et al.* 1971 : 111–112.

FONTÉCHEVADE (Charente). In 1949 at the request of Mlle G. Henri-Martin the fluorine-dating method was applied to the Fontéchevade skulls. No one would question the provenance of Fontéchevade I and II found in 1947, now known as Fontéchevade 4 and 5 (Petit-Maire *et al.* 1971 : 115). They were unearthed from an Eemian (clayey gravel) deposit containing a Tayacian industry and sealed by a stalagmitic layer ('*plancher*') which in turn was overlain by layers containing Mousterian and Aurignacian industries. The analytical results obtained were instructive and worth recording here.

Fontéchevade 1 skull fragment, *Homo sapiens sapiens* (found before 1913), Aurignacian: $F = 0{\cdot}05\%$, $100F/P_2O_5 = 0{\cdot}2$, $N = 0{\cdot}91\%$

Fontéchevade 4 (formerly I) calotte, *Homo* sp., Tayacian: $F = 0{\cdot}4\%$, $100F/P_2O_5$ not determined.

Fontéchevade 5 (formerly II) calotte, *Homo* sp., Tayacian: $F = 0{\cdot}5\%$, $100F/P_2O_5 = 2{\cdot}4$, $N = 0{\cdot}63\%$ (w), $U_3O_8 = 3{\cdot}2$ ppm (determined as uranium $= 3{\cdot}8 \pm 0{\cdot}4$ ppm)

Mammal bones from Tayacian deposits, Niveau 2 (lower level): $F = 0{\cdot}9\%$, $100F/P_2O_5 = 2{\cdot}8$; $F = 0{\cdot}7\%$, $100F/P_2O_5 = 2{\cdot}3\%$, $N = 2{\cdot}7\%$ (w), $e\ U_3O_8 = 6$ ppm.

Ditto, Niveau 1 (upper level): $F = 0{\cdot}6\%$, $100F/P_2O_5 = 1{\cdot}9$, $N = 1{\cdot}87\%$, $e\ U_3O_8 =$ nil; $F = 0{\cdot}5\%$, $100F/P_2O_5 = 1{\cdot}7$, $N = 1{\cdot}62\%$ (w)

Mammal bone from Mousterian sandy lens within stalagmite, interior of bone: $F = 0{\cdot}05\%$, $100F/P_2O_5 = 0{\cdot}2$; exterior of bone: $F = 0{\cdot}2\%$, $100F/P_2O_5 = 0{\cdot}7$

Mammal bone from Aurignacian breccia: $F = 0{\cdot}1\%$, $100F/P_2O_5 = 0{\cdot}6$

See Tables 8, p. 35, and 9, p. 36.

In this very small series of analysed bones there is only a slight increment in the fluorine content from Aurignacian and Mousterian deposits above, to the Tayacian layers below. The fluorine contents of Fontéchevade 4 and 5 are in conformity with the Tayacian controls. The nitrogen contents of Tayacian and Aurignacian (Fontéchevade 1) bones are not significantly different. It is notable that the average fluorine content of the Mousterian bone places it between the Tayacian and the Aurignacian. The difference in fluorine content between the outer layer of this bone (0·2%F) and the interior (0·05%F) illustrates the importance of only using for comparison samples which are representative of the whole bone. Each of the samples of the Tayacian calottes submitted for analysis included the outer table and the diploic layer and was therefore fully representative.

A sample of charred bone from the Tayacian Niveau 2 (lower level) was found to contain an appreciably lower fluorine content (0·3%) than unburnt bones from the Tayacian layers (0·4–0·7%F). This is in accordance with expectations, for it has been found experimentally that charring inhibits subsequent fluorination of bone.

References: Henri-Martin 1951, Oakley & Hoskins 1951, Petit-Maire *et al.* 1971 : 113–115.

MOULIN-QUIGNON (Somme). In March 1863, the left side of a human mandible, with the second molar in place, was allegedly found by workmen at a depth of 4·5 m in high terrace gravels, containing extinct mammalia and palaeolithic hand-axes, exposed in the Moulin-Quignon pit near Abbeville (Somme). In the following year, a second mandible was reported from the same gravels. These discoveries led to heated controversy, but eventually the conclusion was reached that the Moulin-Quignon mandibles were not older than Neolithic and had been 'planted' by the gravel diggers wishing to please M. Boucher de Perthes. That the Moulin-Quignon mandibles were intrusive in the gravels has been confirmed by chemical assays of samples of these specimens taken by permission of the Director of the Musée de l'Homme, Paris, in 1950.

Moulin-Quignon mandible no. 1: F = 0·12%, $100F/P_2O_5$ = 0·4, N = 2·05% (w)
Moulin-Quignon mandible no. 2: F = 0·05%, $100F/P_2O_5$ = 0·2
Palaeoloxodon molar (dentine), Moulin-Quignon pit: F = 1·7%, $100F/P_2O_5$ = 5·1
Homo sapiens, calvaria, Neolithic, Champs-de-Mars (Somme): F = 0·05%, $100F/P_2O_5$ = 0·2
See Table 7, p. 34.

References: Delesse 1863, Oakley 1964*c* : 111–115, 117.

SOLUTRÉ (Saône). Although skeletal remains of more than 60 individuals of *Homo sapiens* were obtained from the early excavations at the open site, Crôt du Charnier, Solutré, the archaeological provenance of the material is uncertain; some of it may be Upper Palaeolithic, but most of it is now considered to be Neolithic or later.

Human mandible from early excavations: F = 0·1%, $100F/P_2O_5$ = 0·4, *e* U_3O_8 = nil, N = 2·16% (w)

A fragment of human mandible from the 1923 excavations was submitted by Dr Nicole Petit-Maire for determination of its nitrogen content, which proved to be 2·27%, high enough on an open site to allow reference to the Holocene.

Reference: Petit-Maire *et al.* 1971 : 177–178.

VEYRIER (Haute-Savoie). A skeleton and also cranial and post-cranial bones of 9 other individuals (*Homo sapiens*) were found in the Veyrier rock-shelters at Étrembières, Annemasse, Saint-Julien, during explorations in 1833–34, 1916 and 1934 onwards. With the exception of one humerus regarded as Holocene, this skeletal material has been attributed to the Magdalenian. Analyses indicated a wide range of collagen content in these bones.

Veyrier 1 (adult skeleton): N = 3·73% (w)
Veyrier human bones (14): N = 1·2–4·6%
Rangifer bone: N = 2·61% (w)
Rupicapra bone: N = 2·81%

The fact that in no less than seven of the tested bones attributed to Magdalenian man, the nitrogen content proved to be 4% (a level common in modern bone) suggests that collagen may

Table 7 Analyses, France, Middle Pleistocene.

BM(NH) Lab. No.	Locus and Description	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3$%	N%	*e* U_3O_8 ppm	Collection
F. 1	30 m or 45 m terrace of Somme, Abbeville, bovid bone	0·9	24	3·7	—	—	—	Musée de l'Homme
F. 2	30 m or 45 m terrace of Somme, Abbeville, '*Elephas*' dentine	1·6	36	4·4	—	—	—	Musée de l'Homme
F. 3	Moulin-Quignon *Palaeoloxodon* dentine	1·7	33	5·1	—	—	—	Boucher de Perthes Coll., Musée de l'Homme
F. 52	Fissure deposit, E slopes, La Denise, *Dicerorhinus* occipital	1·53	31·29	4·89	9·8	0·74	nil	Musée Crozatier, Le-Puy-en-Velay, (Haute-Loire)
F. 72-F. 80	Sand-dune deposits, Mindelian? Terra Amata, nine mammal bones	—	—	—	—	nil	—	H. de Lumley Coll., Marseilles

Table 8 Analyses, France, early Upper Pleistocene.

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	$P_2O_5\%$	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3\%$	N%	$e\,U_3O_8$ ppm	U ppm	Collection
F. 4	10 m terrace Somme, Menchecourt, *Equus* metatarsal	—	1·1	33	3·2	—	—	—	—	Musée de l'Homme
F. 5	10 m terrace Somme, Menchecourt, *Dicerorhinus* talus	—	1·2	35	3·4	—	—	—	—	Musée de l'Homme
F. 19	Tayacian cave-deposits, Fontéchevade, Bed E1′ *Homo* parietal	F5	0·5	21	2·4	—	0·63 (w)	3·2	3·8	Villebois-Lavalette, Charente. G. Henri-Martin Coll.
F. 23	Tayacian cave-deposits, Fontéchevade, Bed E0 *Homo* frontal	F4	0·4	—	—	—	—	—	—	Villebois-Lavalette, Charente. G. Henri-Martin Coll.
F. 18	Tayacian cave-deposits, Fontéchevade, Bed E1′ animal bone	—	0·5	29	1·7	9	1·62 (w)	—	—	Villebois-Lavalette, Charente. G. Henri-Martin Coll.
F. 17	Tayacian cave-deposits, Fontéchevade, Bed E1′ animal bone	—	0·6	31	1·9	—	1·87	nil	—	Villebois-Lavalette, Charente. G. Henri-Martin Coll.
F. 16	Clacto-Tayacian cave-deposits, Fontéchevade, Bed E2 animal bone	—	0·9	32	2·8	—	—	—	—	Villebois-Lavalette, Charente. G. Henri-Martin Coll.
F. 15	Clacto-Tayacian cave-deposits, Fontéchevade, Bed E2 *Dama* bone	—	0·7	30	2·3	—	2·72 (w)	6	—	Villebois-Lavalette, Charente. G. Henri-Martin Coll.
F. 25	Clacto-Tayacian cave-deposits, Fontéchevade, Bed E2 burnt animal bone	—	0·3	31·0	1·0	—	—	—	—	Villebois-Lavalette, Charente. G. Henri-Martin Coll.
F. 45	Clacto-Tayacian cave-deposits, Fontéchevade, Bed E2 animal bone	—	—	—	—	—	0·32	—	—	Villebois-Lavalette, Charente. G. Henri-Martin Coll.

Table 9 Analyses, France, late Upper Pleistocene

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	$P_2O_5\%$	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3\%$	N%	$e\ U_3O_8$ ppm	^{14}C yrs bp	Collection and Register No.
F. 21	Aurignacian, Fontéchevade, *Homo sapiens sapiens* parietal	1	0·05	33·0	0·2	—	0·91 (w)	—	—	Dugonthier Coll.
F. 24	Aurignacian breccia, Fontéchevade, *Saiga* bone	—	0·1	16·5	0·6	—	—	—	—	G. Henri-Martin Coll.
F. 26	Mousterian stalagmite, Fontéchevade, *Equus* phalange, inner zone	—	0·05	29·0	0·2	—	—	—	—	G. Henri-Martin Coll.
	Ditto, outer zone	—	0·2	27·5	0·7	—	—	—	—	
F. 48	Magdalenian, Trou des Forges, Bruniquel, *Homo* humerus	—	0·44	31·1	1·41	10·89	1·64	nil	—	BM(NH) EM 546
—	Upper Magdalenian antler harpoon fragments, Trou des Forges, Bruniquel	Cf. B4–23	—	—	—	—	—	—	11 750 ± 300 (BM-302)	F. de Lastic Coll., Musée de l'Homme
F. 34	Aurignacian, Grotte d'Aurignac, *Rangifer* antler	—	0·70	30·5	2·3	—	1·03	—	—	E. Lartet Coll., BM(NH)
F. 36	La Chapelle-aux-Saints, *Homo neanderthalensis* skeleton	LC-S1	0·36	16·5	2·2	7·0	2·12 (w)	12	—	Musée de l'Homme
F. 37	Cro-Magnon, evolved Aurignacian *Homo* 'Le Vieillard' skeleton	C-M1	0·12	31·4	0·38	3·05	0·49	<1	—	Musée de l'Homme
F. 38	La Ferrassie *Homo neanderthalensis* footbone	F1	0·06	16·3	0·37	5·9	2·74 (w)	nil	—	Musée de l'Homme

have survived longer in bones preserved under cold damp conditions. An additional factor may have been the sealing in of the bone pores by films of calcite.

Reference: Sauter 1971*b* : 184–186.

Germany

KÖSTRITZ (Thuringia). It is recorded that in 1820, in Winter's Gypsum Quarry at Köstritz, 30 km east of Jena, a Dr Schammerring collected a hominid parietal bone and femur fragment from a depth of about 15 m in diluvial deposits below bones of '*Rhinoceros*'.

Analyses did not suggest high antiquity: F = 0·11%, $100F/P_2O_5$ = 0·35, *e* U_3O_8 = 2 ppm, N = 1·6% (w).

Radiocarbon dating of the residual collagen in the femur indicate that the bones are Post-Pleistocene: 1480 ± 125 bp (BM-373). The specimens are of historic interest in view of the early date at which E. F. von Schlotheim reported this alleged association of man with a locally extinct mammal. The specimens are preserved in the BM(NH), M 16805–6.

References: Barker, Burleigh & Meeks 1971 : 167, Gieseler 1971 : 196–197.

MAUER (Heidelberg). The Heidelberg mandible was found by a workman, D. Hartmann, and recognized by Professor O. Schoetensack on 21 October 1907. The discovery was made in Sandgrube Rösch, 900 m north of Mauer, 16 km SE of Heidelberg. Although the depth from the surface at which the jaw occurred was not recorded, Schoetensack (1908) published photographs on which its original position in the section is clearly indicated. The stratigraphical age of the Mauer Sands from which this historic specimen undoubtedly came is generally given as Cromerian, but in the opinion of Dr Karl D. Adam it is more precisely Mosbachian. Schoetensack recorded that a specimen of *Palaeoloxodon antiquus* occurred at the same level 11·5 m south from the human mandible.

In September 1965 I visited the Geologisch-Paläontologisches Institut of Heidelberg University, where the Mauer mandible is preserved, and through the courtesy of the Director, Professor Schonenberg, obtained samples of the mandible and of associated fauna for analysis in London. A microsample of the mandible was taken close to the symphysis and another microsample of the left first premolar.

Analyses for fluorine, phosphate and nitrogen of these samples were made in the Laboratory of the Government Chemist, London. Radiometric assays of the larger samples were carried out in the Subdepartment of Anthropology, BM(NH). Residual grains of the human mandible sample and of a small piece of associated bone of *Dicerorhinus etruscus* were sent to Dr R. L. Fleischer at the General Electric Research Laboratory at Schenectady, New York, who kindly determined their uranium content, here recalculated as U_3O_8.

	F%	$100F/P_2O_5$	N% (w)	U_3O_8 ppm
Homo heidelbergensis, mandible bone	1·13	10·0	0·08	6
Palaeoloxodon antiquus, *Homo* layer, bone	2·1	6·6	0·12	11[7]
Dicerorhinus etruscus, bone	2·2	7·4	<0·01	15

See Table 10, p. 38.

It is notable that the percentage of fluorine in the sample of the Mauer mandible that was analysed is lower than that in the sample of associated *Palaeoloxodon* bone, but the level of fluorination in the mandible, measured as $100F/P_2O_5$, is actually higher.

References: Gieseler 1971 : 197–198, Oakley 1958*a*, Schoetensack 1908.

OFNET (Bavaria). In 1908 R. R. Schmidt excavated a nest of about 30 human crania in the cave of Grosse Ofnet, 4 km SW of Nördlingen, Bavaria. They were described as a Mesolithic burial.

Analysis of the cranium Ofnet 27 showed: F = 0·05%, $100F/P_2O_5$ = 0·24, *e* U_3O_8 = 2 ppm, N = nil.

[7] determined as *e* U_3O_8

Table 10 Analyses, Germany, early Middle Pleistocene. All specimens in the collection of Geol. Pal. Inst. Univ., Heidelberg.

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3$%	N%	eU_3O_8 ppm	U ppm
G. 1	Mauer sand, *Homo heidelbergensis* mandible	M1	1·13	11·5	10	48	0·08 (w)	6	7
G. 2	Mauer sand, *Homo heidelbergensis* premolar dentine	M1	4·2	31·4	13	—	—	—	—
G. 3	Mauer sand, *Palaeoloxodon* skull	—	2·11	31·8	6·6	9·1	0·12 (w)	11	—
G. 4	Mauer sand, *Palaeoloxodon* tusk dentine	—	1·67	35·0	4·8	7·6	nil	15	—
G. 6	Mauer sand, *Palaeoloxodon* tusk dentine	—	2·36	33·4	7·1	9·1	0·07	—	—
G. 5	Mauer sand, *Dicerorhinus etruscus* molar dentine	—	3·06	34·0	9·0	10·7	nil	—	—
G. 7	Mauer sand, *Dicerorhinus etruscus* mandible	—	2·21	29·7	7·4	10·7	<0·01 (w)	15	18

Table 11 Analyses, Germany, late Middle Pleistocene. All specimens in the collection of Staatliches Mus. Natur., Stuttgart.

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3$%	N%	eU_3O_8 ppm	U ppm	Register No.
G. 29	Steinheim Gravels, *Homo steinheimensis* cranium	S1	1·2	11·8	10·2	—	0·37 (w)	2	2·5	—
G. 9	Steinheim Gravels, *Bison* horn-core	—	1·88	31·6	5·9	14·7	—	—	—	—
G. 10	Steinheim Gravels, *Homotherium* maxilla	—	1·40	32·5	4·3	12·2	nil (w)	—	—	—
G. 12	Steinheim Gravels, *Palaeoloxodon* level, rolled bone	—	1·98	30·9	6·4	13·9	0·23	13	—	—
G. 13	Steinheim Gravels, *Mammuthus* tusk dentine	—	1·55	33·4	4·7	13·2	—	—	—	—
G. 31	Steinheim Gravels, '*Elephas*' tusk dentine	—	1·46	22·4	6·5	9·6	—	—	—	17492
G. 32	Steinheim Gravels, '*Elephas*' tusk dentine	—	1·10	19·9	5·5	11·7	—	—	—	17753
G. 33	Steinheim Gravels, '*Elephas*' tusk dentine	—	2·20	31·4	7·0	13·8	—	—	—	19022
G. 34	Steinheim Gravels, '*Elephas*' tusk dentine	—	1·51	24·3	6·2	11·0	—	—	—	18070b

The nitrogen determination 'nil' in fact means not detected, but the element is probably present although at less than 0·01 %. As 51 cervical vertebrae are available in the Ofnet collection, further nitrogen estimations should be made. Early Holocene series of bones are known in which the nitrogen content varies from $<0{\cdot}01\,\%$ to 3 %. The aim of this additional work would be to find material containing sufficient collagen for reliable radiocarbon dating.

Collagen extracted from one of the Ofnet skulls is said to have been dated by ^{14}C as *c.* 13 000 BP (when Magdalenian culture prevailed). Judgement on this result must be suspended until details of the sample UCLA-1783 have been published with full comments in *Radiocarbon*. All the Ofnet skulls appear to have been buried contemporaneously, so the UCLA date contradicts the evidence of the geometric microliths associated with two of these crania, indicating a Mesolithic culture of less than 10 000 years before present.

References: Gieseler 1971 : 201–202, Glowatzki & Protsch 1973, Newell *et al.* 1979.

RHÜNDA (Hessen). On 20 July 1956, Herr Glatzer found a hominid skull at a depth of 0·8 m in argillaceous silts near the village of Rhünda in the Melsungen district of Hessen. It consists of the right half of a cranium with occipital bone and isolated molars and premolars. At first it was interpreted as a female *Homo neanderthalensis*, but full investigation showed it to be a skull of *Homo sapiens* dating from early Holocene times.

Homo cranium: $F = 1{\cdot}29\,\%$, $100F/P_2O_5 = 4{\cdot}8$, $e\ U_3O_8 = 8$ ppm, $N = 1{\cdot}34\,\%$ (w)

No well-dated fossil bones from the locality were available to compare. Comparison with analyses of bones of known age from further afield suggested that the Rhünda skull was not older than Würmian. Measurement of ^{13}C and ^{14}C in carbonate forming a calc-sinter incrustation of the cranium indicated an age of *c.* 9000 bp (H. 571-981). The inferred stratigraphical age is Pre-Boreal/Boreal.

References: Gieseler 1971 : 203–204, Oakley 1958*a*.

STEINHEIM (Württemberg). On 24 July 1933 K. Sigrist found an adult hominid cranium in the Sigrist Gravel pit on the northern outskirts of Steinheim an der Murr, 20 km north of Stuttgart. F. Berckhemer recognized that it was from the *Palaeoloxodon antiquus* bed of gravel, which he regarded as, at latest, of Saalian interstadial age. Further investigation by K. D. Adam indicated that the probable stratigraphical age is Elster-Saale (= Mindel-Riss) interglacial.

Homo cranium: $F = 1{\cdot}2\,\%$, $100F/P_2O_5 = 10{\cdot}16$, $e\ U_3O_8 = 2$ ppm, $N = 0{\cdot}37\,\%$ (w)

Mammalian bone from *Palaeoloxodon* gravel: $F = 1{\cdot}98\,\%$, $100F/P_2O_5 = 6{\cdot}4$, $e\ U_3O_8 = 13$ ppm, $N = 0{\cdot}23\,\%$

Homotherium ('*Epimachairodus*'): $F = 1{\cdot}40\,\%$, $100F/P_2O_5 = 4{\cdot}3$, N = nil (w).

See Table 11, p. 38.

References: Adam 1954, 1961, Berckhemer 1933, Gieseler 1971 : 206–207.

Hungary

SUBALYUK. In 1932 neandertalian skeletal material (1 adult, 1 child) was found at the cave known as Mussolini-barlang in the Bukk Mountains. The fluorine content of hominid and mammalian bones from this cave was determined as $<0{\cdot}1\,\%$.

Reference: Thoma & Vértes 1971 : 226–227.

VÉRTESSZÖLLŐS. On 21 August 1965, L. Skoflek and J. Futó, working under direction of L. Vértes, discovered a hominid occipital in lime-mud at the bottom of a calc-tufa basin exposed in the travertine quarry near Vértesszöllős, 50 km west of Budapest. The mammalian fauna from the same stratigraphical level indicates that the deposits belong to an Elsterian interstadial (i.e. inter-Mindel.) The associated Buda industry has Clactonian traits, but it could be referred either to the pebble-tool tradition, or to the chopper/chopping-tool tradition.

Hominid occipital (Vértesszöllős 2): F = 1·6%, $100F/P_2O_5$ = 5·6, *e* U_3O_8 = 3 ppm, N = nil, $CaCO_3$ = 18%

Directly associated mammal bone, cultural horizon 1: F = 1·5%, $100F/P_2O_5$ = 5·3, *e* U_3O_8 = 3 ppm, N = 0·1%, $CaCO_3$ = 20%

Other mammal bones from Vértesszöllős:
Cultural horizon 1: F = 1·8%, $100F/P_2O_5$ = 5·5, *e* U_3O_8 = 9 ppm, N = 0·1%, $CaCO_3$ = 11%
Cultural horizon 2: F = 2·0%, $100F/P_2O_5$ = 6·6, *e* U_3O_8 = 9 ppm, N = 0·1%, $CaCO_3$ = 12%
Cultural horizon 2/3: F = 1·5%, $100F/P_2O_5$ = 6·4, *e* U_3O_8 = 9 ppm, N = nil, $CaCO_3$ = 12%
Cultural horizon 3: F = 1·5%, $100F/P_2O_5$ = 5·1, *e* U_3O_8 = 18 ppm, N = 0·1%, $CaCO_3$ = 12%
Cultural horizon 3: F = 1·63%, $100F/P_2O_5$ = 5·0, *e* U_3O_8 = 14 ppm, N = 0·1%, $CaCO_3$ = 13·2%
Loess overlying cultural horizon 3: F = 1·8%, $100F/P_2O_5$ = 4·3, *e* U_3O_8 = 9 ppm, N = <0·1%, $CaCO_3$ = 12%

References: Oakley 1966, Thoma & Vértes 1971 : 228–229.

Italy

CASTENEDOLO (Lombardia). In 1860, G. Ragazzoni discovered hominid skeletal fragments on the hill of Castenedolo near Brescia, but since there was doubt about their stratigraphical age they were discarded as of no importance. In 1880, G. Ragazzoni found close to the same site several hominid skulls, with some associated post-cranial bones, including an adult female calvaria (Castenedolo 1), fragments of parietal and occipital bones of an adult male (Castenedolo 2) and isolated cranial fragments of a child (Castenedolo 3). These remains were embedded in shelly marine clay identified as of Tertiary (Astian) age by G. B. Cacciamali (1896), who cautiously rejected the opinion of those who regarded the human bones as contemporaneous with the clay. In 1889 further human bones were found at this site, but A. Issel (1889) recognized them as recent burials. G. Sergi agreed with Issel's opinion about the 1889 finds, although he maintained his earlier view (Sergi 1884) that those of 1880 (Castenedolo 1, 2 and 3) constituted proof that man with modern morphology (*Homo sapiens*) existed in Pliocene times.

Castenedolo 1–3 are still encrusted with their original matrix, and with the co-operation of Professor G. Genna were re-investigated in 1965. Analyses of the bones showed that their residual collagen (assessed by percentage of nitrogen) is higher than that of any fossil bones from central and northern Italian sites which have been tested with the exception of a few from Upper Pleistocene levels.

	%N
Castenedolo 1, cranial fragment:	1·6
Castenedolo 1, costae:	2·6
Castenedolo 2, cranial fragment:	2·2
Castenedolo 3, cranial fragment:	1·2
Middle Pleistocene bones from Italian sites:	<0·1–0·3
Upper Pleistocene bones from Italian sites:	<0·1–3·7
Holocene bones from Italian sites:	0·5–4·4

From this evidence it was inferred that Castenedolo 1–3 were intrusive burials into the Astian clays. In 1969 the British Museum Research Laboratory undertook radiocarbon dating of bones of Castenedolo 1, which proved to be 958 ± 116 years bp (BM-496) on the basis of ^{14}C dating of residual collagen in its vertebrae and costae (Barker, Burleigh & Meeks 1971 : 183).

Radiometric assays of the Castenedolo bones indicated an unexpectedly high uranium content:

Castenedolo 1, cranial fragment: *e* U_3O_8 = 29 ppm
Castenedolo 1, costae: *e* U_3O_8 = 32 ppm
Castenedolo 2, cranial fragment: *e* U_3O_8 = 17 ppm
Castenedolo 3, cranial fragment: *e* U_3O_8 = 9 ppm

The uranium content of the matrix of the bones was measured by Dr T. K. Ball of the Institute of Geological Sciences. He reported 3·9 ± 0·2 ppm.

The most likely explanation of the radioactivity of the bones is that the local ground-water is

Table 12 Analyses, Hungary, Middle Pleistocene.

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$	N%	$CaCO_3$%	$e\,U_3O_8$ ppm	Collection & Register No.
H. 1	Vértesszöllős, *Homo* occipital bone	V2	1·6	28·4	5·6	nil	18	3	Magyar Nemzeti Muzeum Pb65/1264
H. 2	Vértesszöllős, mammal bone (associated with *Homo*) cultural horizon 1	—	1·5	29·1	5·3	0·1	20	3	Magyar Nemzeti Muzeum —
H. 3	Vértesszöllős, cultural hor. 1 animal bone	—	1·8	32·4	5·5	0·1	11	9	K. P. Oakley Coll. unreg.
H. 4	Vértesszöllős, cultural hor. 2 animal bone	—	2·0	30·4	6·6	0·1	12	9	K. P. Oakley Coll. unreg.
H. 5	Vértesszöllős, cultural hor. 2/3 calcreted animal bone	—	1·5	33·8	6·4	nil	12	9	K. P. Oakley Coll. unreg.
H. 6	Vértesszöllős, cultural hor. 3 animal bone	—	1·5	30·1	5·1	0·1	12	18	K. P. Oakley Coll. unreg.
H. 15	Vértesszöllős, cultural hor. 3 animal bone	—	1·63	32·4	5·03	—	13·2	14	K. P. Oakley Coll. unreg.
H. 7	Vértesszöllős, Late Mindelian loess overlying cultural hor. 3 animal bone	—	1·8	41·6	4·3	<0·1	12·4	9	K. P. Oakley Coll. unreg.
H. 8	Vértesszöllős, cult. hor. 1 *Cervus elaphus* enamel	—	1·9	32·4	5·8	0·1	12·5	9	K. P. Oakley Coll. unreg.
H. 9	Vértesszöllős, Mindelian interstadial calcareous deposit ungulate bone	—	2·02	33·9	6·0	0·1	11·6	15	L. Vértes Coll., BM(NH) E.6190
H. 10	Vértesszöllős, Mindelian interstadial calcareous deposit animal bone	—	1·33	34·0	3·9	0·1	11·9	7	L. Vértes Coll., BM(NH) unreg.

rich in uranyl ions. Professor E. Anati of the Centro Camuno di Studi Preistorici, Brescia, sent a sample of well water from Castenedolo to the Centro di Studi Nucleari E. Fermi in Milan, where Professor Terrani determined 180 ml contained 1·58 ± 0·39 micrograms of uranium. As this is an unusually high proportion of uranium for ground-water, it probably accounts for accumulation of this element in the bones to the levels recorded after an exposure of less than 1000 years.

The fluorine content of the Castenedolo bones is also high for bones of late Holocene age. The Laboratory of the Government Chemist, London, could not detect fluorine in a sample of well water from Castenedolo, but in this tectonically rather unstable region the composition of ground-water is probably liable to considerable variation in the course of a millennium. The fluorine content of the Castenedolo bones is occasionally exceeded by that of bones of comparable age in other parts of Europe, for example County Durham:

Castenedolo bones: $F = 0{\cdot}4\text{–}0{\cdot}6\%$, $100F/P_2O_5 = 1{\cdot}4\text{–}2{\cdot}3$
Human bone from Mediaeval site, Barnard Castle, Co. Durham: $F = 1{\cdot}3\%$, $100F/P_2O_5 = 4{\cdot}1$

References: Barker, Burleigh & Meeks 1971 : 183, Cacciamali 1896, Issel 1889, Oakley *in* Sergi, Cardini & Leonardi 1971 : 235–236, Ragazzoni 1880, Sergi 1884.

CIRCEO (Latina). The neandertal skull Circeo 1 was found in 1939 occupying a hollow in the surface of an indurated cave filling formed by beach and sandy continental deposits in Grotta Guattari, 300 m SE of San Felice Circeo, Latina. Partial analysis of a nasal bone of the skull showed: $F = 0{\cdot}57\%$, $100F/P_2O_5 = 5{\cdot}5$, $N = 0{\cdot}28\%$, $CaCO_3 = 36{\cdot}1\%$.

The carbonate content is unusually high. In Pleistocene bones from other Italian sites $CaCO_3$ ranged from 3% to 27%. The exceptionally high carbonate content of this skull is presumably due to the macropores of the bone containing microcrystals of calcite or aragonite deposited by the stalagmite-forming water in this cave. In future research a thin section of the skull bone should be prepared for examination under a petrographic microscope.

The neandertal mandible Circeo 3 from breccia at the entrance to Grotta Guattari was tested for nitrogen representing residual collagen: $N < 0{\cdot}1\%$ (w).

Reference: Sergi, Cardini & Leonardi 1971 : 237–239.

OLMO (Tuscany). I. Cocchi obtained in 1863 a calotte of *Homo* from the cutting of the Florence–Rome railway at Olmo near Arezzo. The cutting exposed Pleistocene gravels overlain by clay, but the layer of origin of the human skull fragment was uncertain. Analytical dating at the BM(NH) indicated that the calotte probably came from the gravel, which contained a blade of Upper Palaeolithic type.

Homo calotte: $F = 0{\cdot}13\%$, $100F/P_2O_5 = 2{\cdot}5$, $N = 3{\cdot}32\%$
Equus bones, probably from gravel: $F = 0{\cdot}3\%$, $100F/P_2O_5 = 1{\cdot}3$, $N = 2{\cdot}64\%$
Elephas dentine, probably from underlying clay: $F = 2{\cdot}3\%$, $100F/P_2O_5 = 7{\cdot}5$, $N = 0{\cdot}92\%$

Reference: Sergi, Cardini & Leonardi 1971 : 247–248.

POFI (Rome). In November 1959 a neandertal ulna was found in rearranged pozzolana underlying lacustrine deposits with diatomites in a quarry 6 km from Pofi, SSE of Frosinone, Lazio, Rome. The containing deposit is probably Riss–Würm in age. Analysis of the bone showed: $F = 1{\cdot}5\%$, $100F/P_2O_5 = 6{\cdot}4$, $e\ U_3O_8 = 9$ ppm, $N = 0{\cdot}2\%$. See Table 13, p. 44.

Reference: Sergi, Cardini & Leonardi 1971 : 249–250.

QUINZANO (Verona). In 1938 workmen directed by G. Montresor found a human occipital fragment in alluvial deposits within Cava Vecchia, exposed in a clay pit at Ca'Rotta Quinzano, near Verona. According to Montresor the human fragment came from the base of layer III (Upper Palaeolithic?), but the degree of mineralization, colour and limestone caking suggested to R. Battaglia that it had been derived from a much older layer.

Analytical dating carried out by the BM(NH) gave results which supported the view that the occipital fragment antedated layers III-V (Würm), and was probably derivative from layers VI/VII.

Homo occipital (Quinzano 1): F = 0·75%, 100F/P_2O_5 = 3·9, *e* U_3O_8 = 11 ppm, N = 0·3% (w)
Equus hydruntinus dentine, layer III: F = 0·16%, 100F/P_2O_5 = 0·6, *e* U_3O_8 = nil, N = 1·46% (w)
Mammal bones from layer V: F = 0·4–1·1%, 100F/P_2O_5 = 2·5–6·6, N = 0·11 (w)
Antler, bone and dentine from layers VI/VII: F = 0·5–1·5%, 100F/P_2O_5 = 4·4–6·6, *e* U_3O_8 = 31 ppm, N = 0·33%
See Table 13, p. 44.

Layer VII, the oldest layer, contained flakes of Clactonian facies and biface of 'Chellean' type (= Acheulian). Layer VI contained a molar of *Mammuthus trogontherii intermedius*. A. Pasa correlated VI with Riss–Würm interglacial and VII with Riss, but differentiation of material from these two layers was not clear.

Reference: Sergi, Cardini & Leonardi 1971 : 250–251.

SACCOPASTORE (Rome). Two neandertal skulls were found in fluviatile gravel forming the lowest terrace of the River Aniene exposed in a gravel pit at Saccopastore, 3·5 km from Porta Pia, Rome. Saccopastore 1 was found on 13 May 1929 by S. Sergi; Saccopastore 2 on 16 July 1935 by A. C. Blanc and H. Breuil. In chemical composition the bone of these skulls conforms with that of associated *Hippopotamus* dentine.

Saccopastore 1: F = 1·8%, 100F/P_2O_5 = 8·1, N = 0·14%
Saccopastore 2: F = 1·7%, 100F/P_2O_5 = 8·3, N = 0·12%
Hippopotamus dentine: F = 1·6%, 100F/P_2O_5 = 5·6, *e* U_3O_8 = 52 ppm, N = 0·16%
See Table 13, p. 44.

The samples of human bone were inadequate for radiometric analysis, but if needed their uranium content could be determined by microchemical analysis.

The terrace gravel is attributed to the Riss–Würm interglacial. The radiocarbon age of *Abies* wood from a correlated deposit in the Mussolino channel near Latina has been reported as 58 000 ± 500 yrs bp (GrN-2572).

Reference: Sergi, Cardini & Leonardi 1971 : 254–255.

SEDIA DEL DIAVOLO (Rome). In 1956 a femur fragment and a metatarsal of a hominid were found in Nomentanan (= Riss) gravels at Sedia del Diavolo quarry overlooking the river Aniene, about 3·5 km from Porta Pia, Rome. Analyses showed:

femur: F = 1·83%, 100F/P_2O_5 = 6·64, N = nil
metatarsal: N = 0·19% (w)

Reference: Sergi, Cardini & Leonardi 1971 : 257–258.

Malta

Two taurodont molar teeth of *Homo* were found in Ghar Dalam Cave in 1917, associated in broad sense with fossil bones of *Cervus*. Sir Arthur Keith referred the teeth to *Homo neanderthalensis* on the basis of their taurodontism. Although obsidian artefacts of Neolithic type occurred in the cave-earth with the teeth, it was suggested that the latter might have been derived from a much older deposit in the cave, which had been partly filled in Pleistocene times. During a visit to Malta in 1962 I obtained permission from the Director of the National Museum to take samples of the Ghar Dalam specimens (including one of the taurodont teeth) for nitrogen analysis in London. The results were as follows:

Ghar Dalam 2 (r. M^3) dentine: N = 1·85%
Cervus long bone from Red Earth, Late Pleistocene or Early Holocene: N = 0·13%
Hippopotamus dentine from Pleistocene Bone Breccia: N = nil.
Dentine of teeth from various Neolithic sites, Malta: >0·3%

These analyses indicated that Ghar Dalam 2 is not older than Neolithic. In 1936, another taurodont molar (l. M_3) was found by Dr J. G. Baldacchino in black clayey earth containing artefacts of the first or Ghar Dalam phase of the Maltese Neolithic.

Table 13 Analyses, Italy, early Upper Pleistocene.

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3$%	N%	$e\,U_3O_8$ ppm	Collection
It. 30	Cava Pompi, Pofi str I (with *Palaeoloxodon*), *Homo* tibia	P1	1·48	23·3	6·4	3·3	0·18	9	L. Cardini Coll. Museo della Preistoria del Lazio, Rome
It. 6	Cava Vecchi, Quinzano str VI, *Mammuthus trogontherii* bone	—	0·5	11·5	4·4	—	—	—	Museo Storia Naturale, Verona
It. 8	Cava Vecchi, Quinzano str VI, '*Elephas*' tusk dentine	—	1·5	33	4·5	—	0·33 (w)	—	Museo Storia Naturale, Verona
It. 9	Cava Vecchi, Quinzano str VI, '*Elephas*' bone	—	1·2	27·5	4·4	—	—	—	Museo Storia Naturale, Verona
It. 10	Cava Vecchi, Quinzano str VII, *Megaloceros* antler	—	0·35	4·0	8·7	—	—	—	Museo Storia Naturale, Verona
It. 11	Cava Vecchi, Quinzano str VII, cervid bone	—	0·6	9·0	6·6	—	0·11 (w)	31	Museo Storia Naturale, Verona
It. 28	Low terrace gravel Aniene, Saccopastore, Rome, *Hippopotamus* dentine	—	1·61	28·7	5·6	2·9	0·16	52	Istituto di Antropologia, University of Rome
It. 29	Low terrace gravel Aniene, Saccopastore, Rome, *Hippopotamus* bone	—	—	—	—	—	0·13	50	Istituto di Antropologia, University of Rome
It. 31	Low terrace gravel Aniene, Saccopastore, Rome, *Homo* cranium	S1	1·76	21·7	8·1	15·3	0·14	—	Istituto di Antropologia, University of Rome
It. 33	Low terrace gravel Aniene, Saccopastore, Rome, *Homo* cranium	S2	1·67	20·0	8·3	26·6	0·12	—	Istituto di Antropologia, University of Rome

The dental surgeon Dr J. J. Mangion of the Royal University of Malta recorded in 1962 that he had extracted taurodont teeth from the jaws of two modern Maltese patients.

References: Keith 1925, Mangion 1962, Oakley 1971*b*.

Netherlands

Beegden. A dozen or so hominid bones (cranial and post-cranial) were salvaged between 1962 and 1966 from material dredged from the gravel bed of the river Meuse at Beegden, south of Roermond, Limburg. According to C. J. Overweel, when the X-ray powder-diffraction method was applied, the fluorine content of two of these bones (Beegden 1 and 2) showed close agreement with dentine of *Mammuthus* dredged from river gravel and sand in the same region. This may be of late Weichselian age. However, analyses of nine of the Beegden human bones showed that they had such a high collagen content (measured as %N) that unquestionably they are not of great antiquity and are certainly post-Pleistocene.

Beegden 5: N = 3·91%
Beegden 6: N = 4·35%
Beegden 7: N = 4·43%
Beegden 8: N = 4·17%
Beegden 9: N = 4·04%
Beegden 10: N = 3·04%
Beegden 11: N = 4·26%
Beegden 12: N = 3·88%
Beegden 13: N = 3·53%

References: Erdbrink & Overweel 1971 : 226–267, Erdbrink, Meiklejohn & Tacoma 1975, Newell *et al.* 1979 : 181.

Hengelo. Two human calottes were found in yellowish brown sand and dark grey marl during harbour excavations *c.* 2 km south of the railway station at Hengelo, Overijssel, in 1934–35. Although Hengelo 1 was originally believed to be of Upper Pleistocene age, both calottes are now considered to be Early Holocene (Mesolithic). It may be regarded as the first authenticated find in the series known as the 'River Valley' people, who occupied a large area of the Rhine delta and surrounding plains, from Norfolk (e.g. Strumpshaw), England, to Téviec, France. They had an industry of somewhat Maglemosian aspect.

According to J. Butter (1952, *in lit.*) analysis of Hengelo 1 showed F = 0·28–0·30%.

References: Erdbrink & Overweel 1971 : 267–268, Erdbrink, Meiklejohn & Tacoma 1975, Newell *et al.* 1979 : 182.

Russia

Kiik-Koba (Crimea). Although no material from this limestone cave was investigated at the BM(NH), for comparative purposes it is worth recording here that samples of bone from this Mousterian site were analysed by V. V. Danilova.

Kiik-Koba 1 (*Homo neanderthalensis*): F = 0·36%, 100F/P_2O_5 = 0·12
Saiga tatarica: F = 0·7%, 100F/P_2O_5 = 0·22–0·3

References: Danilova 1946, Klein, Ivanova & Debetz 1971 : 318–319.

Spain

Barranc Blanc. In 1951, a hominid frontal bone was discovered by M. Jorda working with J. & P. Cubero Garcia in an Epigravettian occupation layer in cave-earths at Barranc Blanc, a cave near Rótova, about 10 km from Gandia, Valencia. In 1953, the cranium of a young adult hominid was found at approximately the same archaeological horizon. Analyses of these hominid bones indicated that their nitrogen content was sufficiently low (0·15–0·38 %) to be consistent with an Upper Palaeolithic age. The *e* U_3O_8 content proved to be nil detected.

Reference: Garralda & Irwin 1971 : 288–289.

CARIGÜELA. In 1955, J.-C. Spahni discovered a series of hominid bones at two occupation levels in the cave-earths at Carigüela, the cave 1 km east of the village of Pinar, Granada. At levels 6–7 the hominids (Carigüela 1–3) were associated with a typical Mousterian industry; at level 2 the hominids (Carigüela 4–6) were accompanied by a Mousterian industry showing slight Aurignacian influences.

Samples of the hominid bones (and one associated animal bone from level 6) were analysed. They all showed a low fluorine content (*c.* 0·1 %), but this is commonly the case with bones from cave deposits. The protein residue measured as N % had been reduced to a very low or negligible level as was to be expected. The *e* U_3O_8 content proved to be nil detected.

Reference: Garralda & Irwin 1971 : 290–291.

CÒVA NEGRA. In 1933, a neandertalian parietal bone was found by P. Gonzalo Vines in a Mousterian occupation layer in the cave of Nova Negra, near the village of Játiva, Valencia.

Analyses of the bone showed a very low fluorine content (0·08 %) but the protein residue (measured as nitrogen) had been reduced to a level consistent with Upper Pleistocene age. The *e* U_3O_8 content proved to be nil detected.

Reference: Garralda & Irwin 1971 : 292–293.

PARPALLÓ. In 1930, L. Pericot Garcia discovered the skull of a hominid child at a Solutrean occupation level in the cave of Parpalló, 10 km NW of the village of Candia, Valencia.

Analyses showed an exceptionally low level of fluorine (0·06 %) but the protein residue had been reduced to 0·3 % N, which is consistent with Late Pleistocene antiquity. The *e* U_3O_8 content proved to be nil detected.

Reference: Garralda & Irwin 1971 : 295.

Switzerland

BIRSMATTEN (Berne). In 1944, Carl Lüdin discovered the greater part of a human skeleton with skull in argillaceous deposits on the floor of the Birsmatten rock-shelter, overlooking the River Birse in the Laufen district. Mesolithic industries (at level D resembling Sauveterrian, at level E resembling Tardenoisian) occurred in these sediments. The skull and skeleton clearly represented a penecontemporaneous burial, but it is uncertain whether it is contemporary with material of level D or level E.

Birsmatten 1: N = 1·1 %
Animal bone level D: N = 1·5–2·1 %
Animal bone level E: N = 1·6 %
Radiocarbon dating of animal bones gave the following results:
level D = 6970 ± 120 BP (B-1236)
level E = 7670 ± 120 BP (B-237)

Level D (III) has been correlated by pollen as of Boreal age, and level E (II) as belonging to the Boreal/Atlantic transition.

References: Oakley 1964*a*, Sauter 1971*a* : 304–305.

LE SCÉ (Vaud). In 1868–69, fragmentary post-cranial bones of several individuals (*Homo sapiens*) were found in Late Pleistocene and Early Holocene bone-breccias in the rock-shelter known as Le Scé du Château at Villeneuve in the Aigle district.

Table 14 Analyses, Spain, Upper Pleistocene.

BM(NH) Lab. No.	Locus and Description	CFH No.	F%	$P_2O_5\%$	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3\%$	N%	$e\,U_3O_8$ ppm	Collection and Register Number
SP. 43	Barranc Blanc cave, Solutrean, *Homo* frontal	BB1	—	—	—	—	0·38 (w)	nil	Museo del Servicio de Investigaciones Prehistoricas, Valencia Cr. 91
SP. 44	Barranc Blanc cave, Epigravettian, *Homo* calotte	BB2	—	—	—	—	0·15 (w)	nil	Museo del Servicio de Investigaciones Prehistoricas, Valencia, Cr. 117
SP. 31	Carigüela cave, occ. level 2, *Homo sapiens* mandible	C4	—	—	—	—	0·23 (w)	nil	Museo Arquelogico Provincial de Granada, 5.873
SP. 32	Carigüela cave, occ. level 2, *Homo sapiens* parietal	C5	0·17	26·5	0·6	11·1	2·2 (w)	nil	Museo Arquelogico Provincial de Granada, 5.874
SP. 33	Carigüela cave, occ. level 2, *Homo sapiens* tibia	C6	—	—	—	—	1·3 (w)	nil	Museo Arquelogico Provincial de Granada, 5.878
SP. 37	Carigüela cave, occ. level 2, *Cervus elaphus* mandible	—	0·04	21·7	0·2	20·5	—	nil	Museo Arquelogico Provincial de Granada
SP. 38	Carigüela cave, occ. level 3, *Panthera spelaea* humerus	—	—	—	—	—	0·25 (w)	nil	Museo Arquelogico Provincial de Granada
SP. 34	Carigüela cave, occ. level 6, *Homo neanderthalensis* parietal	C3	0·1	20·8	0·5	21·3	0·16	nil	Museo Arquelogico Provincial de Granada, 5.875
SP. 39	Carigüela cave, occ. level 6, *Cervus elaphus*	—	0·17	26·7	0·6	24·2	nil	nil	Museo Arquelogico Provincial de Granada
SP. 35	Carigüela cave, occ. level 7, *Homo neanderthalensis* parietal	C1	0·08	21·0	0·4	23·1	nil	nil	Museo Arquelogico Provincial de Granada, 5.876
SP. 36	Carigüela cave, occ. level 7, *Homo neanderthalensis* frontal	C2	—	—	—	—	nil	nil	Museo Arquelogico Provincial de Granada, 5.877
SP. 40	Carigüela cave, occ. level 7, *Dicerorhinus mercki* skull	—	—	—	—	—	0·37 (w)	nil	Museo Arquelogico Provincial de Granada
SP. 41	Còva Negra cave, *Homo neanderthalensis* parietal	CN1	0·08	28·5	0·3	9·1	0·25 (w)	nil	Museo del Servicio de Investigaciones Prehistoricas, Valencia, Cr. 92
SP. 42	Parapalló cave, *Homo sapiens* occipital	P1	0·06	10·8	0·6	0·5	0·31 (w)	nil	Museo del Servicio de Investigaciones Prehistoricas, Valencia, Cr. 90

Human femur ('Scé III'): N = 1·74% (w)
Human bone (unspecified): N = 4·06% (w)
Rangifer long-bone, Late Pleistocene: N = 2·59% (w)

Reference: Sauter 1971*a* : 306–307.

Yugoslavia[8]

Krapina, Croatia. Neandertal hominid bones were excavated by K. D. Gorjanović-Kramberger in 1899 (and subsequent years) at the rock-shelter of Krapina on the right bank of the River Krapinica, NNW of Zagreb, Croatia. The hominid bones, representing about 25 individuals (including five children) were embedded in sandy loams derived from weathering débris of the Miocene sandstone in which the shelter had been cut. The shelter deposits are underlain by fluviatile sand and gravel.

In 1967, aided by a grant from the Wenner-Gren Foundation, Miss T. I. Molleson and Dr J. C. Vogel visited Krapina, and other bone-bearing sites in Yugoslavia, with the aim of collecting samples for relative dating and for radiocarbon measurement. They obtained a series of samples from the Krapina hominid and animal bones preserved in the Geološko-Paleontološki Muzej, Zagreb, by kind permission of the Director, Professor I. Crnolatac. They were unable to collect any field samples at Krapina, because the rock-shelter deposits have been totally removed—not even a witness section has been left at the site.

It is of historic interest that a hominid bone from Krapina was analysed for fluorine in preparation for the report on the original excavations (Gorjanović-Kramberger 1901). The value recorded was 0·7%.

Bone samples from most Mousterian levels in the shelter deposits were analysed in the Laboratory of the Government Chemist for fluorine and phosphate following the 1967 expedition, but no trend was detectable in the fluorine/phosphate ratio. However, nor was there any inconsistency between the ratio found in the hominid fragments and in the animal bones of the level with which they were reputed to be associated. These results may be summarized as follows:

Human bones (7): F = 0·73–1·04%, 100F/P_2O_5 = 2·6–4·1
Animal bones (11): F = 0·22–1·53%, 100F/P_2O_5 = 0·7–5·6

A series of hominid and animal bones samples from Krapina were submitted to radiometric assay in the BM(NH) and the results are summarized in Table 15. The counts obtained on the Krapina samples fall within the range for the Upper Pleistocene in Yugoslavia. No significance

Table 15 Uranium in bones from Mousterian layers at Krapina. *e* U_3O_8 ppm

Human bone, Mousterian layer 9	nil
Animal bone, Mousterian layer 8	11
Animal bone, Mousterian layer 8	6
Animal bone, Mousterian layer 8	4
Animal bone, Mousterian layer 8	8
Animal bone, Mousterian layer 7	8
Animal bone, Mousterian layer 5	7
Animal bone, Mousterian layer 4	nil
Animal bone, Mousterian layer 4	nil
Human bone, Mousterian layer 4	6
Human bone, Mousterian layer 4	nil
Human bone, Mousterian layer 3	4
Human bone, Mousterian layer 3	5
Animal bone, Mousterian layer 1–2	10
Animal bone, Mousterian layer 1	10

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[8] This section was prepared largely on the basis of a script written by Miss T. I. Molleson after her visit to Yugoslavia in September, 1967.

Table 16 Analyses, Yugoslavia, Upper Pleistocene. All specimens in Geološko-Paleontološki Muzej, Zagreb.

BM(NH) Lab. No.	Locus and Description	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3$%	N%	*e* U_3O_8 ppm
Y. 1	Krapina layer 9 *Dicerorhinus* bone	0·39	32·0	1·2	11·7	0·61 (w)	—
Y. 2	Krapina layer 9 *Homo* femur	0·88	31·3	2·8	7·7	0·36 (w)	9
Y. 3	Krapina layer 9 *Bos* mandible	0·73	29·9	2·4	8·4	0·78 (w)	11
Y. 4	Krapina layer 9 *Dicerorhinus* bone	—	—	—	—	0·30 (w)	—
Y. 5	Krapina layer 1 *Castor* bone	1·53	27·2	5·63	9·5	0·27 (w)	10
Y. 6	Krapina layer 1–2 animal bone	0·61	26·8	2·28	11·2	0·57 (w)	10
Y. 7	Krapina layer 3 *Homo* adult skull	0·97	24·3	3·99	10·0	nil	5
Y. 8	Krapina layer 3 *Homo* juvenile skull	1·0	26·9	3·72	12·3	0·24 (w)	4
Y. 9	Krapina layer 4 *Homo* adult skull	1·01	24·5	4·12	11·5	0·36 (w)	nil
Y. 10	Krapina layer 4 *Homo* skull	1·04	37·5	2·7	11·7	0·31 (w)	nil
Y. 11	Krapina layer 4 animal bone	1·28	28·4	4·5	8·6	0·42 (w)	nil
Y. 12	Krapina layer 4 *Homo* skull	1·09	25·2	4·3	6·0	0·30 (w)	6
Y. 13	Krapina layer 5 animal bone	0·98	29·2	3·4	8·8	0·43 (w)	7
Y. 14	Krapina layer 6a (7) animal bone	0·95	29·9	3·19	12·9	0·43 (w)	8
Y. 15	Krapina layer 8 animal bone	0·77	29·2	2·64	6·1	0·51 (w)	8
Y. 16	Krapina layer 6b (8) animal bone	0·88	27·6	3·20	7·6	0·70 (w)	4
Y. 17	Krapina layer 8 animal bone	0·22	31·2	0·70	15·4	0·23 (w)	11
Y. 18	Krapina layer 8 *Dicerorhinus* bone	0·68	28·7	2·37	14·3	0·35 (w)	6
Y. 19	Krapina layer 9g *Homo* nasion	0·73	27·9	2·60	13·4	0·14	nil
Y. 20	Krapina *Homo* skull[9]	0·83	29·9	2·77	14·2	0·08	5

[9] K. D. Gorjanović-Kramberger Coll. 1901. Geološko-Palaeontološki Muzej, Zagreb '4058–4059'.

Table 17 Analyses, Yugoslavia, Upper Pleistocene. All specimens in the M. Malez Coll., Geološko-Paleontolška laboratorij, Zagreb.

BM(NH) Lab. No.	Locus and Description	F%	P_2O_5%	$\frac{F\%}{P_2O_5\%} \times 100$	$CaCO_3$%	N%	*e* U_3O_8 ppm	^{14}C yrs bp
Y. 21	Šandalja Cave Upper Gravettian layer b, *Homo* calotte	—	—	—	—	0·78	—	12 320 ± 100 (GrN-4978)[10]
Y. 22	Šandalja Cave Upper Gravettian layer b, *Homo* calotte	n.d.	32·1	0	12·3	—	—	—
Y. 23	Šandalja Cave Upper Gravettian layer b, animal bone	0·03	32·7	0·09	20·1	0·27 (w)	nil	10 830 ± 50[10] (GrN-4976)
Y. 24	Šandalja Cave Lower Gravettian layer c, animal bone	0·22	28·9	0·75	16·4	1·51 (w)	nil	—
Y. 25	Šandalja Cave Aurignacian layer e, animal bone	0·13	31·7	0·42	13·3	0·93 (w)	nil	23 450 ± 180 (GrN-5013)
Y. 26	Šandalja Cave Aurignacian layer f, animal bone	0·18	28·2	0·62	14·5	1·67 (w)	nil	25 340 ± 170 (GrN-4977)
Y. 27	Šandalja Cave Upper Gravettian layer b (above hearth), animal bone	n.d.	29·0	0	13·0	1·93 (w)	nil	—
Y. 28	Šandalja Cave Upper Gravettian layer b (just above hearth), animal bone	0·05	32·8	0·14	10·0	1·57 (w)	nil	—
Y. 29	Šandalja Cave Aurignacian (?) layer c–d (below hearth), animal bone	0·08	29·5	0·27	15·3	0·55 (w)	5	—
Y. 32	Crvena Stijena, Montenegro, Upper Palaeolithic layer 10/11, animal bone	0·59	31·7	1·87	17·6	0·79 (w)	3	—
Y. 33	Crvena Stijena, Mousterian layer 12, animal bone	0·22	31·2	0·71	14·3	1·37 (w)	5	40 770 ± 900 (GrN-6083)
Y. 34	Crvena Stijena, Mousterian layer 12, animal bone	0·30	28·9	1·02	11·9	1·68 (w)	7	> 46 250 (GrN-4988)

[10] Associated charcoal.

can at this stage be attached to the very low counts for some bones in Mousterian layers 4 and 9. None of the hominid bone fragments contained more than 1·0% nitrogen derived from residual collagen, as was to be expected with Upper Pleistocene material.

Dr J. C. Vogel measured the radiocarbon in collagenous residue from a sample of bone from Mousterian level 1, but the result he obtained, 3200 ± 800 bp (GrN-4983) indicated without any doubt that there had been contamination with recent carbon. He also measured the radiocarbon in a piece of charred bone from a Mousterian level at Krapina that had been obtained by Professor J. S. Weiner when he visited the Geološko-Paleontološki Muzej, Zagreb in 1962. The result was 30 700 ± 750 bp (GrN-4299). Bone from a Mousterian level at Crvena Stijena, Montenegro had a radiocarbon age of 40 770 ± 900 bp (GrN-6083), but there is a growing body of evidence that Mousterian culture survived here and there until at least 32 000 bp (see Mellars 1970; Molleson, Oakley & Vogel 1972).

References: Gorjanović-Kramberger 1901, Malez 1970; 1971 : 338–340, Mellars 1970, Molleson, Oakley & Vogel 1972.

Šandalja, Istria. In 1963 and 1966, M. Malez discovered hominid fragments in a Gravettian occupation level (layer b) in cave deposits exposed in the chalk quarry at Šandalja in southern Istria.

The fluorine content of a hominid fragment found in 1963 was not detectable, but the range of fluorine shown by animal bones from the Upper Palaeolithic levels in this cave is also very low. The nitrogen content of the same bone is within the range shown by animal bones from the Gravettian layers (0·27–1·51%).

Reference: Malez 1971 : 341–342.

Velika Pećina, Croatia. In 1961, M. Malez found a human frontal bone (*Homo* aff. *neanderthalensis*) in association with Proto-Aurignacian industry in layer j in the Velika Pećina cave, NW of Ivanec in Croatia. The nitrogen content of this bone is 0·77% (w). The inferred date of this hominid is > 33 850 ± 520 bp on the basis of ^{14}C dating of charcoal in the overlying layer i.

Reference: Malez 1971 : 342.

Concluding summary with Acknowledgements

Researches on the use of analytical techniques to aid the relative dating of fossil hominid and other skeletal materials have been pursued by the present writer since the end of World War II. In April 1947 I returned from an official visit to East Africa with a collection of fossil bones and teeth, obtained mainly through the co-operation of the late Dr L. S. B. Leakey, from some of the classic hominoid sites in Kenya and Tanganyika (now Tanzania). I was fortunate enough to obtain later that year an offer from Dr H. J. Walls, then Director of the Forensic Science Laboratory, Bristol, to test the fluorine-dating method by analysing a selected series of the fossil specimens that I had brought back from Africa, and which ranged in age from Miocene to Early Holocene (although the majority were Pleistocene). The results showed that Carnot's method was not very dependable when applied to skeletal material from regions where the ground-water is rich in fluorine, as in sediments containing a high proportion of volcanic ash. In such situations the apatite composing buried bones and teeth rapidly approaches mineralogical saturation with fluorine. Under tropical conditions this process is not only accelerated but occurs in a more random fashion. The fluorine content of bones is far from being uniform in any single stratum in the Lower and Middle Pleistocene succession of ashy deposits exposed in the Olduvai Gorge, Tanzania. Some of the bones in the Late Pleistocene pyroclastic deposits at Kuguta, near Homa Mountain, Kenya, have a fluorine content in excess of the maximum for fluorapatite (see p. 3).

As the majority of specimens analysed for fluorine by Carnot were not from tropical/volcanic areas, it is probable that relative dating by fluorine is more reliable when applied to specimens buried in deposits where the ground-water has a low or moderate fluoride content, and where sedimentation and weathering occur under temperate climatic conditions.

In 1948, the late W. N. Edwards, then Keeper of Geology (Palaeontology) at the BM(NH), agreed to approach the Department of the Government Chemist (London) with a view to their undertaking microchemical analyses of bone, antler, dentine and enamel samples collected from Quaternary deposits in the Swanscombe district, Kent, from which several hominid specimens of disputed age had been recovered. The Government Chemist agreed to this co-operative programme of research. The first results were notably successful. Before the end of 1948 it was shown that the controversial Galley Hill skeleton had a very low fluorine content and was therefore evidently intrusively buried into the 100-ft terrace of the Thames during Post-Pleistocene time. In marked contrast the Swanscombe skull showed the relatively high fluorine content which characterizes the Middle Pleistocene fauna contemporaneous with the gravels of the 100-ft terrace.

In this first demonstration in Europe since the nineteenth century of the usefulness of Carnot's test the analysts (R. H. Settle, E. C. W. Maycock and C. R. Hoskins) made the innovation of determining the phosphate as well as the fluorine content of the specimens, and thus found that the fluorine/phosphate ratios were better indicators of the relative ages of buried bones of varied origin than the fluorine percentages on their own.

The following year (1949) microsamples of the hominoid and 'associated' mammalian skeletal remains reported as having been found at Piltdown, near Lewes, Sussex, between *c.* 1910 and 1915, were submitted to the Department of the Government Chemist where they were analysed by Dr C. R. Hoskins. The results which he obtained were extraordinary: the hominoid bones and teeth from both Piltdown sites (Site I and Site II) had such a low fluorine content (in the 1949 results ranging from less than 0·1% to 0·4%) that comparison with the fluorine content of known Pleistocene skeletal remains from sites in southern Britain made it impossible to believe any longer that Piltdown man had the high antiquity which for some 40 years anthropologists and palaeontologists had been claiming. The fossil mammalian bones and teeth said to have been found at the two Piltdown sites showed a wide range of fluorine content, from less than 1% to 2·7%. This was not so surprising because several of the original investigators had concluded that fossil faunas of two or more geological ages had become mixed together in the Piltdown river gravel. It was so difficult to accept the new indications that the Piltdown skull was at the most no older than Upper Pleistocene, that further analytical investigations of the anomalous results of 1949 were set in motion using larger samples and more refined techniques of analysis. The outcome in 1953 was to establish Dr (later Professor) J. S. Weiner's hypothesis that the Piltdown I skull (including mandible and teeth) had been forged. Although it was the application of the 'fluorine test' to the Piltdown specimens in 1949 that triggered off the extensive investigations which eventually led to this result, the removal of all doubt about its correctness was due to teamwork on a scale probably unprecedented in solving a single problem. Thus a whole battery of physical and chemical techniques was brought to bear on the Piltdown problem before complete proof was obtained that the Piltdown skulls I and II and all the mammalian fossils recovered from Site I and Site II were part of an elaborate forgery. Some 25 scientists deserve credit for their contributions to this work: Dr G. F. (later Sir Frank) Claringbull, Mrs A. Foster, Dr M. H. Hey, Dr A. A. Moss and Dr J. D. H. Wiseman of the Department of Mineralogy, BM(NH); A. D. Baynes-Cope, H. L. Bolton, H. J. Dothie, C. F. M. Fryd and Dr C. R. Hoskins of the Department of the Government Chemist, London; Professor W. E. (later Sir Wilfrid) LeGros Clark and Dr J. S. Weiner,[11] Department of Human Anatomy, University of Oxford; Miss R. J. Plesters and Dr A. E. A. Werner, then at the Research Laboratory, National Galley; Dr E. T. Hall, Clarendon Laboratory, Oxford; Dr R. C. Hoather, late of Counties Public Health Laboratories, London; Dr C. Bloomfield, Rothamsted Experimental Station, Harpenden; Dr A. V. W. Martin (now Mrs Angela Brown) and Professor J. T. Randall, Department of Biophysics, King's College, London; Drs G. Weiler and F. B. Strauss, Microanalytical Laboratory, Oxford; F. H. Edmunds, Geological Survey of Great Britain; S. H. U. Bowie and Dr C. F. Davidson[12], Atomic Energy Division, Geological Survey of Great Britain.

[11] Later Professor of Environmental Physiology, London University.
[12] Later Professor of Geology, University of St Andrews.

As the Piltdown investigations were directed from the Department of Geology (Palaeontology), BM(NH), I would like to record my appreciation of the co-operation received from the members of the staff of the Department who made fossils available for comparative tests, notably the late Dr A. T. Hopwood who at the time was in charge of Fossil Mammalia. L. E. Parsons and other members of the laboratory staff in the Department of Geology (Palaeontology) rendered valuable service in the preparation of samples for analysis. I should also like to record the helpfulness of the consultations which I had with the late Dr F. C. Fraser, eventually Keeper of the Department of Zoology. The Director of the Museum at the time, the late Sir Gavin de Beer, gave unreserved encouragement to all this work and played a leading part in presenting a summary of the results at a meeting of the Geological Society of London on the 30th June 1954.

Following the reports of successful applications of analytical techniques for the relative dating of fossil hominids, the late Dr Paul Fejos, Director of Research of the Wenner-Gren Foundation, told me after I had lectured on the subject in New York in 1950 that if I reached a position at which my researches on these lines would benefit by receiving a grant-in-aid, I should let him know and he would submit an application on my behalf for consideration by his Board of Directors. So far the researches had been on a fairly modest scale, but after the publication of the Piltdown investigations, W. N. Edwards agreed that as the Laboratory of the Government Chemist was prepared to continue the co-operation with the Museum, the research should be extended to a wide range of sites in Britain and abroad. Since some of the work would involve foreign travel, employment and purchase of equipment for use in the Museum, he thought that it would be a good idea for me to apply to the Wenner-Gren Foundation for grants-in-aid of the researches. My applications were successful.

The first grant was made in 1952, and was mainly used for the purpose of applying relative dating techniques to fossil hominid sites in southern Africa. After carrying out this programme of work in 1953, the remainder of the grant was devoted to continuing the use and development of analytical methods of dating to fossil hominids and associated faunal material from American, Asiatic and European sites. With a second grant received in December 1954, it was possible to purchase radiometric equipment to aid this work. I should like to record my gratitude to the late Dr Paul Fejos for the interest he took in these researches up to the time of his death in 1963. Mrs Lita Osmundsen (formerly Mrs Fejos) succeeded her late husband as Director of Research of the Wenner-Gren Foundation and continued to give me much help and encouragement in subsequent years. The Board of Directors in New York renewed their grant-in-aid of analytical work on fossil bone and other skeletal materials in 1963 and 1969.

Through the experience in analytical work on the Galley Hill, Swanscombe, Fontéchevade and Piltdown material (and wide-ranging comparative materials) it became an established procedure to analyse the following components of bone, antler, dentine and enamel: fluorine (F), phosphate (P_2O_5) and the ratio ($100F/P_2O_5$), calcium carbonate ($CaCO_3$), nitrogen (N) and uranium (either as U parts per million, as U_3O_8 ppm or as e U_3O_8 ppm). In the research carried out after 1960, the fluorine and phosphate contents were determined microchemically by methods developed by M. J. Glover and G. F. Phillips in the Laboratory of the Government Chemist, London. Where relative dating problems could be solved by estimating the fluorine content of the material by X-ray diffraction data in a long series of samples, the work was undertaken by G. F. Claringbull and R. J. Davis in the Department of Mineralogy at the Museum. Nitrogen determinations were made microchemically by E. I. Johnson in the Laboratory of the Government Chemist or by G. C. Ross in the Department of Zoology at the Museum, or by G. Weiler and F. B. Strauss in the Microanalytical Laboratory, Oxford. The uranium content of samples was determined in the Subdepartment of Anthropology at the Museum using the method of radiometric assay introduced by Davidson & Bowie (1955) during the Piltdown researches. Over 1200 radiometric assays were carried out in the Subdepartment of Anthropology between 1955 and 1975, the work being supervised first by A. E. Rixon and then mainly by Miss T. I. Molleson. When it was necessary to determine the uranium content on samples weighing less than a milligram, the work was generously undertaken by Dr R. L. Fleischer in the General Electric Research Laboratories at Schenectady, New York. (See Note on the Tables, p. 14).

In cases where it was desirable to have the chronometric age of a fossil hominid estimated as closely as possible, the Research Laboratory of the British Museum (Bloomsbury) was asked to include one or more samples for radiocarbon dating in their 'human palaeontology' programme. I would like to acknowledge the help received from Messrs Harold Barker and Richard Burleigh of the British Museum Laboratory, in discussing problems of bone-dating relevant to the preparation of parts of the present paper.

The uses to which the research described in this paper can be put are quite varied. Perhaps partly as a result the use of fluorine, uranium and nitrogen in relative dating of bones which I have described in previous papers, a number of radiocarbon laboratories now include determinations of these elements in their reports. In the *Catalogue of Fossil Hominids* (BM(NH), London, 1967–1977), whenever they were obtainable, the results of analysing the hominid remains and of associated fauna have been recorded under item 9 as explained in the Introduction of each part of the Catalogue. The analyses were for the most part only obtainable through the co-operation of museum curators who had charge of the original specimens and who arranged for them to be lent for sampling at the BM(NH), or alternatively themselves supplied the requisite samples. Where analyses quoted in this Bulletin were made possible by co-operation of this kind, my indebtedness to the persons concerned has been expressed in the descriptions of the various sites.

Relative dating of skeletal material by nitrogen analysis has proved particularly useful when considered in relation to radiocarbon dating of specimens close to the Upper Palaeolithic/Holocene boundary (see under Robin Hood's Cave, p. 16). Since the breakdown of the collagen of skeletal materials into amino-acids, and the leaching out of these through weathering, have a bearing on the regression of the nitrogen content of buried bones, researches on these processes were carried out in the Department of Palaeontology in co-operation with other laboratories between 1953 and 1969. It is therefore appropriate to acknowledge here the help provided by the late Professor J. T. Randall and Miss A. V. W. Martin (now Mrs Angela Brown) in the Department of Biophysics, King's College London, who obtained the first electron micrographs of collagen fibrils in fossil ivory and fossil bone (p. 9). Further help on these lines was provided by D. Claugher, assisted by C. G. Ogden in the Electron Microscope Unit of the BM(NH), who in 1967 made a detailed study of the collagen fibres in the 30 000 years old rhinoceros bone from the Lloyd's site in the City of London (Fig. 5, p. 21). A related study was the identification of the amino-acids retained in the organic matrix of bones during their various stages of fossilization. This was undertaken by using chromatography, first by A. E. Rixon in the Department of Palaeontology using paper-chromatography, and later by G. C. Ross in the Department of Zoology, using a more sophisticated type of chromatography (Fig. 6, p. 21).

Further research is required on the ecological aspects of collagen degradation in buried skeletal materials. When ivory from ancient Egyptian sites is analysed prior to the use of any washing technique it is found to contain almost as much nitrogen as fresh ivory, and nearly the full range of the amino-acids. But if the analyses are carried out after a sample of the same ivory has been washed in warm (70°C) water and acetone, the nitrogen content has been greatly reduced and only a few of the amino-acids retained. Evidently under warm and relatively dry climatic conditions, the amino-acids in the collagenous residue are retained through many millennia, but they are loosely bound together, so that after washing in warm water they undergo dissolution. Buczko and his colleagues have found that the nitrogen content of bones buried in alluvial deposits in Hungary is lost most rapidly during warm climatic phases (Buczko *et al.* 1978). In Britain evidence has been found that the type of mineral matrix enclosing the fossil bones greatly affects the influence of the climatic factor in the rate of regression of nitrogen content. For example, the nitrogen content of the rhinoceros ulna encased by clay at the Lloyd's site in London was 3·4%, whereas in a mammoth bone embedded in sand on the same stratigraphic horizon at that site the nitrogen content had been reduced to 0·1%.

Altogether about a thousand skeletal samples ranging in age from Oligocene to late Holocene from sites in Africa, Asia, Australasia, Indonesia, Malaysia, North, Central and South America, and the Pacific Islands have been analysed. Dr Susan Limbrey, while working temporarily in the Subdepartment of Anthropology, BM(NH), prepared a slip index on which the essential details regarding each analysed sample are recorded, including the name of the analyst and the laboratory. Arrangements can be made for visitors to consult this data-bank when required.

From 1965 onwards Miss T. I. Molleson aided me in all phases of the programme of research described in this *Bulletin*. In thanking her for this co-operation, I should like to say how glad I am that since my retirement she has continued to use, and has made further developments in, the analytical studies of fossil skeletal materials which rather tentatively I initiated at the Museum some 30 years ago.

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Origin, evolution and systematics of the dwarf Acanthoceratid *Protacanthoceras* Spath, 1923 (Cretaceous Ammonoidea)

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Contents

Synopsis

Protacanthoceras Spath, 1923 is a dwarf acanthoceratid of middle and late Cenomanian age. Individuals are adult at diameters of 15–50 mm and some populations show apparent size dimorphism indicating that the genus is genuinely diminutive, not the microconch of some larger acanthoceratid.

The earliest species, *P. tuberculatum* Thomel, is a paedomorphic derivative of contemporary *Acanthoceras rhotomagense* (Brongniart); later species diverged considerably from the basic long-ranging ribbed,

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square-whorled prototype. Decline in ornament led to *P. tuberculatum mite* subsp. nov., whence was derived *P. arkelli* sp. nov. in the late Middle Cenomanian, and the early Upper Cenomanian *P. asgeirri* sp. nov. In the early Upper Cenomanian *P. arkelli* gave rise to a further paedomorphic offshoot which led to the aberrant *P. tegulicium* sp. nov. During middle Upper Cenomanian time there arose three rectangular-whorled forms, a small robust subspecies, *P. tuberculatum devonense* subsp. nov., *P. tuberculatum cyclopeum* subsp. nov. (the largest form of the genus), and the compressed *P. bunburianum* (Sharpe). *P. tuberculatum devonense* gave rise to a round-whorled form which lost its tubercles, *P. proteus* sp. nov., with two subspecies *P. p. proteus* and *P. p. baylissi* subsp. nov.

The late Cenomanian *Protacanthoceras* assemblage exhibits in miniature the features of the early growth stages of several latest Cenomanian and early Turonian genera.

Protacanthoceras is best known in England and France but a further species, *P. imperatoris* sp. nov., is described from Madagascar.

Other species have been referred to the genus incorrectly.

Introduction

Protacanthoceras Spath, 1923 is among the most variably interpreted of Cenomanian acanthoceratid genera. Originally described, on the basis of misconceptions about its stratigraphic range, as an intermediate between *Calycoceras* Hyatt, 1900 of the Mantelliceratinae and *Acanthoceras* Neumayr, 1875 of the Acanthoceratinae, the generic name has been, and still is, applied to diverse convergent acanthoceratids linked only by their closely trituberculate peripheries. The genus in fact comprises genuine dwarfs, adult at diameters of 15–50 mm, and, unlike some other dwarf taxa which subsequent work has shown to be no more than microconchs of normal-sized ammonites, it appears to be dimorphic within these size limits. *Protacanthoceras* at its origin is thus an exception to the widely quoted phenomenon of progressive size increase amongst ammonites (Cope's Rule, e.g. Stanley 1973). As discussed below, evolution within the genus demonstrates both size increase and size decrease, whilst both at its origin and subsequently paedomorphosis produced abrupt species transformations. Furthermore, the late Cenomanian array of *Protacanthoceras* reproduces in miniature several latest Cenomanian and early Turonian genera.

Evolutionary origins

Spath's original view (1923 : 144) that *Protacanthoceras* preceded *Acanthoceras*, with *P. triseriale* (J. de C. Sowerby) as the passage form closest to *Calycoceras*, was probably based on his ideas on the sequence of Cenomanian ammonites which derived from faunas collected by T. F. Grimsdale and others from the Chalk Basement Bed in south Dorset and the Cenomanian Limestone of Devon. In 1926 he noted that *Hyphoplites* occurred with '*Protacanthoceras*' of the '*hippocastanum*' group in this area, without realising that these condensed units contained mixed faunas (cf. Kennedy 1970). In fact work on the expanded chalk sequences of south-east England shows quite clearly that *Acanthoceras* precedes *Protacanthoceras* and that its origins in all probability lie in robustly ornamented *Acompsoceras* of the group of *sarthense* (Guéranger) or *landesi* Cobban (= *Paracompsoceras* Cobban, 1971).

Thomel (1972 : 99, text-fig. 3) suggested that *Protacanthoceras* evolved from early *Pseudocalycoceras* Thomel, 1969 and placed both in the Mantelliceratinae. Again stratigraphic evidence renders this view untenable. The earliest known *Pseudocalycoceras* appears in the Upper Cenomanian, while *Protacanthoceras* appears low in the Middle Cenomanian. Juvenile *Pseudocalycoceras* are so different in their ribbing and tuberculation (Cobban & Scott 1972 : pl. 13, figs 11–25) that no close relationship can be inferred and the similar clavate ventral ornament of adults is merely homoeomorphy (Figs 8, 9). Thomel's view (1972 : 99) that *Protacanthoceras* might be the microconch of *Pseudocalycoceras* cannot be supported. The two genera show none of the features in common which are seen in dimorphic pairs and have quite different stratigraphic and geographic distributions.

Morphological evidence points very clearly to *Acanthoceras* of the *rhotomagense* (Brongniart) group as the immediate ancestor of *Protacanthoceras*. Immature specimens of the earliest species, *P. tuberculatum* Thomel, show such striking similarities to juveniles of strongly-ribbed variants such as *A. rhotomagense sussexiense* (Mantell) and *confusum* (Guéranger) (Figs 11, 12) that affinity cannot be doubted. Indeed, only the parallel sides and more markedly clavate outer ventrolateral and siphonal tubercles allow the inner whorls of *tuberculatum* to be distinguished, although the adult ornament of *Protacanthoceras* (e.g. Fig. 8) is immediately diagnostic, as is the change from alternately long and short ribs of the juvenile *Acanthoceras rhotomagense* to the wholly long ribs of middle and later growth.

Whereas adult sutures of *Acanthoceras* differ at first sight from adult sutures of *Protacanthoceras*, they are on the same essential plan, as is indicated by the resemblance between the sutures of juvenile *Acanthoceras* and adult *Protacanthoceras* (Fig. 1), whilst the very earliest ornamented stage of *A. rhotomagense* and *P. tuberculatum*, with round whorls and sparse, band-like tuberculate ribs, are identical.

No intermediates are known between *Acanthoceras* of the *rhotomagense* group and *Protacanthoceras tuberculatum* and the generic transformation does not appear to have involved progressive size decrease. Sudden paedomorphosis seems to be the most probable explanation of the evolution from a species group that is adult between 150–200 mm to one whose macroconchs are adult at 30–37 mm.

The smallest adult *Acanthoceras* is that described as *A. basseae* by Kennedy & Hancock (1970 : pl. 47, figs 2a–c) from the Middle Cenomanian, but even here the holotype shows a change to adult *Acanthoceras* ornament with all the ribs extending to the umbilicus, whilst its general proportions and whorl section are sufficiently different from *P. tuberculatum* to preclude it from any direct relationship.

We have suggested (Wright & Kennedy *in* Juignet *et al.* 1973 : 26) that certain *Thomelites* might be the macroconchs of *Protacanthoceras*. It now appears that *Protacanthoceras* is itself dimorphic and that the '*Protacanthoceras*' species we there referred to are in fact small *Thomelites*, and indeed microconchs. Differences between *Thomelites* and *Protacanthoceras* (Figs 6, 8) are clarified in the taxonomic part of the paper.

Dimorphism

Dimorphism, although well documented in many groups of Jurassic and some Cretaceous ammonites (Makowski 1962; Callomon 1963; Le Hégerat 1973; Kennedy & Cobban 1976), has not been generally recognized amongst normally-coiled Upper Cretaceous ammonites. *Protacanthoceras* (and probably other acanthoceratids–see, for instance, Berthou *et al.* 1976, Cooper 1978) appears to show dimorphism that is largely a matter of bimodal size distribution, with microconchs only slightly smaller, around 70% of the size of the macroconch, and without lappets, rostra or other apertural modifications. This is in marked contrast to Jurassic groups, where the size difference is often two- to four-fold. Figs 24–33, 36–45 show presumed dimorphic pairs of typical *Protacanthoceras* species. Our samples are generally too small to quantify ratios of the members of pairs with any precision, but samples of *P. tuberculatum* and *P. bunburianum* suggest a ratio of one to one. This size dimorphism, though strongly suggested, is not proved; the spread of size in presumed macroconchs and microconchs within a species may be greater than the gap between the two. However, virtually all the material has been collected from condensed phosphatic beds; the real constituents of any momentary population and exact contemporaneity of individuals cannot be established and it is probable that there was some variation in size during the time represented by each condensed bed.

Localities

To save repetition, full details are given here of localities frequently mentioned in the text (National Grid references in brackets):

Askerswell, Dorset (SY 529923), temporary section 300 m S of church (Kennedy 1970: 644).
Bindon Slips, Devon (SY 272886), *in situ* and slipped masses at top of cliff west of where coastguard path dips over cliff edge.
Chardstock, Devon (ST 316044), old quarries on eastern side of Storridge Hill (Kennedy 1970: 651).
Chilfrome Lane, Maiden Newton, Dorset (SY 593979), old quarry (Kennedy 1970: 634).
Durdle Cove, Dorset (SX 805803), natural exposures west of Durdle Door.

Evershot, Dorset (ST 578050), old quarry behind Rock Cottages (Kennedy 1970: 632).
Furley, Devon (SY 208999), disused quarries (Kennedy 1970: 654).
Hooken Beach, Devon (SY 222878), fallen blocks on beach.
Hooken Cliff, Devon (SY 220880), slipped masses.
Horn Hill, Beaminster, Dorset (ST 470032), old quarry on Horn Hill, east of road (Kennedy 1970: 640).
Humble Point, Devon (SY 307889), fallen blocks on beach (Kennedy 1970: 658).
Lulworth Cove, Dorset (SX 825800), natural exposures at back of Cove.
Man-of-War Cove, Dorset (SY 815810), natural exposures at back of Cove.
Osmington, Dorset (SY 726819), blocks on beach and in landslips inland, west of Osmington Mills.
Ringstead Quarry, Dorset (SY 747818), disused quarry on west side of road between Upton and Ringstead (Wright *in* Arkell 1947: 211).
Shapwick Grange, Devon (SY 313918), working limepit close to farm.
Snowdon Hill, Chard, Somerset (ST 313089), old quarry on south side of road A30 west of town (Kennedy 1970: 648).
Toller Porcorum, Dorset (SY 567982), disused quarry (Kennedy 1970: 637).
White Hart Sandpit, Wilmington, Devon (SY 208999), working sandpit at western end of village, opposite White Hart Inn.
White Nothe, Dorset (SY 772806), cliff exposures and slipped masses below Holworth House.
Whitlands, Pinhay Bay, Devon (SY 313905), slipped masses in undercliff.

Stratigraphy

The basic succession of Cenomanian ammonite faunas in the expanded chalk sequences of south-east England (Kennedy 1969, 1971) provides the framework against which the evolution of *Protacanthoceras* has been worked out. In this region, however, the genus is rare and only the sequence of the main *Protacanthoceras tuberculatum–P. bunburianum* rootstock of the genus can be traced. In contrast, the condensed phosphatic Basement Beds of the Chalk of south-west England (Kennedy 1970) yield many more ammonites, and provided most of our *Protacanthoceras* material. These Basement Beds can be precisely correlated with the Chalk sequence and allow dating of the remaining species. It must, however, be stressed that these Basement Beds are in some cases equivalent to many metres to the Chalk sequence and species and subspecies of slightly differing ages are present in a single bed. Here evolutionary relationships are established on the basis of either morphology or relative degrees of mineralization and abrasion.

Systematic descriptions

Superfamily **ACANTHOCERATACEAE** Grossouvre, 1894

Family **ACANTHOCERATIDAE** Grossouvre, 1894

Subfamily **ACANTHOCERATINAE** Grossouvre, 1894

Genus ***PROTACANTHOCERAS*** Spath, 1923

TYPE SPECIES. *Ammonites bunburianus* Sharpe (1853 : 25; pl. 9, figs 3a–c), by the original designation of Spath (1923 : 144).

DIAGNOSIS. Small. Adult at diameters of 15–50 mm. Moderately involute, compressed to depressed, flat-sided or round-whorled, bearing primary and intercalated ribs, typically with prominent umbilical and inner[1] ventrolateral tubercles and closely spaced clavate outer ventrolateral and siphonal tubercles; tuberculation declines at the end of the body chamber and the ribs become broad and flat. Dimorphic, microconchs generally less densely and more strongly ribbed than macroconchs, although both show essentially similar styles of ornament. In a few species some or all tuberculation except for the umbilical is suppressed during part or all of ontogeny. Suture simple, with broad bifid L and smaller bifid U_2. E/L larger, bifid; L/U_2 small, simple. Auxiliaries may be pseudoceratitic.

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[1] The *Treatise* terms 'upper' and 'lower', as applied to ventrolateral tubercles, are illogical. 'Inner' and 'outer' are therefore used instead.

DISCUSSION. *Protacanthoceras* was introduced by Spath in 1923 without diagnosis. He included *P. triseriale* (J. de C. Sowerby), *P. compressum* (Jukes-Brown) and *P. hippocastanum* (J. de C. Sowerby) in the genus at that time and regarded it as intermediate between *Calycoceras* and *Acanthoceras*. Subsequently Collignon (1937) included a series of Madagascan and Algerian ammonite species in the genus and later (*in* Roman 1938 : 443) gave the first diagnosis of the genus: 'Acanthocératidés comprimés, aux côtes plus ou moins flexueuses, parfois droites, de section ogivale, à trois rangées de tubercles ventraux serrées l'une contre l'autre. Cloison du type general d'*Acanthoceras*. Les caractères distinctifs sont la compression de l'Ammonite et la présence de trois rangées de tubercles ventraux serrées, l'une contre l'autre'. This diagnosis was widely accepted and diverse Cenomanian ammonites with three rows of closely spaced clavate ventral tubercles were referred to *Protacanthoceras*, most of them much larger than the type species, including forms up to 150–200 mm diameter.

In 1951 Wright & Wright pointed out that the genus was in fact a genuine dwarf and that most of the species referred to the genus by other authors belonged elsewhere. Thomel (1969) proposed the genus *Pseudocalycoceras* to accommodate the *harpax* group, with their diagnostic rursiradiate ribs, whilst we (*in* Juignet *et al.* 1973) proposed *Thomelites* to accommodate various other species which closely resembled *Protacanthoceras* but grew to much larger sizes. At that time we suggested that some *Protacanthoceras* might be microconch *Thomelites*; our subsequent work indicated that these specimens are indeed microconchs, but are *Thomelites*.

The characteristic ornament of the end of the body chamber, appearing at small sizes, is the easiest way of separating *Protacanthoceras* from other genera, but when juveniles only are available problems may arise.

Acanthoceras Neumayr, 1875 reaches a large size (commonly in excess of 400 mm) when adult. Early whorls may be separated from *Protacanthoceras* in that most individuals are much less strongly ribbed at the same size as adult *Protacanthoceras* and do not show the same closely-spaced ventrolateral tubercles (Fig. 11A). The sutures of juvenile *Acanthoceras* are always more complex than those of mature *Protacanthoceras* of similar size. Flat ventral ribbing without tubercles is never seen in juvenile *Acanthoceras*. The earliest *Protacanthoceras*, *P. tuberculatum* (Fig. 8), is at

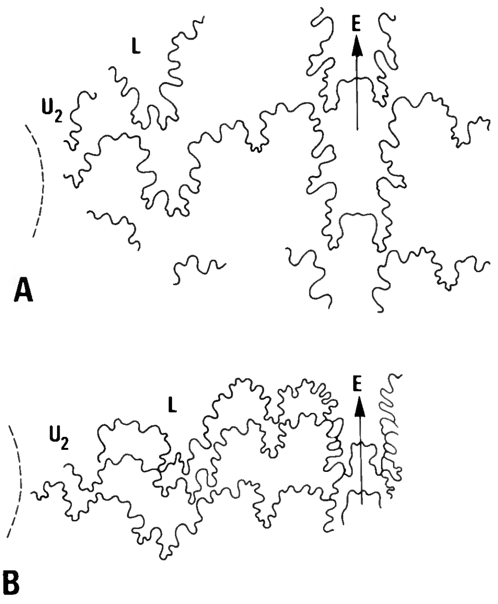


Fig. 1 Sutures of adult Middle Cenomanian *Protacanthoceras* and juvenile *Acanthoceras* compared. 1A, *Acanthoceras rhotomagense* (Brongniart). P. Juignet coll. no. 1-159, from the phosphatic *costatus* Zone fauna at the base of the Craie de Théligny of Sarthe, France, × 4. 1B, *Protacanthoceras tuberculatum tuberculatum* Thomel from the *acutus* Zone fauna of the Chalk Basement Bed, Snowdon Hill, Chard, Somerset. OUM K4437, × 4.

first glance indistinguishable from some contemporary *Acanthoceras rhotomagense* variants in all but size, suture and grouping of ventral tubercles (Figs 11, 12).

Pseudocalycoceras Thomel, 1969 reaches a moderate size, up to 100 mm. Most species bear dense, rounded ribs, which become markedly rursiradiate during middle and later growth (Fig. 9), a feature never seen in *Protacanthoceras*. The juveniles of *P. dentonense* (Moreman), as figured by Cobban & Scott (1972 : pl. 13, figs 11–23), do not develop the strong clavate ventral tuberculation which characterizes the adult and which led previous authors to refer species such as *Pseudocalycoceras harpax* (Stoliczka) and its allies to *Protacanthoceras*.

Thomelites Wright & Kennedy, 1973 reaches a large size. All species retain siphonal tubercles to a much larger size than *Protacanthoceras* (Fig. 6). Compressed forms may lose their inner ventrolateral tubercles at an early stage, leaving a flat venter with the siphonal tubercle weaker than the outer ventrolaterals. Robust forms develop massive inner ventrolateral spinose or subspinose tubercles on primary ribs, with two or three intercalated ribs lacking such a tubercle, a style of ornament never seen in *Protacanthoceras*. The suture of *Thomelites* (Fig. 23E, p. 81) is deeply incised and subdivided compared with that of *Protacanthoceras*.

Metoicoceras Hyatt, 1903 reaches a large size. Juveniles of most species lack siphonal tubercles at all stages in ontogeny (e.g. Cobban 1953 : pl. 6, figs 1–11), have a tiny shallow umbilicus with an outward-sloping umbilical shoulder and have a suture which tends toward development of entire, pseudoceratitic auxiliaries on the suspensive lobe (Fig. 23C, p. 81). Two species, *M. praecox* Haas and *M. latoventer* Stephenson, develop siphonal tubercles when young; in neither are they closely-spaced and clavate as in *Protacanthoceras*.

The largest known individuals of *Neocardioceras* Spath, 1926 are somewhat larger than adult *Protacanthoceras*. All *Neocardioceras* bear dense, flexuous sharp ribs, all or virtually all of which are long. The coiling is very evolute; whilst the inner ventrolateral tubercles disappear early in ontogeny, the outer are bullate rather than clavate and those of the siphonal row are small and separated from the ventrolateral row by a smooth band. Adults never develop the late body chamber ornament of *Protacanthoceras*.

Nigericeras Schneegans, 1943 reaches a large size. Juveniles (Fig. 10) of *Nigericeras costatum* Barber (1957 : pl. 10, figs 3a–b) bear band-like ribs similar to those on the phragmocone of *P. asgeirri* (Figs 20–21) and the earliest ornamented growth stages of other *Protacanthoceras* (Figs 24, 28). The great difference in size and distinctive ornament of later stages in both genera preclude confusion.

The type species of the interesting genus *Quitmaniceras* Powell, 1963, *Q. reaseri* Powell (1963 : 313; pl. 32, figs 5, 13; text-fig. 2A–B), is densely and flexuously ribbed with a carinate venter and is thus readily distinguished from all *Protacanthoceras*. *Q. brandi* Powell (1963 : 314; pl. 32, figs 6, 8, 11, 12, 14–16), however, closely resembles late *Protacanthoceras* like *P. bunburianum* but has flexuous ribs and a crenulate siphonal keel rather than a row of discrete tubercles. The sutures of the two genera are both rather simple.

Calycoceras Hyatt, 1900 species are moderately to very large and have rounded whorls and only faintly clavate tubercles which may be lost at an early stage (Fig. 7). Juvenile *C.* (*Conlinoceras*) Cobban & Scott, 1972 closely resembles *Protacanthoceras* of the *tuberculatum* group, especially subspecies *mite*, but the ventral tuberculation is never so clavate nor so closely spaced as in *Protacanthoceras*, and *Conlinoceras* lose their tubercles and develop a rounded venter as size increases. Juveniles of *C.* (*Newboldiceras*) Thomel, 1972 are usually densely ribbed and never show such strong close-spaced ventral tuberculation as *Protacanthoceras*. The sutures of *Calycoceras* (Fig. 23B, p. 81) include broad, sometimes intricately divided lobes and saddles, whilst the auxiliary elements on the suspensive lobe are far more divided than in *Protacanthoceras*.

OCCURRENCE. *Protacanthoceras* first appears as a great rarity at the top of the *Turrilites costatus* Zone, in the lower third of the Middle Cenomanian. It ranges to the middle of the Upper Cenomanian, the higher parts of the *Calycoceras naviculare* Zone.

The genus is best known from southern England (Middle and Upper Cenomanian of Devon and Dorset; Middle Cenomanian of Somerset, Wiltshire, Kent and Sussex). There are also records from the Middle Cenomanian of Rouen, Normandy (Kennedy & Hancock 1970), Sarthe (specimens in the collection of P. Juignet, Caen, and the Faculté des Sciences, Rennes) and Provence (Thomel 1972) in France. Collignon noted a species from Tinhrert, Algerian Sahara (1965 : 12); the description however suggests it may be a *Pseudocalycoceras*. *Ammonites tropicus* Stoliczka, previously suggested as a possible Indian representative of *Protacanthoceras* (Kennedy 1971 : 97), is a *Thomelites* (p. 101); the Madagascan specimens referred to *tropicum* are indeed *Protacanthoceras* and are described below (p. 97) as a new species, *Protacanthoceras imperatoris*, of presumed Upper Cenomanian age. '*Acanthoceras*' *cuspidum* Stephenson (p. 99) is shown to be a juvenile *Acanthoceras* or *Dunveganoceras* and a homoeomorph of *Protacanthoceras*. Matsumoto, Saito & Fukada's (1957 : 39; pl. 14, fig. 3) specimen from Japan is too juvenile for certain determination.

Protacanthoceras is generally very rare; in the Middle Cenomanian *Turrilites costatus* and *acutus* Zones it accounts for less than 0·1 % of the ammonite fauna. It is a little commoner in the succeeding *jukesbrownei* and basal *naviculare* Zones, but still forms less than 1 % of the fauna. In the high *naviculare* Zone faunas of south Devon, however, it is one of the commonest ammonites. In England most specimens come from the condensed phosphatic Basement Beds of the south-west. This reflects merely the selective preservation of small ammonites in this facies and the fact that our collections from these fossil concentrates are far larger than from the standard Chalk facies.

Only eight specimens definitely referable to the genus are known from outside the United Kingdom.

Protacanthoceras tuberculatum Thomel

1972 *Protacanthoceras tuberculatum* Thomel: 101; pl. 32, figs 9–12.

Holotype. G. Thomel colln no. 17523, a macroconch, from the Upper Cenomanian of Peille, Alpes-Maritimes, France, by monotypy. The associated fauna suggests that the specimen is from a horizon equivalent to the lower part of the English *naviculare* Zone.

Diagnosis. A species of *Protacanthoceras* with generally robust ornament of 12–19 alternately long and short ribs per whorl (although feebly ornamented subspecies are known) and a quadrate, angular costal whorl section. Long ribs bear strong umbilical bullae and all ribs bear blunt to spinose inner ventrolateral tubercles and well-developed clavate outer ventrolateral and siphonal tubercles.

Protacanthoceras tuberculatum tuberculatum Thomel
(Figs 1B, 2, 8, 14–17)

1969 *Protacanthoceras* sp. Kennedy : 469, 485, 487, 500, 538 and 542.
1970 *Protacanthoceras* sp. Kennedy : 633, 634, 638, 641, 653 and 654.
1970 *Protacanthoceras* sp. Kennedy & Hancock: pl. 97, figs 4a–b.
1971 *Protacanthoceras* sp. a; Kennedy : 644.
1972 *Protacanthoceras tuberculatum* Thomel : 101; pl. 32, figs 9–12.

Holotype. G. Thomel colln no. 17523, as above.

Material. Numerous specimens, including the following (National Grid references in brackets). From the *Turrilites costatus* Zone fauna of the Chalk Basement Bed, Worbarrow Bay, Dorset (SY 865804): BM(NH) C82006. From the *Turrilites acutus* Zone fauna of the Chalk Basement Bed: BM(NH) C9424 from Maiden Newton, Dorset (precise locality unknown); BM(NH) C9563 and OUM K4432 from Evershot; OUM K4436–7 from Toller Porcorum; OUM K4483 from Chilfrome Lane, Maiden Newton; BM(NH) C72911 and OUM K4470 from Horn Hill, Beaminster; OUM K4436–39 from Snowdon Hill. From the Chalk Basement Bed blocks in the landslips west of Osmington, Dorset (*Acanthoceras jukesbrownei* Zone): BM(NH) C72919–24, C81904–9. Of like age and from the same horizon at Ringstead, Dorset are BM(NH) C81910–5; from Chaldon, Dorset (precise locality unknown) is GSM 36927; from Holworth House, White Nothe, Dorset (SY 773807) is BM(NH) C72939; C70956 is also from White Nothe, as is, presumably, a specimen labelled 'White Nose Cape', C55867; C81916 is from Durdle Cove;

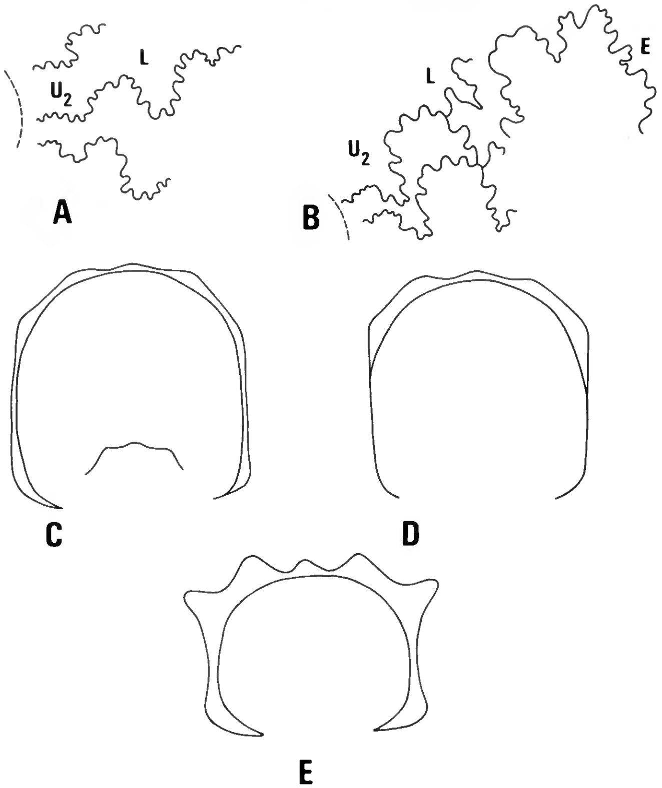


Fig. 2 *Protacanthoceras tuberculatum tuberculatum* Thomel. 2A, juvenile sutures of OUM K4429, × 4. 2B, mature sutures of OUM K4436, × 4. 2C, whorl section of BM(NH) C81905 at aperture, × 2. 2D, whorl section of body chamber of BM(NH) C81906 through an intercalated rib, × 2. 2E, whorl section of BM(NH) C81904 at back of body chamber, × 2.

C81917–9 are from Man-of-War Cove and a specimen in J. M. Hancock's collection is from Furley.

C81920 and C81922 are from the top of the local equivalent of Division B of the Cenomanian Limestone at the White Hart Sandpit, Wilmington and of Middle Cenomanian age.

Calycoceras naviculare Zone: OUM K4426–31 are from the Chalk Basement Bed at Askerswell, Dorset. BM(NH) C81921 and C81923 are from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone near Whitlands, Pinhay Bay and from a higher level in the *naviculare* Zone.

Specimens from the Chalk facies of south-east England include OUM K4481 from the *costatus* Zone (Band 6f) below Beachy Head, near Eastbourne, Sussex (TQ 593955); OUM K4482 from the *acutus* Zone (Band 6), Bluebell Hill, Burham, Kent (TQ 735618) and OUM K4480 from the *jukesbrownei* Zone at Newington's Pit, Glynde, Sussex (TQ 430922).

Diagnosis. A subspecies of *Protacanthoceras tuberculatum* characterized by strong ornament, 17–19 alternately long and short straight ribs per whorl, the long ribs bearing variable but generally strong umbilical bullae. All ribs bear subequal, conical to spinose inner ventrolateral tubercles and strong, equal, clavate outer ventrolateral and siphonal tubercles borne on strong transverse ribs. Body chamber modifications include decline in strength of flank ribs and all tubercles, with strengthening and projection of ventrolateral and ventral ribs into a marked chevron.

Description. The coiling is moderately involute on the phragmocone, tending to be rather more evolute on the adult whorl, the umbilical seam of the body chamber being markedly eccentric

(Figs 16b, 17b). The umbilicus is of variable breadth, 20–25% of the total diameter in most specimens, tending towards the lesser figure in juveniles and the greater in adults, as indicated in the table of measurements below.

The umbilicus is of moderate depth, with a rounded umbilical wall and a crenulate umbilical seam to accommodate the ribs on the previous whorl. The umbilical shoulder is sharply rounded. The intercostal section displays flattened, subparallel flanks and a broadly rounded venter, the greatest breadth being around mid-flank. It is always depressed, breadth to height ratios varying greatly, from 1·41 to 1·04. The costal section is also generally depressed, the breadth to height ratio varying from 1·34 to 1·00. The whorl section becomes relatively less depressed towards the adult aperture, in association with a decline in ornament. The greatest breadth is at the inner ventrolateral tubercle, when present.

Ornament is variably developed, tending to become stronger as the whorl breadth to height ratio (*Wb* : *Wh*) increases.

The smallest individual we have seen (OUM K4429; Fig. 28) shows the early stages of ornament at a diameter of 4 mm, with sparse, broad ribs bearing relatively massive, conical inner ventrolateral tubercles and clavate outer ventrolateral and siphonal tubercles. Our other material shows the ornament from 12 mm onwards. On the phragmocone there are 17–19 ribs per whorl. Nine variably-developed umbilical bullae are borne at the umbilical shoulder; from these arise one or two strong to weak, broad, rounded, radial to prorsiradiate straight ribs, whilst shorter intercalated ribs arise low on the flanks, one or rarely two such ribs being intercalated between the bullate ribs or groups or ribs.

Virtually all ribs bear spinose to conical inner ventrolateral tubercles which are of equal development on both primary and intercalated ribs. Only rarely does a short rib lack such a tubercle, although the strength of tubercles varies greatly. From the inner ventrolateral tubercles the ribs strengthen and broaden, passing somewhat forwards across the ventrolateral shoulder to well-marked clavate outer ventrolateral tubercles, between which a lower, broader rib passes straight across the venter, bearing a clavate siphonal tubercle of similar size and shape to the outer ventrolateral. There is wide variation in the relative dominance of ribbing over tuberculation in our material, some specimens showing very delicate flank ribs and bullae, although all show strong ventrolateral ornament (compare Fig. 17a–b and Fig. 15a–b).

Modification of body chamber ornament associated with maturity is similar in both macroconchs, maturing between 30 and 37 mm, and microconchs, maturing between 20 to 27 mm. Ornament on the earliest parts of the body chamber resembles that of the phragmocone. Towards the aperture, however, the whorl section becomes less depressed, the umbilical bullae and flank ribs decline markedly (Figs 16b, 17b) whilst ventrolateral and ventral ribbing becomes stronger and more crowded and is projected into a distinctive tongue-shaped fold; the ventrolateral tubercles decline markedly (Fig. 15a).

The suture (Fig. 2A–B) is of basic *Protacanthoceras* type, with a deep E, broad bifid L and smaller bifid U_2. E/L is large and bifid, L/U_2 smaller, but also bifid. There is a series of small rather simple auxiliaries.

DIMENSIONS. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
OUM K4432	25·3 (100)	11·4 (45)	11·4 (45)	1·0	5·0 (20)
BM(NH) C81924	34·5 (100)	15·0 (43)	15·2 (44)	0·99	7·9 (23)
BM(NH) C81904 at c	—	16·0	11·9	1·34	—
Ic	—	14·4	10·2	1·41	—
BM(NH) C81908 at c	22 (100)	11·9 (54)	10·2 (46)	1·16	4·5 (20)
Ic	22 (100)	10·2 (46)	8·7 (39)	1·17	—
BM(NH) C74796 at c	27·3 (100)	14·5 (53)	12·8 (47)	1·13	6·8 (25)
Ic	27·3 (100)	12·2 (45)	11·7 (42)	1·04	—
OUM K4427	37·2 (100)	17·2 (46)	15·4 (41)	1·11	8·9 (24)
OUM K4436	25·0 (100)	11·5 (46)	11·3 (45)	1·01	6·7 (26·8)
BM(NH) C9424	24·3 (100)	11·3 (46)	10·5 (43)	1·07	4·6 (19)

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
BM(NH) C9563	28·0 (100)	13·1 (47)	12·5 (45)	1·04	7·5 (27)
BM(NH) C72923	20·5 (100)	—	8·9 (43)	—	4·1 (20)
BM(NH) C72924	22·5 (100)	12·9 (57)	10·5 (46)	1·22	5·4 (24)
BM(NH) C72911	27·5 (100)	12·9 (46)	12·5 (45)	1·03	5·6 (20)

DISCUSSION. The holotype of *P. tuberculatum tuberculatum* is crushed and distorted, but nevertheless recognizable as either a juvenile or the phragmocone of a macroconch. Our uncrushed material shows the very distinctive ornament and proportions of the subspecies which of all *Protacanthoceras* most closely resembles the ancestral *Acanthoceras*. Indeed, juveniles pose difficulties of separation, but the following features of *P. t. tuberculatum* are distinctive: flattened whorls, strong, equal, clavate ventrolateral tubercles and, when preserved, the adult body chamber modifications.

The subspecies is readily distinguishable from most other *Protacanthoceras*, most closely resembling *P. tuberculatum cyclopeum* subsp. nov. (p. 80). That subspecies, which comes from a higher stratigraphic horizon than that of the acme of *P. t. tuberculatum*, is larger, has much blunter, coarser ornament throughout and inner ventrolateral tubercles which are strongly developed on long ribs and weakly developed on short ribs, in contrast to the far more uniform development of *P. t. tuberculatum*.

Macroconchs and microconchs of *P. tuberculatum devonense* subsp. nov. (p. 76) are significantly smaller than their equivalents in *P. t. tuberculatum*, much more coarsely ribbed and tuberculate (generally around 12 ribs per whorl rather than 17–19), and have umbilical bullae which are stronger than the inner ventrolateral, the reverse of the situation in *P. t. tuberculatum*. Many specimens of *P. t. devonense* show irregularities in ventral ribbing and a highly distinctive rounding of the venter which is transitional towards *Protacanthoceras proteus* sp. nov. (p. 95).

P. t. tuberculatum differs from *P. tuberculatum mite* subsp. nov. (below) in having strong rather than weak tubercles, broad straight rather than delicate flexuous or sometimes effaced flank ribs and stronger and far more clavate ventral tuberculation.

OCCURRENCE. *P. tuberculatum tuberculatum* is the most widespread *Protacanthoceras* in the Chalk Basement Beds of south-west England, first appearing as a great rarity high in the *Turrilites costatus* Zone, commonest in the *Acanthoceras jukesbrownei* Zone of the area and also occurring in the basal *naviculare* Zone Basement Bed fauna at Askerswell (Dorset). A few specimens are known from Division C of the Cenomanian Limestone of the coast; the two specimens from Wilmington are from a local equivalent of Division B of the Cenomanian Limestone and are of Middle Cenomanian age. The species is also known from the chalk facies of south-east England, being recorded from *costatus*, *acutus* and *jukesbrownei* Zones as a great rarity (Kennedy 1969 : 469, 487, 500, 538 and 542, as *Protacanthoceras* spp.). A *Protacanthoceras* from 'Ventnor' (BM(NH) 98206) may belong here, whilst some records of *Protacanthoceras compressum* from Wiltshire and Surrey (Wright & Wright 1951) may refer to this species. French records include the holotype from Provence and a specimen from the Rouen Fossil Bed figured by Kennedy & Hancock (1970 : pl. 97, figs 4a–b; BM(NH) C74796).

Protacanthoceras tuberculatum Thomel ***mite*** subsp. nov.
(Figs 3, 18–19)

1971 *Protacanthoceras* spp. nov. Kennedy : 103 (*pars*).

TYPES. The **holotype**, BM(NH) C81925, is a macroconch from the remanié phosphatic fauna of the Chalk Basement Bed at Ringstead (*Acanthoceras jukesbrownei* Zone). Paratypes BM(NH) C81926–8 are from the same horizon and locality and C81929–30 from the slightly older *Turrilites acutus* Zone Chalk Basement Bed at Lulworth Cove, Dorset; C81931–2 are from the *Acanthoceras jukesbrownei* Zone, Osmington landslips; C81933 (*ex* Mottram collection) is of the same age and from the same horizon below White Nothe; OUM K4425 is from the basal *Calycoceras naviculare* Zone Chalk Basement Bed at Askerswell.

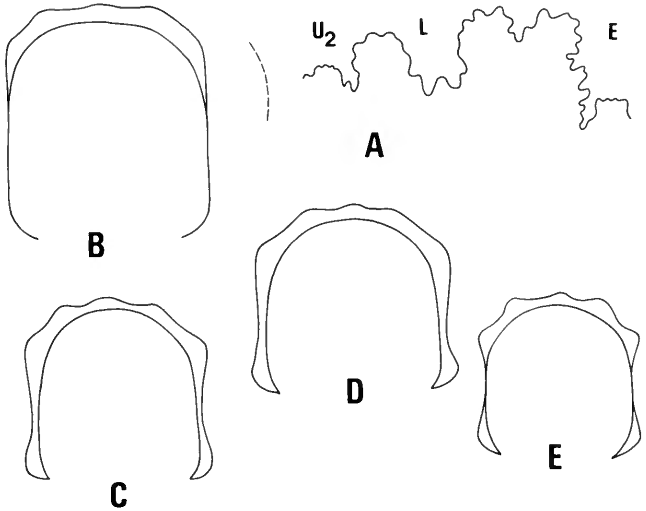


Fig. 3 *Protacanthoceras tuberculatum* Thomel *mite* subsp. nov. 3A, suture of BM(NH) C81926, × 4. 3B, whorl section of BM(NH) C81925 at aperture of body chamber, × 2. 3C, whorl section of BM(NH) C81929, × 2. 3D, whorl section of OUM K4425, × 2. 3E, whorl section of BM(NH) C81926, × 2.

NAME. Latin *mitis*, mild, in reference to the difference in ornament between it and *P. t. tuberculatum*.

DIAGNOSIS. A subspecies of *Protacanthoceras tuberculatum* characterized by weak tuberculation, flank ribbing weak and slightly flexed or effaced and ventral tubercles only weakly clavate.

DESCRIPTION. This subspecies shows a similar size dimorphism to *P. t. tuberculatum*, with macroconchs adult at around 27–30 mm and microconchs generally at less than 25 mm. The umbilicus is generally smaller, 20% of diameter in juveniles, increasing to only 22% in mature individuals. The umbilical wall is vertical and rounded, with an abruptly rounded shoulder, the sides are flattened and subparallel in intercostal section, with the greatest breadth around mid-flank; the venter is broadly rounded. The costal section is more angular, with the greatest breadth at the umbilical bullae or inner ventrolateral tubercles. Relative proportions change throughout ontogeny, with the whorl breadth to height ratio (*Wb* : *Wh*) declining from 1·19 in specimens of 4–8 mm diameter to slightly less than unity in adults.

Juveniles have approximately 20 ribs per whorl, increasing to an estimated 22–24 at maturity. The arrangement of ribs and tubercles is as in *P. t. tuberculatum* but much feebler, the umbilical bullae consistently weaker, the ribs low, effaced at mid-flank and sometimes flexuous. The inner ventrolateral tubercles are generally weak, and always weaker than in the *P. t. tuberculatum*, as are the ventral ribs and tubercles. The latter are much less prominent, delicate and less elongated radially.

Modifications of the later parts of the mature body chamber are as in *P. t. tuberculatum* but with distinct flexure of ribbing in some individuals.

The suture is simpler than that of the nominate form, as shown in Fig. 3A.

DIMENSIONS. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
BM(NH) C81926	18·9 (100)	9·8 (52)	8·2 (43)	1·19	3·7 (20)
OUM K4425	22·4 (100)	10·5 (47)	10·3 (46)	1·02	4·4 (20)
BM(NH) C81929	—	11·5	12·1	0·95	—
	—	10·5	10·3	1·02	—
BM(NH) C81927	26·5 (100)	11·9 (45)	11·8 (45)	1·0	5·3 (21)

DISCUSSION. Differences between *P. tuberculatum tuberculatum* and *P. t. mite* are brought out in the description. The subspecies is intermediate between *tuberculatum sensu stricto* and *P. arkelli* sp. nov. (p. 82), to which we believe it led by way of *arkelli verrucosum* subsp. nov. (p. 86); *mite* and *verrucosum* can be distinguished by virtue of the delicate but well-defined flank ribs of the latter, combined with delicate, barely clavate outer ventrolateral and siphonal tubercles and a stronger projection of ribs on the ventrolateral shoulder.

OCCURRENCE. Scarce in the *acutus*, *jukesbrownei* and basal *naviculare* Zone faunas of the Chalk Basement Bed in Dorset.

Protacanthoceras tuberculatum devonense subsp. nov.
(Figs 13, 36–40, 52)

1896 *Ammonites hippocastanus* var. *compressus* Jukes-Browne, *in* Jukes-Browne & Hill : 157 (*pars*); pl. 5, figs 3, 3a.
1970 *Protacanthoceras* spp. Kennedy : 660, 664, 666 (*pars*).
1971 *Protacanthoceras* sp. nov. Kennedy : 99 (*pars*); pl. 32, figs 4a–c.
1971 *Protacanthoceras* spp. nov. Kennedy: 103 (*pars*).

TYPES. The **holotype**, BM(NH) C81934, is a microconch from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone, Whitlands; high *Calycoceras naviculare* Zone. Paratypes, from the same horizon and locality: BM(NH) C81935–7 and OUM K4461–72; in the Pinhay Humble Point–Whitlands Bay area: BM(NH) C7282, C73051, C73060, C81938–52, C81896, C81898 (labelled 'Chardstock' but clearly from the coast); GSM 53483, one of the syntypes of Jukes-Browne's *Ammonites hippocastanus* var. *compressus*; BM(NH) C81853 from the same horizon at the White Hart Sandpit, Wilmington; GSM Zn 9089, BM(NH) C81954 from Hooken Beach, Devon; C81955–6 from Hooken Cliff, Devon; numerous specimens in the O. H. Bayliss collection, from Shapwick Grange, Devon.

NAME. From the county of Devon.

DIAGNOSIS. A rectangular-whorled, depressed, coarsely ribbed *Protacanthoceras* with 12–15 alternately long and short ribs per whorl. Long ribs with strong conical umbilical tubercles, all ribs with strong conical inner ventrolateral tubercles and strongly clavate, closely-spaced, equal outer ventrolateral and siphonal tubercles.

DESCRIPTION. The coiling is involute on the inner whorls, the umbilicus 16–20% of the diameter, with a marked uncoiling of the body chamber to give a more evolute appearance at maturity, the umbilicus widening to 25% of the diameter (Fig. 42).

Figs 4–5 *Ammonites tropicus* Stoliczka, × 1. 4a–c, BM(NH) C12590, *ex* F. A. Bather collection, from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone, Beer Head, Devon. 5a–b, copies of the original figures (Stoliczka 1865 : pl. 34, figs 2, 2a) of the holotype, from the Utatur Group near Odium, southern India.

Fig. 6a–b *Thomelites* aff. *sornayi* (Thomel), OUM K4443, *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone, Humble Point, Devon. × 1.

Fig. 7 *Calycoceras* (*Gentoniceras*) *gentoni* (Brongniart), OUM K4479, Chalk Basement Bed, *Turrilites acutus* Zone, Snowdon Hill, Chard, Somerset. × 1.

Fig. 8a–b *Protacanthoceras tuberculatum tuberculatum* Thomel, OUM K4426, Chalk Basement Bed, *Calycoceras naviculare* Zone, Askerswell, Dorset. × 2.

Fig. 9a–b *Pseudocalycoceras harpax* (Stoliczka) *ankomakaensis* Collignon, Ankomaka II (Manera), Madagascar. Original of Collignon 1964 : pl. 373, fig. 1621 (photographs supplied by W. A. Cobban). × 1.

Fig. 10a–b *Nigericeras costatum* Barber, BM(NH) C47700, Lower Turonian, Pindiga, Nigeria. × 1.

Figs 11–12 *Acanthoceras rhotomagense* (Brongniart), two juveniles from the *Turrilites costatus* Zone, base of Craie de Théligny, Sarthe, France (P. Juignet collection). × 2.


4a


4b


4c


6a


6b


7


8a


8b


5a


5b

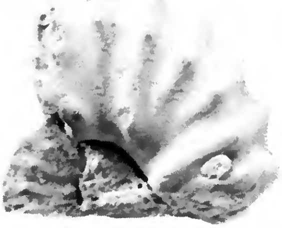

9a


9b


10a


10b


11a


11b


12a


12b

Microconchs and macroconchs are essentially similar in ornament, with a size ratio of between 1 : 1·25 and 1 : 1·40. The umbilicus is of moderate depth, with a vertical, rounded wall and abruptly rounded shoulder. The whorls are depressed; the breadth to height ratio in intercostal section varies between 1·25 and 1·48, with the greatest breadth low on the flattened flanks and the venter flattened with broadly rounded shoulders. The breadth to height ratio (*Wb* : *Wh*) in the trapezoidal costal section varies from 1·19 to 1·48, with the greatest breadth at the umbilical tubercles. The ornament consists of 12–15 ribs per whorl, weaker on the phragmocone than on the body chamber and alternately long and short. Long ribs arise at the umbilical shoulder, originating in variable umbilical bullae, generally 7–8 per whorl, relatively weak on the phragmocone but stronger on the body chamber. They give rise to single, well-differentiated ribs, stronger on the body chamber, recti- or slightly prorsiradiate, straight, with strong conical inner ventrolateral tubercles. Thence, the ribs strengthen and project markedly across the shoulder to strong clavate outer ventrolateral tubercles, connected across the venter by a broad subdued rib bearing a clavate siphonal tubercle. The ventral tubercles are closely spaced and generally equal.

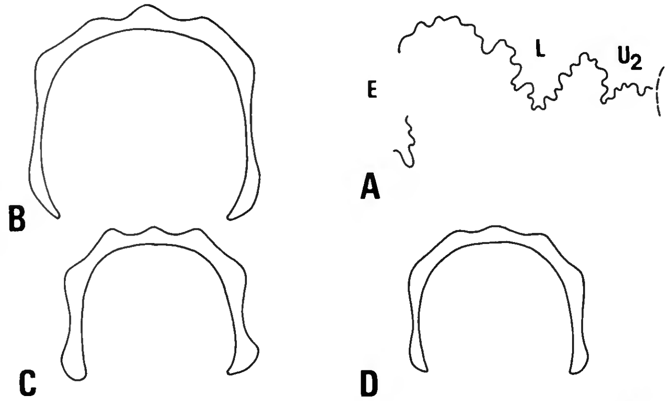


Fig. 13 *Protacanthoceras tuberculatum devonense* sp. nov. 13A, suture of BM(NH) C81935, × 4. 13B, whorl section of body chamber of BM(NH) C81936, × 2. 13C, whorl section of body chamber of BM(NH) C81935, × 2. 13D, whorl section of body chamber of BM(NH) C81934, × 2.

Most of the intercalated ribs arise low on the flank and may show a tenuous connection to an umbilical bulla. They are as strong as the major ribs and bear a similar complement of ventrolateral and siphonal tubercles. Some specimens also bear occasional intercalated ribs without inner ventrolateral tubercles.

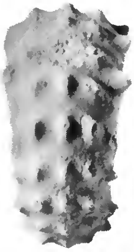
Figs 14–17 *Protacanthoceras tuberculatum tuberculatum* Thomel. 14a–b, a juvenile, BM(NH) C81908 from the *Acanthoceras jukesbrownei* Zone fauna of the Chalk Basement Bed, Osmington, Dorset. 15a–d, BM(NH) C81904, and 17a–b, BM(NH) C81924, both macroconchs, from the same horizon and locality. 16a–b, BM(NH) C81922, from the Middle Cenomanian equivalent of Bed B of the Cenomanian Limestone at the White Hart Sandpit, Wilmington, Devon.

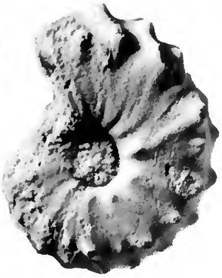
Figs 18–19 *Protacanthoceras tuberculatum mite* subsp. nov. 18a–c, BM(NH) C81929, a macroconch body chamber from the *Turrilites acutus* Zone fauna of the Chalk Basement Bed at Lulworth Cove, Dorset. 19a–c, **holotype** BM(NH) C81925, a macroconch from the *Acanthoceras jukesbrownei* Zone fauna of the Chalk Basement Bed, Ringstead Quarry, Dorset.

Figs 20–21 *Protacanthoceras asgeirri* sp. nov., both from the basal *Calycoceras naviculare* Zone fauna of the Chalk Basement Bed at Askerswell, Dorset. 20a–c, paratype, OUM K4434. 21a–d, **holotype,** OUM K4433.

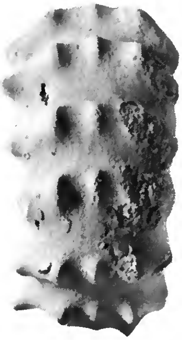
Fig. 22a–b *Protacanthoceras tuberculatum* Thomel. OUM K4439, the subspecifically indeterminate nucleus of an individual from the *Turrilites acutus* Zone fauna of the Chalk Basement Bed at Snowdon Hill, Chard, Somerset.

All figures are × 1·125.


14a


14b


15a

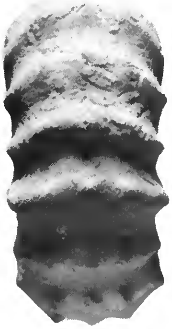

15b


15c


16a

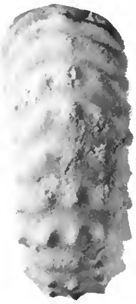

16b


15d


17a


17b


18a


18b


18c

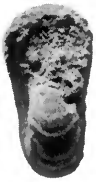

19a

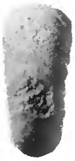

19b


19c


20a


20b


20c


21a


21b


21c


21d


22a


22b

The subspecies shows typical adult features, consisting of a decline in the umbilical bullae and a strengthening of the ventrolateral and ventral ribbing at the expense of the tubercles.

The suture is of basic rather simple *Protacanthoceras* type, with little-divided bifid elements (Fig. 13A).

Dimensions. Typical specimens are as follows; percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*	Ribs per whorl
BM(NH) C81934 at c	20·8 (100)	11·5 (55)	8·0 (38)	1·43	5·3 (25)	12
Ic	20·8 (100)	9·9 (48)	6·7 (32)	1·48	5·3 (25)	14
BM(NH) C81935 at c	17·9 (100)	10·5 (59)	7·1 (40)	1·48	4·2 (23)	14
Ic	17·9 (100)	8·9 (50)	6·6 (37)	1·35	4·2(23)	—
BM(NH) C81936 at c	25·0 (100)	12·8 (51)	10·8 (43)	1·19	5·0 (20)	7 (½ whorl)
Ic	25·0 (100)	11·5 (46)	9·2 (37)	1·25	5·0 (20)	—

Discussion. Typical *P. tuberculatum devonense* are readily separable from other forms such as *P. bunburianum* and *P. tuberculatum tuberculatum* by their coarse, sparse ribs and strong tuberculation. Some variants (e.g. Figs 36, 52) show rather subdued ornament and a rounding of the venter which recall *Protacanthoceras proteus proteus* and *P. p. baylissi*, but all possess distinctive ventrolateral and ventral tuberculation throughout ontogeny and are easily recognizable.

P. t. devonense originated in *P. t. tuberculatum* by decrease in size, coarsening of ribbing and tuberculation and a great reduction in rib density.

Occurrence. This subspecies is widespread in the *Calycoceras naviculare* Zone faunas of Division C of the Cenomanian Limestone and its equivalents in Devon.

Protacanthoceras tuberculatum cyclopeum subsp. nov.

(Figs 34, 45)

Types. The **holotype** is BM(NH) C81299, formerly Col. O. H. Bayliss' coll. no. 193; a paratype remains in the same collection. Both are from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone, high *Calycoceras naviculare* Zone, Shapwick Grange, Devon.

Name. Latin *cyclopeus*, in allusion to the size and locality (Shapwick = sheep farm) of the holotype; cyclopses were giants and the best known, Polyphemus, kept sheep.

Diagnosis. A large (52 mm diameter) subspecies of *P. tuberculatum* with 16 broad, blunt, alternately long and short ribs per whorl. Long ribs bear strong conical umbilical bullae; all ribs bear prominent inner ventrolateral tubercles which are stronger on long ribs than intercalated ribs, whilst ventral tuberculation declines and strong ventral chevron-ribbing develops on the apertural parts of the mature body chamber.

Description. The holotype is a well-preserved, phosphatic internal mould, with just under two-thirds of a whorl of body chamber. The last few septa are crowded and overlap, suggesting the specimen to be a mature adult.

The coiling is evolute, becoming increasingly so on the outer whorl, where the umbilical seam of the body chamber egresses somewhat so that, at the aperture, *c.* 40% of the previous whorl is covered. The umbilicus is of moderate size (*c.* 30% of diameter) with a rounded wall of moderate elevation and an abruptly rounded shoulder. The whorl section is depressed. The flanks are flat intercostally, with the maximum breadth on the inner third of the whorl side. The outer third of the flanks converge somewhat; the ventrolateral shoulder is rounded and the venter somewhat flattened. The costal section is more angular, with the greatest breadth on the phragmocone at the spinose lower ventrolateral tubercle and on the body chamber at the umbilical bulla.

There are eight strong, conical to bullate umbilical tubercles per whorl, positioned on the umbilical shoulder and extending to the umbilical seam as broad, rounded, subdued swellings. From the bullae arise single, broad, relatively low, rounded and more or less radial ribs which pass straight across the flanks to connect to prominent subspinose inner ventrolateral tubercles. These are very prominent on the earlier portions of the outer whorl, become less prominent and

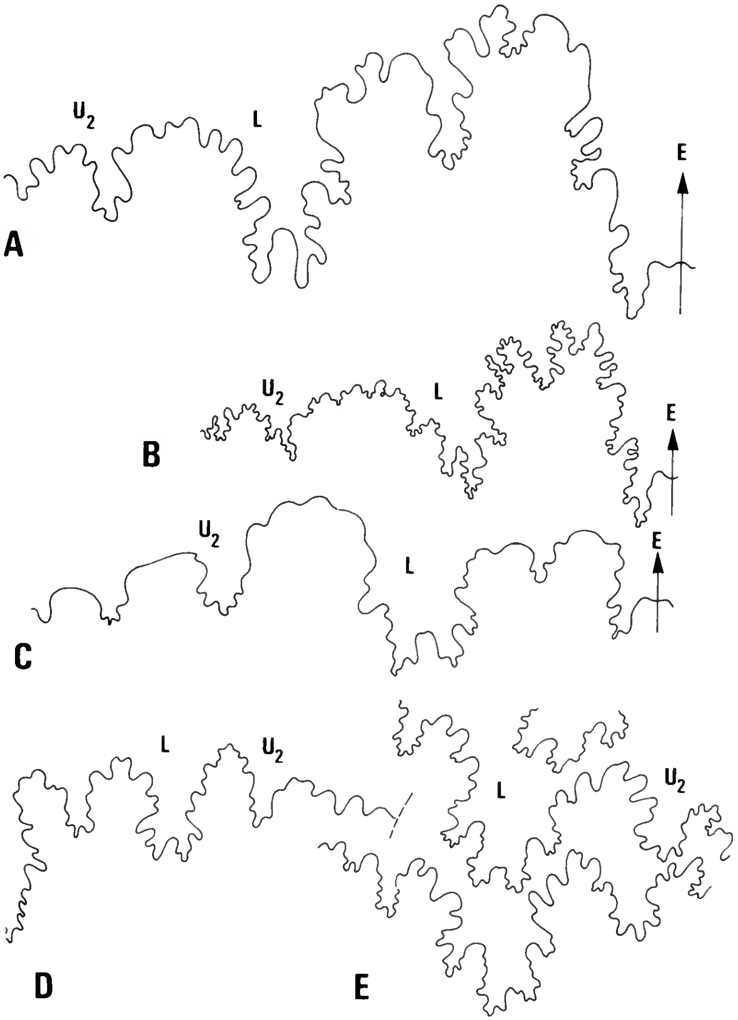


Fig. 23 Suture lines of selected mature acanthoceratacean compared. 23A, *Acanthoceras rhotomagense* (Brongniart). P. Juignet coll. no. 1-161, from the phosphatic *Turrilites costatus* Zone fauna at the base of the Craie de Théligny, Sarthe, France, × 4. 23B, *Calycoceras naviculare* (Mantell). OUM K4442, *Calycoceras naviculare* Zone fauna of Division C of the Cenomanian Limestone, Humble Point, Devon, × 2. 23C, *Metoicoceras geslinianum* (d'Orbigny). OUM KT22, *Sciponoceras gracile* Zone, Eagle Ford Shale, Dallas/Fort Worth, Texas, × 2. 23D, *Pseudocalycoceras* aff. *dentonense* (Moreman). *Sciponoceras gracile* Zone, Ikushumbets, Hokkaido (modified after Matsumoto & Kawano 1975: text-fig. 3), × 2. 23E, *Thomelites* aff. *sornayi* (Thomel). OUM K4443, *Calycoceras naviculare* Zone, Division C of the Cenomanian Limestone, Humble Point, Devon, × 2.

subdued, with a tendency towards clavation on the early parts of the body chamber, declining towards the aperture. From them a broad rounded, straight rib passes forwards across the ventrolateral shoulder to strong clavate siphonal tubercles, sharp at the smallest diameters visible but declining on the body chamber and merging with the inner ventrolateral tubercles into strong transverse and elevated ribs. Low broad ribs extend across the venter and bear a strong clavate siphonal tubercle, somewhat more elongate than the outer ventrolateral. This tubercle declines towards the body chamber but retains its identity to the aperture. Shorter ribs, arising low on the flank and lacking umbilical bullae (although some connect tenuously to the bulla of the long ribs next to them), alternate regularly with the longer ribs. These intercalated ribs bear the same complement of ventrolateral and ventral tubercles as the long ribs, but the inner ventrolateral tubercles are always weaker than the corresponding ones on the long ribs.

Modifications of the adult body chamber include a sudden decline of umbilical bullae, weakening and crowding of ribs, development of striae and a fusion of inner and outer ventrolateral tubercles into obliquely placed bar-like ribs, which, with broadening and accentuation of the ventral ribbing, give the venter a scale-like appearance.

The suture line is quite deeply subdivided for the genus, with a deep and relatively narrow E, a deep, narrow, asymmetrically bifid L and a much smaller U_2. E/L is broad and asymmetrically bifid; L/U_2 is symmetrically bifid.

DIMENSIONS. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
BM(NH) C81299	51·9 (100)	23·2 (45)	20·9 (40)	1·11	15·3 (29)
at c	42·5 (100)	22·8 (54)	17·8 (42)	1·28	12·1 (28)
Ic	42 (100)	20·7 (49)	15·8 (37)	1·31	12·1 (28)
at c	38·0 (100)	15·6 (41)	11·0 (29)	1·42	11·5 (30)
Ic	38·0 (100)	11·9 (31)	9·4 (25)	1·27	11·5 (30)

DISCUSSION. *P. tuberculatum cyclopeum* is the largest form of *Protacanthoceras* we have seen. It is readily differentiated from its contemporaries, in that *P. proteus proteus* and *P. p. baylissi* are round-whorled, with quite distinctive changes in ornament, whilst *P. bunburianum* and its variants have a compressed whorl section and finer ornament, and are much smaller.

P. t. cyclopeum is like an extremely large *P. t. tuberculatum* Thomel (Figs 14–17), but is separable not only because of its size, well outside that of populations of the latter before us, but also by having fewer ribs and coarser ornament; furthermore in *P. t. tuberculatum* tubercles are similar on all ribs, whilst in *P. t. cyclopeum* ribs are generally sharply differentiated from much flatter flanks.

OCCURRENCE. As for types.

Protacanthoceras arkelli sp. nov.

TYPES. The **holotype**, BM(NH) C81957, is a macroconch from the remanié phosphatic fauna of the Chalk Basement Bed, Ringstead Quarry, *Acanthoceras jukesbrownei* Zone. Paratypes, all microconchs, are BM(NH) C81958–9 from the same horizon and locality, and C81960–1, from the same horizon in the Osmington landslips.

NAME. After the late W. J. Arkell, at whose Ringstead house the collector of the holotype (C.W.W.) was staying at the time.

Figs 24–26 *Protacanthoceras arkelli arkelli* subsp. nov., all from the *Acanthoceras jukesbrownei* Zone fauna of the Chalk Basement Bed at Ringstead, Dorset. 24, BM(NH) C81961, showing details of the inner whorls, × 1·5. 25a–d, **holotype,** BM(NH) C81957, a macroconch, × 1·125. 26a–b, BM(NH) C81958, microconch paratype, × 1·125.

Fig. 27a–c *Protacanthoceras arkelli verrucosum* subsp. nov. **Holotype,** BM(NH) C81962, from the *Acanthoceras jukesbrownei* Zone fauna of the Chalk Basement Bed at Ringstead Quarry, Dorset. × 1·125.

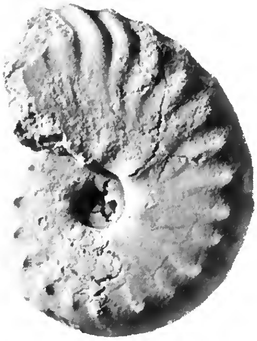
Fig. 28 *Protacanthoceras tuberculatum* Thomel, subspecies undetermined. Inner whorls of OUM K4429, from the basal *Calycoceras naviculare* Zone of Askerswell, Dorset. × 1·5.

Figs 29–33 *Protacanthoceras bunburianum* (Sharpe). Figs 29–30, 32–33 from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone, Humble Point, Devon. Juvenile microconchs: 29a–b, OUM K4445, and 30a–b, BM(NH) C81968. Macroconchs: 32a–d, BM(NH) C81969, and 33a–b, BM(NH) C81965. Fig. 31a–d, holotype, BM(NH) 50155, figd Sharpe 1853 : pl. 9, figs 3a–c. An adult macroconch, said to be from Chardstock, Devon, but more likely to be from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone of the Devon Coast (see Kennedy 1971 : 98 for discussion). All × 1·125.

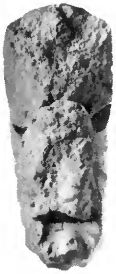

24


25a

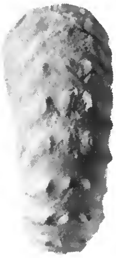

25b

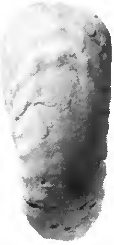

25c


25d


27a


27b


27c


26a


26b


29a


29b


28


30a


30b

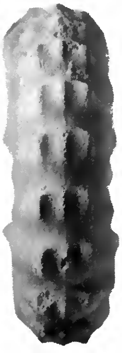

31a


31b


31c


31d


32a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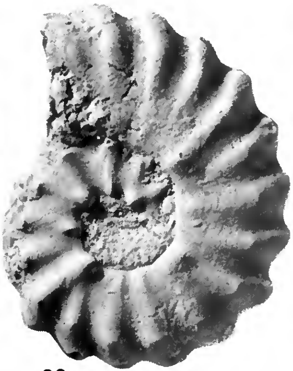
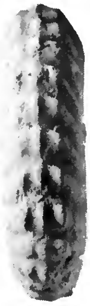

32c


32d


33a


33b

Diagnosis. An involute, compressed *Protacanthoceras* characterized by very weak to obsolete flank ribs and delicate lateral and ventral tuberculation, which latter may disappear during middle growth. The body chamber develops well-defined lateral and ventral ribbing only towards the adult apertural margin.

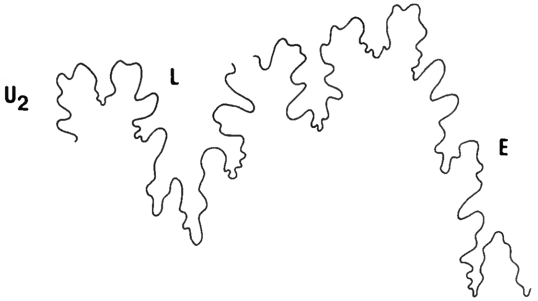


Fig. 34 *Protacanthoceras tuberculatum cyclopeum* subsp. nov. Suture of holotype, BM(NH) C81299 (OB 193), × 4.

Protacanthoceras arkelli arkelli subsp. nov.
(Figs 24–26, 35A–H)

? 1970 *Protacanthoceras* sp. Kennedy & Hancock: pl. 97, figs 7a–b.

Types. As above.

Diagnosis. An involute, compressed subspecies of *P. arkelli* with an initial stage characterized by delicate umbilical bullae which give rise to groups of delicate falcoid ribs bearing tiny inner and outer ventrolateral and siphonal tubercles, a second growth stage in which outer ventrolateral and siphonal tubercles disappear, their place being taken by spiral striae, and a third stage in which distinct crowded ribs, stronger than those of the earlier stage, reappear bearing weak umbilical bullae and well-developed ventrolateral and siphonal tubercles. On the latter part of the body chamber the ventral ribs are strong and the outer ventrolateral and siphonal clavi virtually disappear. Microconch and macroconch are essentially similar, with a size ratio of 1 : 1·3.

Description. The holotype is a well-preserved phosphatic internal mould of a macroconch, retaining traces of iridescent phosphatized shell. The last few sutures are crowded, suggesting the specimen is adult, whilst the last two-thirds of the outer whorl are body chamber, showing modifications indicating the specimen to be a mature adult.

Two specimens, C81959 and C81961, show nuclei at diameters of 4–6 mm (Figs 24, 34G, H). At this stage, the coiling is moderately involute, with a small, relatively deep umbilicus and a depressed reniform whorl section.

The flanks bear low, broad, sparse ribs, *c*. 10 per whorl, strengthened into bullate tubercles at the umbilical shoulder and terminating in relatively strong conical ventrolateral tubercles. The venter of C81959 is smooth and completely lacks ribs; on the inner whorls of C81961 there are periodic broad chevron-like constrictions at intervals of two per half-whorl (Fig. 24); behind one of these constrictions there is a low rib. *P. arkelli arkelli* undergoes distinctive morphological changes during middle and late growth. Up to 15–20 mm, the coiling is involute, with over half the previous whorl being covered. The umbilicus is small, < 20% of diameter, of moderate depth with a flattened vertical wall and an abruptly rounded shoulder. The whorls are compressed and flat-sided (breadth to height ratio *Wb* : *Wh c*. 0·9) with the greatest breadth at the umbilical bulla. The sides are more or less parallel and the venter broad and strongly convex. Ornament consists of 7–8 weak, comma-shaped umbilical bullae, from which arise low, weak, gently flexed ribs or striae in groups of two or three; occasional shorter intercalated ribs are also present low on the flanks as mere striae. All ribs bear small, delicate, sharp, conical inner ventrolateral tubercles at the junction of the flattened sides and the arched venter. These give rise to a much broader, flat-topped rib which passes forwards across the ventrolateral tubercles. These in turn are connected by a very subdued transverse rib, which bears a small but clearly differentiated and somewhat clavate siphonal tubercle.

From 15–20 mm to the early parts of the body chamber the proportions, coiling and whorl sections remain unchanged. However, the flank ribs become subdued, the inner ventrolateral tubercles are slightly weakened and virtually all of the remaining ventral ornament becomes suddenly weaker, leaving a smooth rounded venter (Figs 25b, 26a) ornamented by delicate transverse and low spiral ridges and striae, the former corresponding in position to outer ventrolateral and siphonal tubercles. Where transverse striae and spiral ridges intersect, there is the merest suggestion of an incipient tubercle.

On the later portions of body chamber there is a revival of ornament that is as abrupt as the previous decline. Umbilical bullae give rise to two or three faint, low, broad ribs, with occasional additional ribs intercalated. Inner ventrolateral tubercles become stronger and are joined by a strong, forward-directed rib across the ventrolateral shoulder to markedly clavate outer ventrolateral tubercles. A low, broad rib extends across the venter (Figs 25d, 26a) and bears a distinct to subdued siphonal tubercle. Towards the aperture, ventral and ventrolateral ribbing becomes stronger and all tuberculation declines, to give the distinct *Protacanthoceras* ventral ribbing (Fig. 25a).

The sutures (Fig. 35A, B) are of the basic, rather simple *Protacanthoceras* type, with a deep and rather narrow E, bifid and relatively broader L and a very small U_2. E/L is asymmetrically bifid,

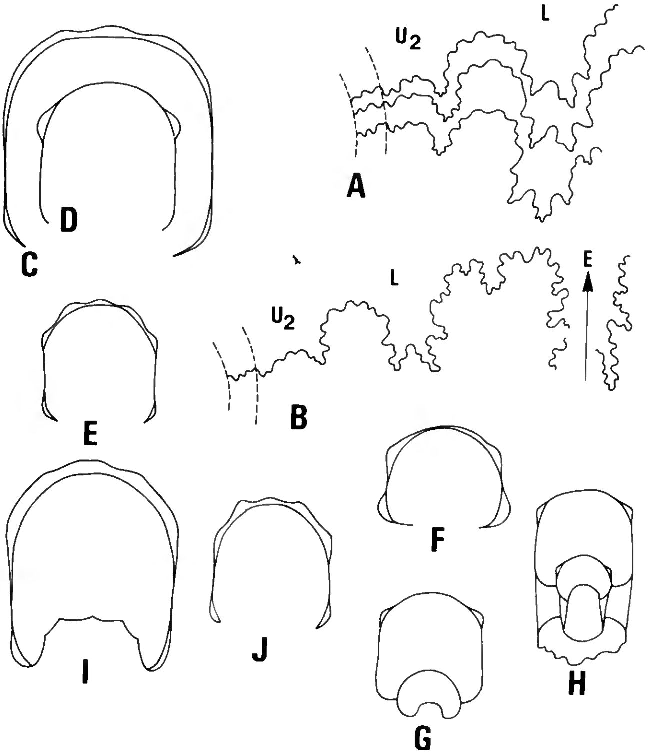


Fig. 35 *Protacanthoceras arkelli* sp. nov. 35A–H, *Protacanthoceras arkelli arkelli*. 35A, adult sutures of BM(NH) C81957, × 4. 35B, suture of BM(NH) C81958, × 4. 35C, D, whorl sections of BM(NH) C81957 at aperture and at tuberculate stage, × 2. 35E, whorl section of BM(NH) C81958 at tuberculate stage, × 2. 35F, whorl section during early development shown by BM(NH) C81959, × 2. 35G, H, whorl sections during early development as shown by BM(NH) C81961, × 2. 35I–J, *Protacanthoceras arkelli verrucosum* subsp. nov. Whorl sections of BM(NH) C81962, × 2.

L/U_2 is very little divided, whilst there is a series of small, smoothly rounded frills on the suspensive lobe.

DIMENSIONS. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
BM(NH) C81957	28·2 (100)	11·8 (42)	12·5 (44)	0·94	5·5 (19·5)
at	21·2 (100)	9·1 (43)	10·6 (50)	0·89	4·1 (19·3)
BM(NH) C81958	22·8 (100)	9·9 (43)	10·5 (46)	0·94	4·3 (19·0)

DISCUSSION. The very distinctive ontogenetic changes shown by *P. arkelli arkelli*, and its weak flank ornament, compressed whorl section and rounded venter serve to distinguish it from all other described *Protacanthoceras* species. It differs from *P. arkelli verrucosum* subsp. nov. (below) in the presence of an intermediate growth stage during which ventral ornament declines; *verrucosum* retains a full complement of tubercles throughout ontogeny.

There is very striking resemblance between the very earliest stages of *Protacanthoceras tegulicium* (p. 88) and the second growth stage of *P. arkelli arkelli*, both showing a smooth arched venter, distinct tubercles at the juncture of venter and flank and distinctive flank ribs (compare Fig. 44 with 24). As discussed below, this may be the key to the origin of the otherwise very distinctive *P. tegulicium*.

OCCURRENCE. As for type material. The specimen of *Protacanthoceras* from the Rouen Fossil Bed figured by Kennedy & Hancock (1970 : pl. 97, figs 7a–b) may be a poorly preserved *P. arkelli arkelli*.

Protacanthoceras arkelli verrucosum subsp. nov.

(Figs 27, 35I, J)

TYPES. The **holotype,** BM(NH) C81962, is a microconch (?), from the remanié phosphatic fauna of the Chalk Basement, *Acanthoceras jukesbrownei* Zone, Ringstead Quarry. Paratype OUM K4440 is from the *Turrilites acutus* Zone fauna of the Chalk Basement Bed at Snowdon Hill, Chard.

NAME. In reference to the subspecies' distinctive delicate tubercles. One meaning of *verruca* is an excrescence on a precious stone (Pliny).

DIAGNOSIS. A subspecies of *Protacanthoceras arkelli* in which inner and outer ventrolateral and siphonal tubercles with associated ribs are retained throughout development, declining only at the mature aperture.

DESCRIPTION. The holotype is a phosphatic internal mould, retaining traces of iridescent phosphatized shell. It consists of all the body chamber and a nucleus (which is poorly visible). Changes in ornament on the body chamber suggest that the specimen is adult.

Figs 36–40 *Protacanthoceras tuberculatum devonense* subsp. nov., all from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone. Figs 36, 37 and 39 are from Humble Point, Fig. 38 from Shapwick Grange and Fig. 40 from Pinhay Bay, all in Devon. 36a–b, BM(NH) C81937, and 37a–b, BM(NH) C81935, microconchs. 38a–b, BM(NH) C81302 (*ex* O. H. Bayliss coll. no. OB 271), a microconch transitional to *P. proteus baylissi* subsp. nov. 39a–b, BM(NH) C81936, a macroconch paratype. 40a–c, **holotype.** BM(NH) C81934, a microconch.

Figs 41–43 *Protacanthoceras bunburianum* (Sharpe), all from the *Calycoceras naviculare* Zone fauna of Division C of the Cenomanian Limestone. Fig. 41 from near Whitlands, Fig. 42 from Hooken Beach, and Fig. 43 from Humble Point, all in Devon. 41a–b, BM(NH) C81992, and 42a–b, BM(NH) C81999, both microconchs. 43a–c, BM(NH) C81967, a macroconch.

Fig. 44a–c *Protacanthoceras tegulicium* sp. nov. **Holotype,** OUM K4435, from the basal *Calycoceras naviculare* Zone fauna of the Chalk Basement Bed at Askerswell, Dorset.

Fig. 45a–c *Protacanthoceras tuberculatum cyclopeum* subsp. nov. **Holotype,** BM(NH) C81299 (*ex* O. H. Bayliss coll. no. OB 193), from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone at Shapwick Grange, Devon.

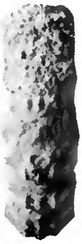
All figures are × 1·125.

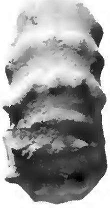

36a


41a


41b


42a

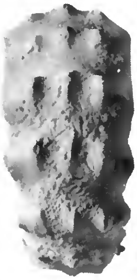

42b


37a


37b

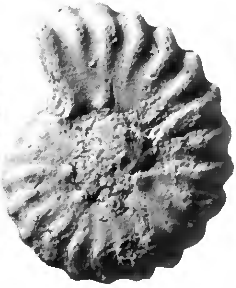

36b

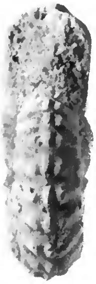

38a

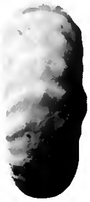

39a


39b


43a


43b


43c


38b


44a


44b

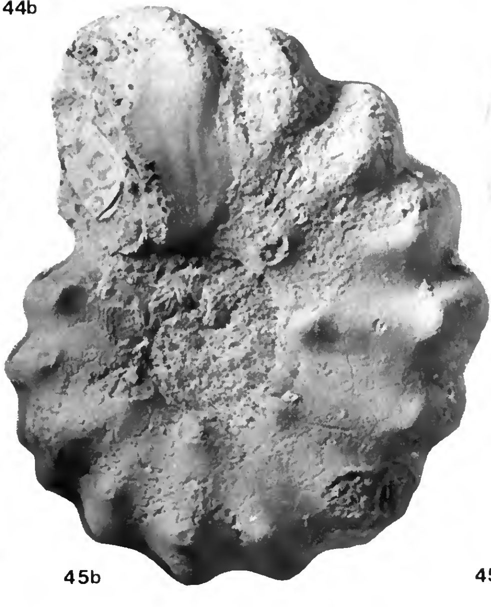

44c


40a


40b


40c


45a


45b


45c

The coiling is involute, over half the previous whorl being covered. The umbilicus is small (19% of diameter) and of moderate depth. The umbilical wall is vertical, rounded, with an abruptly rounded shoulder. The whorl sides are flattened; the greatest breadth is at the umbilical bulla at the beginning of the body chamber but towards the ventrolateral shoulder at the aperture. The venter is broadly rounded in intercostal but more flattened in costal section (Fig. 35J). There are five small umbilical bullae on the half whorl of body chamber. From these arise pairs of gently flexed, radial ribs, very subdued at the middle of the flank, being sometimes reduced to mere striae, but stronger and broader across the outer flank. There are occasional intercalated ribs which arise low on the flank and may extend to the umbilicus as mere striae. In all there are 13 ribs on the last half whorl.

All but the last few ribs bear distinct, sharp, conical inner ventrolateral tubercles, whence arise broader, stronger ribs, which project forwards across the ventrolateral shoulder to sharp, distinctly clavate outer ventrolateral tubercles. A low subdued rib extends across the venter, bearing a clavate siphonal tubercle. Modifications of the last few ribs towards the mature aperture include a strengthening of the ventral and ventrolateral portion into a strong rounded rib and a decline of the inner ventrolateral tubercles to virtual obsolescence, and a loss in identity and definition by the outer ventrolateral and siphonal tubercles.

The holotype is broken across the last septum and the suture is damaged; it appears to have been simple and of basic *Protacanthoceras* design.

Dimensions. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
BM(NH) C81962	24·5 (100)	10·4 (42)	11·2 (46)	93	47 (19)

Discussion. *P. arkelli verrucosum* differs from the nominate form in retaining distinctive inner and outer ventrolateral and siphonal tubercles with associated ventral and ventrolateral ribbing, as compared to the smooth-ventered second growth stage of *arkelli arkelli*, which generally extends to at least the early parts of the body chamber. *P. tuberculatum tuberculatum* and *P. t. mite* are robust, coarsely-ribbed forms by comparison, in which the ventral tubercles are markedly pinched and clavate. *P. arkelli verrucosum* is morphologically transitional in many respects between *P. tuberculatum mite* and *P. arkelli arkelli*, but the specimens come from a condensed Basement Bed facies and there is no stratigraphic evidence for or against this inferred relationship.

Occurrence. As for types.

Protacanthoceras tegulicium sp. nov.

(Figs 44, 46)

1970 *Protacanthoceras* sp. Kennedy : 644.
1971 *Protacanthoceras* spp. nov. Kennedy : 103 (*pars*).

Holotype. OUM K4435 from the Chalk Basement Bed, low *Calycoceras naviculare* Zone, at Askerswell, Dorset.

Name. Late Latin *tegulicius*, tiled, a reference to the imbricate appearance of the venter, the ribs upon which resemble overlapping roof tiles.

Diagnosis. Whorl section reniform. No siphonal or outer ventrolateral tubercles, but with periodic strengthened primary ribs bearing subspinose umbilical bullae and inner ventrolateral tubercles at maturity. The strengthened primaries have a shallow rear and steep front slope giving the appearance of constrictions. These ribs are separated by two or three weaker, untuberculated ribs.

Description. The holotype is a phosphatic internal mould retaining traces of iridescent phosphatized shell. The specimen is adult, and two-thirds of the outer whorl is body chamber.

The coiling is moderately evolute, with almost half of the previous whorl covered. The umbilicus is moderately broad (31% of diameter) and of moderate depth. The whorl section is slightly depressed (*Wb* : *Wh* is 1·28 at a diameter of 22·2 mm), reniform in intercostal section (Fig. 46B)

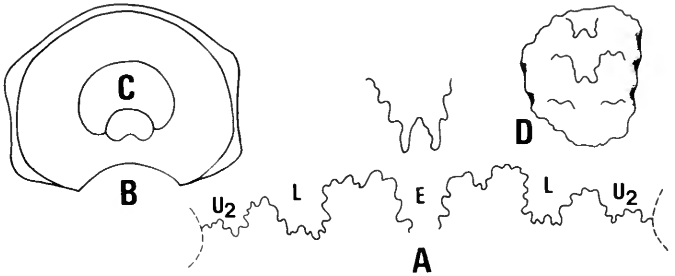


Fig. 46 *Protacanthoceras tegulicium* sp. nov., based on the holotype, OUM K4435. 46A, suture, × 4. 46B, whorl section of body chamber, × 4. 46C, whorl section of nucleus, × 8·3. 46D, early sutures on nucleus, × 8·3.

with the flanks strongly rounded and the venter flattened and broadly rounded, the greatest breadth quite low on the flank. The costal section is more angular, flat or even concave on the flanks, with sharp subspinose umbilical and ventral corners and a slight concavity on either side of a broadly rounded venter. The greatest breadth is at the ventrolateral angle.

There are ten irregularly-spaced primary ribs on the outer whorl. These arise as the faintest swellings at the umbilical seam. They develop into sharp, pointed bullae at the umbilical shoulder, which become stronger progressively towards the aperture. The ribs are strong, rounded, recti- to slightly prorsiradiate, low at mid-flank and produced into sharp inner ventrolateral tubercles, which become very strongly developed towards the aperture. At the smallest diameters visible, there are no obvious outer ventrolateral tubercles, although an almost imperceptible deflection of rib direction occurs on some ribs at the outer ventrolateral position. The ribs are strong and rounded, with very shallow rear and steep front slopes, and pass across the venter with a slight forward sweep, in some cases forming a distinct obtuse angle at mid-venter (Fig. 44a).

Between the main ribs are two or three low, relatively broad ribs best developed across the venter, lacking all trace of tubercles. These ribs pass straight across the venter.

The mature adult aperture shows typical *Protacanthoceras* modifications: there is a strong, tuberculate rib followed by a deep intercostal depression; the aperture itself is simple, slightly flared and projected into a short but distinct angular rostrum.

The nucleus was removed during preparation and shows inner whorls (Fig. 46C–D) which are depressed and reniform at a whorl breadth of 1·5 mm., with low, broad ribs on the flank, and a broadly rounded flattened venter quite without tubercles, although crossed by faint striations. At a whorl breadth of 0·8 mm the whorl is depressed and quite without ornament.

The mature suture consists of a deep and relatively narrow E, with a linguiform, little-divided median saddle, less than half as long as high. E/L is broad, asymmetrically bifid, with very minor incisions. L is broad and asymmetrically bifid; L/U_2 is small and little divided, whilst U_2 is very small. There are two very simple auxiliaries on the suspensive lobe external to the umbilical seam.

DIMENSIONS. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
OUM K4435	22·2 (100)	11·8 (53)	9·2 (41)	1·28	6·9 (31)

DISCUSSION. Although represented only by the holotype, this extraordinary species is highly distinctive, with its lack of siphonal and outer ventrolateral tubercles and its *Peltoceras*-like ribs and tubercles. It most closely resembles the later *P. proteus* sp. nov. (Fig. 50), but *proteus* has a more rounded whorl section, has much more subdued inner ventrolateral tubercles and bears small but distinct clavate siphonal and outer ventrolateral tubercles during early growth. *P. proteus baylissi* (Fig. 51), although equally lacking siphonal tubercles, also lacks ventrolateral tuberculation and has a much more rounded whorl section.

The origin of *Protacanthoceras tegulicium* is fairly clearly established in *Protacanthoceras arkelli*, whose nucleus, with broad rounded venter, chevron-like constrictions and flank ribs with strong ventral tubercles is in many respects a miniature *tegulicium*.

Occurrence. As for holotype.

Protacanthoceras asgeirri sp. nov.

(Figs 20–21, 47)

1970 *Protacanthoceras* sp. b Kennedy : 644.
1971 *Protacanthoceras* spp. nov. Kennedy : 103 (*pars*)

Types. The **holotype,** OUM K4433, is from the Chalk Basement Bed, low *Calycoceras naviculare* Zone, at Askerswell, Dorset. A paratype, OUM K4434, is from the same horizon and locality.

Name. From the type locality, Askerswell, deriving from the Old Norse name Asgeirr.

Diagnosis. A small round-whorled *Protacanthoceras*, the middle growth stages characterized by low distant primary ribs with umbilical bullae and subdued, rounded inner and outer ventrolateral and siphonal tubercles and shorter intercalated non-tuberculate ribs. Later growth stages characterized by loss of all ventrolateral and ventral tuberculation, leaving relatively strong umbilical bullae and primary ribs separated by two or three intercalated short ribs.

Description. The holotype is a slightly corroded phosphatic internal mould retaining traces of phosphatized shell. The specimen is adult and two-thirds of the outer whorl is body chamber.

The coiling is moderately involute on the phragmocone, becoming rather more evolute on the outer whorl, the body chamber uncoiling somewhat so that the width of the umbilicus is 26% of the total diameter. The umbilicus is of moderate depth with a vertical wall and abruptly rounded shoulder. The breadth and height are more or less the same, the flanks subparallel, with an evenly rounded arched venter (Fig. 47B). There are seven umbilical bullae on the last half whorl (all of which is body chamber) and an estimated twelve per whorl. On the phragmocone and early parts of the body chamber these bullae give rise to low, broad, gently flexed prorsiradiate ribs, which are strengthened on the shoulder into subdued bullae. From these the ribs become broader and stronger and sweep forwards across the ventrolateral shoulder to faint, low, rounded to transversely elongate outer ventrolateral tubercles. These are linked by a low broad rib, projected across the venter in a marked sinus, and bearing a faintly discernible, rounded siphonal tubercle. Between these strong primary ribs are faint, non-tuberculate ribs and striae, two or three between each tuberculate pair. This type of ornament extends onto the earlier parts of the body chamber. On later parts, ventral and ventrolateral tuberculation declines, but the umbilical bullae become stronger, as do the ribs. The flanks are thus ornamented by long, clearly differentiated broad ribs and one or two intercalated shorter ribs between each pair of long ribs. All ribs sweep forwards across the ventrolateral shoulder but cross the centre of the venter in a shallow curve.

The last few sutures are approximated, indicating the specimen to be mature. No details can be deciphered other than very simple lobes and saddles in a suture of basic *Protacanthoceras* pattern.

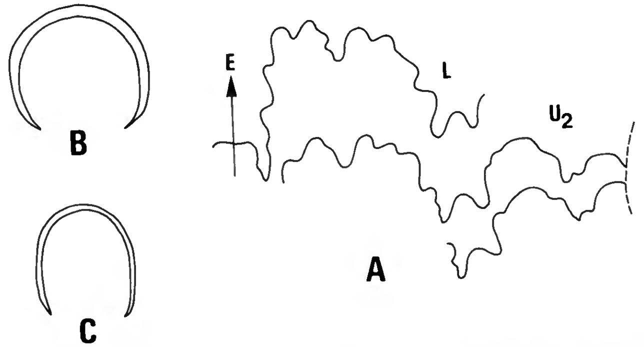


Fig. 47 *Protacanthoceras asgeirri* sp. nov. 47A, sutures, × 8·3, and 47B, whorl section, × 2, of OUM K4433. 47C, whorl section of OUM K4434, × 2.

The paratype is a more robust individual, in which the tuberculate stage is not visible, the outer whorl bearing ribs only. As in the holotype, these are differentiated into flexuous primary ribs with intercalated short ribs. There are *c.* 26 ribs per whorl and three distinct constrictions on the last half whorl. The suture line is very simple (Fig. 47A) with a narrow E, a smaller, asymmetrically bifid L with a few incisions and a smaller U_2 with a single median element. E/L is broad and asymmetrically bifid, U_2 and the auxiliaries on the suspensive lobe are almost ceratitic. This is the simplest suture we have seen in the genus.

DIMENSIONS. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
OUM K4433	14·1 (100)	5·8 (41)	5·6 (40)	1·04	3·6 (26)
OUM K4434	16·0 (100)	7·2 (45)	6·8 (43)	1·05	3·8 (24)

DISCUSSION. This is the smallest species of *Protacanthoceras* we have seen and the whorl section and the ornament of the early and middle growth stages are so distinctive that it is unlikely to be confused with any other. The ornament of juveniles of *P. tuberculatum* at diameters of 5 mm and less is very like that of the present species at much larger sizes, both showing the distinctive broad distant ribs with rather rounded tubercles, and we would suggest that the diminutive *asgeirri* is a paedomorphic derivative of that species.

OCCURRENCE. The species is only known from Askerswell.

Protacanthoceras bunburianum (Sharpe)

(Figs 29–33, 41–43, 48)

1853 *Ammonites bunburianus* Sharpe: 25; pl. 9, figs 3a–c.
1860 *Ammonites bunburianus* Sharpe; Pictet & Campiche : 315.
1896 *Ammonites hippocastanus* var. *compressus* Jukes-Browne *in* Jukes-Browne & Hill : 157; pl. 5, figs 4, 4a only (*non* 1a–b, 3a–b).
1923 *Protacanthoceras bunburianum* (Sharpe) Spath : 144.
1923 *Protacanthoceras compressum* (Jukes-Browne) Spath : 144.
1925 *Ammonites bunburianus* Sharpe; Diener : 24.
1925 *Acanthoceras hippocastanus* (Sow.) var. *compressa* Jukes-Browne et Hill; Diener : 161.
1951 *Protacanthoceras bunburianum* (Sharpe); Wright & Wright : 28.
1951 *Protacanthoceras compressum* (Jukes-Browne); Wright & Wright : 28.
1957 *Protacanthoceras compressum* (Jukes-Browne); Wright : L414, figs 534, 534a, b.
non 1962 *Protacanthoceras* aff. *compressum* Avnimelech & Shoresh : 532; pl. 15, figs 2a–b; text-fig. 2 (= *Thomelites* sp.).
1970 *Protacanthoceras compressum* (Jukes-Browne); Kennedy : 658.
1970 *Protacanthoceras bunburianum* (Jukes-Browne); Kennedy : 658.
1970 *Protacanthoceras* spp. Kennedy : 660, 664, 666 (*pars*).
1971 *Protacanthoceras bunburianum* (Sharpe); Kennedy : 97; pl. 31, figs 1a–c.
1971 *Protacanthoceras compressum* (Jukes-Browne); Kennedy : 98; pl. 32, figs 2a–d.
1972 *Protacanthoceras bunburianum* (Sharpe); Thomel : 99.
1972 *Protacanthoceras compressum* (Jukes-Browne); Thomel : 100.

HOLOTYPE. By monotypy the original specimen figured by Sharpe (1853 : pl. 9, figs 3a–c), BM(NH) 50155. It is said to be from Chardstock but as discussed by Kennedy (1971 : 98) this is, in all probability, an error, for all other known specimens of the species come from the *Calycoceras naviculare* Zone fauna of Division C of the Cenomanian Limestone and its equivalents and are of middle Late Cenomanian age; the phosphatic Basement Bed of the Chalk at Chardstock is of Middle Cenomanian age (Kennedy 1970).

OTHER MATERIAL. Numerous specimens, including the lectotype (GSM 53484, sel. Wright & Wright 1951) of *Protacanthoceras compressum* (Jukes-Browne), from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone of the Devon coast between Pinhay Bay and Humble Point: BM(NH) 47736, C8006–7, C73049–50, C73052, C81897, C81963–93; GSM Zn 9082–3, Zn 9085–7; JMH CC328, CC774; OUM K4445–53. From the same horizon

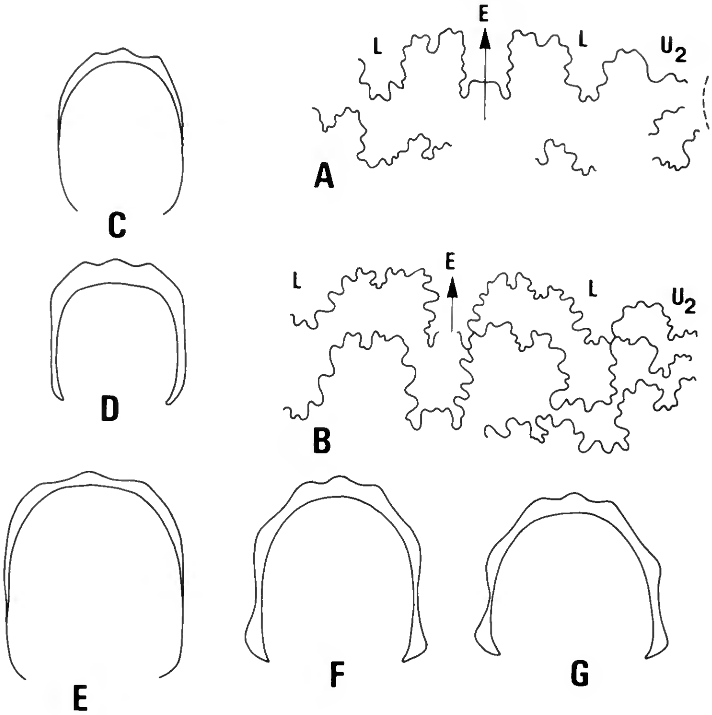


Fig. 48 *Protacanthoceras bunburianum* (Sharpe). 48A, suture of BM(NH) C81968, × 4. 48B, suture of BM(NH) C82001, × 4. 48C, whorl section of BM(NH) C81968, × 2. 48D, whorl section of BM(NH) C81992, × 2. 48E, whorl section of adult body chamber of BM(NH) C81969, × 2. 48F, whorl section of body chamber of BM(NH) C81993, × 2. 48G, section of phragmocone of BM(NH) C81969, × 2.

at the White Hart Sandpit, Wilmington, Devon: BM(NH) C76263, C78575, C81994–7 and OUM K4474–5; 'West of Culverhole', Devon: BM(NH) C73038; 'Landslips at Bindon', Devon: BM(NH) C72983; 'Beer Head': BM(NH) C12591; Hooken Beach, C81998–9; Haven Cliff,

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Figs 49–50 *Protacanthoceras proteus proteus* subsp. nov., from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone, Whitlands, Pinhay Bay, Devon. 49a–b, paratype, BM(NH) C82003. 50a–d, **holotype**, BM(NH) C82002.

Fig. 51a–d *Protacanthoceras proteus baylissi* subsp. nov. **Holotype**, BM(NH) C81300 (*ex* O. H. Bayliss coll. no. OB 268), from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone at Shapwick Grange, Devon.

Fig. 52a–b *Protacanthoceras tuberculatum devonense* subsp. nov. A paratype, BM(NH) C81953, from the *Calycoceras naviculare* Zone fauna of Bed C of the Cenomanian Limestone at White Hart sandpit, Wilmington, Devon.

Fig. 53a–b *Protacanthoceras* sp. nov. (?) of Matsumoto, Saito & Fukada (1957 : 39; pl. 14, fig. 3) from the Trigonia Sandstone (Middle Cenomanian) of Katsurazawa, Ikushumbets, Hokkaido, Japan.

Fig. 54a–d *Protacanthoceras imperatoris* sp. nov. **Holotype**, from Ankomaka, Madagascar, and in the late General M. Collignon's collection.

Fig. 55a–b *Acanthoceras* aff. *cuspidum* Stephenson. BM(NH) C82005, from the *Calycoceras naviculare* Zone fauna of Division C of the Cenomanian Limestone of Whitlands, Pinhay Bay, Devon.

Fig. 56a–b *Acanthoceras cuspidum* Stephenson. Paratype, USNM 105975, from the Templeton Member of the Woodbine Formation, gullies just south of the Old Sherman Highway, 2·8 miles E of Whitsboro, Grayson County, Texas, U.S.A.

All figures are × 1·125.


49a


49b


51a


51b


51c


51d


50a

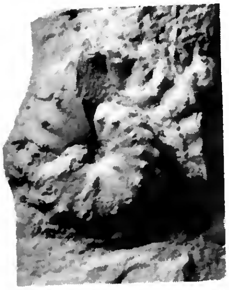

50b


50c


50d


52a


52b


53a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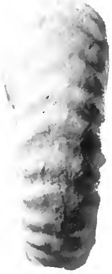
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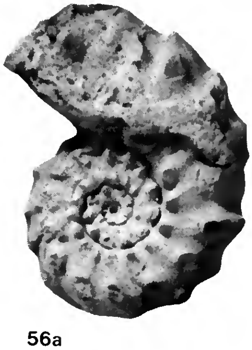
56a


56b

Seaton, BM(NH) C82000–1; also numerous specimens from Shapwick Grange, in the O. H. Bayliss collection.

Diagnosis. Compressed, flat-sided, with 16–28 ribs per whorl, mostly long and bearing umbilical bullae and rounded inner ventrolateral tubercles. Outer ventrolateral and siphonal tubercles are clavate and closely spaced.

Description. The holotype of *Protacanthoceras bunburianum* is a well-preserved phosphatic internal mould of which just over half the last whorl is body chamber. The whorl section is compressed, the breadth to height ratio (*Wb* : *Wh*) being 0·74, with the greatest breadth below mid-flank; the coiling is involute, with half the previous whorl covered.

The whorl sides are flat, parallel, with a broadly rounded ventrolateral shoulder and narrow, arched venter, rounder between the ribs, but angular in costal section. The umbilicus is small (8% of diameter), shallow, with a low wall and broadly rounded shoulder.

There are 27–28 ribs on the outer whorl. On the phragmocone these are broad and flat and separated by narrow interspaces. All ribs are long, every other rib bearing a faint umbilical bulla. There is a faint swelling at the inner lateral position and a delicate outer ventrolateral and siphonal clavus. On the body chamber the ribs become markedly broader and flatter across the ventrolateral shoulder, with a gently inclined back and steep front slope. Towards the aperture transverse striae appear on all ribs, the umbilical bullae disappear and the ventral tubercles become weaker.

The suture is of standard *Protacanthoceras* pattern, with plump and little-divided elements.

Dimensions. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*	Ribs per whorl
a. Macroconchs						
Holotype, BM(NH) 50155	32·8 (100)	11·0 (33)	14·8 (45)	0·74	8·0 (24)	27–28
BM(NH) C81969	32·0 (100)	9·8 (31)	11·0 (34)	0·89	11·4 (35)	18–19
BM(NH) C81974	29·2 (100)	11·0 (37)	11·9 (41)	0·92	8·6 (29)	—
BM(NH) C81967	24·8 (100)	8·2 (33)	9·5 (38)	0·86	6·4 (26)	23
b. Microconchs						
BM(NH) C81992	18·3 (100)	7·8 (42)	7·4 (40)	1·05	4·3 (23)	19
BM(NH) C81999	21·7 (100)	7·2 (33)	8	—	—	18
BM(NH) C82001	22·4 (100)	8·6 (38)	7·5 (33)	1·14	—	16
BM(NH) C81968	22·5 (100)	7·0 (31)	8·8 (39)	0·79	5·5 (24)	20

Discussion. The examination of large collections of *Protacanthoceras* from Division C of the Cenomanian Limestone on the Devon coast has convinced us that there is every gradation between the feebly ornamented holotype of *Protacanthoceras bunburianum* and the robustly ornamented lectotype of *P. compressum*, and that the two specimens represent the extremes of variation within one species. There also emerge strong indications of dimorphism, with macroconchs generally mature at diameters ranging from 26 to 33 mm and with 18 to 28 ribs on the outer whorl and microconchs mature between 17 and 22 mm and generally with 16 to 20 ribs on the outer whorl. The types of both *bunburianum* and *compressum* are macroconchs, and as can be seen from a comparison of Figs 29–33, 41–43, the range of variation is similar in both macroconchs and microconchs.

P. bunburianum is readily distinguished from all its contemporaries. The closest similarities are between microconchs of *bunburianum* and macroconchs of *P. tuberculatum devonense* subsp. nov. (p. 76). These latter are, however, invariably more coarsely and sparsely ribbed and tuberculate, with a much more depressed whorl section. Rare compressed individuals of *Protacanthoceras tuberculatum tuberculatum* also resemble this species.

Occurrence. *Protacanthoceras bunburianum* is one of the commonest ammonites in the remanié phosphatic *Calycoceras naviculare* Zone fauna of Division C of the Cenomian Limestone on the south Devon coast and its equivalents inland at Beer, Wilmington and Furley.

Protacanthoceras proteus sp. nov.

TYPES. The **holotype** is BM(NH) C82002, and there are two paratypes, C82003 and C82004, all from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone, fallen blocks near Whitlands, Humble Point, Charton Bay, between Lyme Regis and Axmouth, Devon (high *Calycoceras naviculare* Zone).

NAME. After the sea god Proteus, who could assume many different forms, in allusion to the distinctive forms taken up by the species at various stages in ontogeny.

DIAGNOSIS. Depressed, round-whorled with strong umbilical bullae giving rise to pairs of flexuous ribs; conical inner ventrolateral and clavate outer ventrolateral and siphonal tubercles variably developed, effaced during later growth.

Protacanthoceras proteus proteus subsp. nov.

(Figs 49–50, 57)

TYPES. As above.

DIAGNOSIS. Depressed, round-whorled with strong umbilical bullae giving rise to pairs of flexuous ribs bearing distinct conical inner ventrolateral tubercles, and clavate outer ventrolateral siphonal tubercles. Occasional ribs are intercalated. The clavate ventral tuberculation declines on the body chamber.

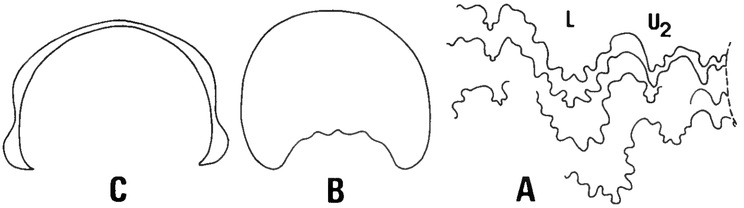

Fig. 57 *Protacanthoceras proteus proteus* subsp. nov., based on the holotype, BM(NH) C82002. 57A, suture, × 4. 57B, whorl section at back of body chamber, × 2. 57C, whorl section at aperture, × 2.

DESCRIPTION. The holotype is a phosphatic internal mould of an adult. About three-fifths of the outer whorl are body chamber and the last few sutures are approximated.

The coiling is moderately involute, with just less than half the previous whorl covered. The umbilicus is moderately broad (25% increasing to 28% at the largest diameter) and deep. The umbilical seam is crenulate to accommodate the ventrolateral tubercles of the preceding whorl. The umbilical wall is low and abruptly rounded. The whorl section is slightly depressed in intercostal section, with gently inflated convergent flanks and an evenly rounded venter. The costal proportions give a much greater whorl breadth to height ratio, 1·67 at the umbilical bulla on the early body chamber and 1·20 closer to the aperture where this bulla is lost. The greatest breadth is at the bulla, where present.

The visible parts of the phragmocone are ornamented by strong, pointed umbilical tubercles, 7–8 to a whorl, which arise from broad low ribs on the umbilical wall. From the bullae there generally arise two well-marked but low rounded ribs, which flex slightly across the flanks and carry small, sharp inner ventrolateral tubercles which become stronger as size increases. From these tubercles the ribs project strongly forwards and become stronger across the shoulder, to join small, delicate, clavate outer ventrolateral tubercles, linked by a very subdued rib to somewhat stronger clavate siphonal tubercles. Occasional intercalated ribs arise low on the flank and sometimes connect to an umbilical bulla on the opposed flank; these bear inner and outer ventrolateral and siphonal tubercles. On the body chamber the ornament changes quite markedly. Siphonal and outer ventrolateral clavi disappear, although up to the aperture their site is marked by distinct spiral striations. The inner ventrolateral tubercles strengthen over the rear part of the body chamber, but decline towards the aperture. The ventral ribbing, weak on the phragmocone, increases markedly as tuberculation declines and is strongly projected into a broad linguiform sinus. On the flanks the umbilical bullae strengthen markedly and then disappear suddenly, leaving the last three ribs arising well up the flank and virtually lacking tubercles. The ventral parts of the aperture are thus markedly constricted compared to the same region of the shell in middle growth. The sutures (Fig. 57A) are only incompletely visible but are relatively little incised. E is not discernible; L is shallow and broadly V-shaped, with rounded, finger-like incisions, U_2 shallow and little-divided. E/L is broad and bifid with a shallow median incision. L/U_2 is very simple and almost ceratitic, whilst there is a series of simple, entire frills on the suspensive lobe.

Dimensions. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
Holotype, BM(NH) C82002 at:	20·7 (100)	8·9 (43)	7·4 (36)	1·20	5·8 (28)
at:	16·4 (100)	10·53 (64)	6·3 (38)	1·67	4·1 (25)

Discussion. The larger paratype has stronger ornament on the body chamber (Fig. 49) but of the same style as that of the holotype; the smaller paratype is slender but has identical ventral tuberculation on the outer whorl and ribs and clavate tubercles similar to those of the holotype on the phragmocone.

Only two other species have comparable overall form. Of these *P. tegulicium* sp. nov. (p. 88, Fig. 44) differs in lacking the clavate ventral tuberculation and branching of ribs and in having more strongly imbricate ribs on the body chamber. There are, naturally, close similarities to *P. proteus baylissi* subsp. nov. (Fig. 51) which we separate on the basis of less pronounced umbilical tuberculation, much straighter ribs and indistinct ventral tuberculation (although the smaller paratype has a marked inner ventrolateral angulation). It is clear, however, that the two are intimately related.

The most interesting feature of *P. proteus proteus* is without doubt the striking similarity of the general proportions and style of ornament, in some respects, to the earliest *Vascoceras*, *V. diartianum* (d'Orbigny). Although *Vascoceras* lacks all but umbilical tubercles, the similarities of the body chamber of *P. p. proteus* to the whole shell of *diartianum* may be significant for the evolutionary origins of *Vascoceras*.

Occurrence. As for holotype.

Protacanthoceras proteus baylissi subsp. nov.

(Figs 51, 58)

Holotype. BM(NH) C81300, formerly Col. O. H. Bayliss' coll. no. OB 268, from the remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone, high *Calycoceras naviculare* Zone, Shapwick Grange, Devon. BM(NH) C81301 (OB 266), from the same horizon and locality as the holotype, may also belong to this species.

Name. After Col. O. H. Bayliss, of Spring House, Uplyme, Dorset, who collected the type specimen.

Diagnosis. A depressed, inflated *Protacanthoceras* with rounded whorls ornamented by seven conical umbilical bullae which give rise to groups of 2–3 strong, rounded, recti- to prorsiradiate and more or less straight ribs, with no ventral tuberculation on the outer whorls.

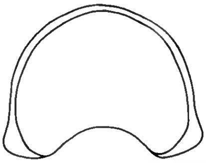

Fig. 58 *Protacanthoceras proteus baylissi* subsp. nov. Whorl section of holotype, BM(NH) C81300 (OB 268), × 4.

DESCRIPTION. The holotype is a phosphatic internal mould retaining approximately half a whorl of body chamber; it appears to be adult.

The coiling is moderately involute during most of development but the adult body chamber uncoils somewhat, giving a lesser degree of involution (Fig. 51a, c). The umbilicus is of moderate breadth and depth (25% of diameter at 20 mm; 24% of diameter at 18 mm). The whorl section (Fig. 58) is depressed and reniform, with an intercostal whorl breadth to height ratio (*Wb* : *Wh*) of 1·25 and the greatest width low on the flanks. The costal whorl section gives an even higher ratio of 1·42, the greatest breadth being at the umbilical bullae.

The umbilical wall is rounded, with seven low, broad ribs arising at the umbilical seam. These strengthen into strong conical to radially elongate bullae at the umbilical shoulder, strength of bullae increasing towards the aperture. Groups of 2–3 ribs are tenuously linked to these bullae and are weak and low on the flank although becoming stronger across the ventrolateral shoulder and venter. The ribs are rounded, narrower than the interspaces and recti- to somewhat prorsiradiate; they vary from straight to slightly concave aperturally and pass gently forwards across the ventrolateral shoulder to be only weakly projected into a very broad and shallow convex ventral sinus. There are perhaps 22 such ribs on the outer whorl, suggesting the presence of rare intercalated ribs. Apart from the umbilical bullae there is no other obvious sign of tuberculation, although the definite strengthening of the ribs on the ventrolateral shoulder may indicate the presence of a tubercle in this position on the inner whorls. In one instance a rib does not complete the loop from flank to flank but dies out on the venter (Fig. 51d).

Occasional interspaces (generally between two ribs groups) are a little more marked than others but scarcely merit the name constriction.

The suture cannot be fully resolved, but consists of very simple, little-divided elements, with rounded, finger-like incisions on both lobes and saddles.

DIMENSIONS. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
Holotype, BM(NH) C81300	20·5 (100)	—	7·9 (39)	—	5·1 (25)
at:	18·4 (100)	11·1 (60)	7·8 (42)	1·42	4·5 (24)

DISCUSSION. The second specimen tentatively referred to *P. proteus baylissi* is a juvenile; it shows traces of inner and outer ventrolateral tubercles. *P. proteus baylissi* most closely resembles the contemporary *P. proteus proteus*, from which it is readily distinguished by lack of strong inner ventrolateral tubercles on the whole of the outer whorl and a lack of delicate clavate outer ventrolateral and siphonal tubercles on the septate parts of the outer whorl. The ribbing style is also different, being concave and projected across the ventrolateral shoulders in *proteus* but much straighter in *baylissi*.

As in the case of *P. p. proteus*, *P. p. baylissi* shows interesting resemblances to the early whorls of certain early Turonian vascoceratids. Whereas *P. p. proteus* may foreshadow *Vascoceras*, *P. p. baylissi* shows some resemblance to juveniles of species of *Fagesia* such as *F. harmanni* Böse; the generic transformation would have involved complete loss of ventral tuberculation, increasing depression of whorls, strengthening of bullae and increase in depth of constrictions (incipient in *P. p. baylissi*) to the prominence they take on in *Fagesia* (Powell 1963 : pl. 34, figs 2–5; Pervinquière 1907 : pl. 20, figs 2a–b, 3a–b, 5a–b).

OCCURRENCE. As for holotype.

Protacanthoceras imperatoris sp. nov.

(Figs 54, 59D)

?1937 *Protacanthoceras tropicum* Stol.; Collignon : 63; pl. 1, figs 1, 1a, 1b.
1964 *Protacanthoceras tropicum* Stol.; Collignon : 146; pl. 373, fig. 1623.

HOLOTYPE. Collignon's (1964) figured specimen from the Cenomanian of Ankomaka, Madagascar; Collignon collection.

NAME. Latin *imperator*, general; in reference to the late General M. Collignon of Moirans, Isère, who collected the type specimen and who helped and encouraged us in many ways.

OTHER MATERIAL. Two specimens from Anabatsifaka, Madagascar, described by Collignon in 1937, may also belong to this species, although we have not examined the original material.

DIAGNOSIS. Compressed, round-whorled with 7–8 conical umbilical bullae giving rise to single flexuous ribs with 2–3 ribs intercalated, showing an early decline of lower ventrolateral tubercles and a body chamber on which all tuberculation but the umbilical is lost.

DESCRIPTION. The coiling is rather involute on the early whorls, although the umbilical seam egresses towards the aperture on the last whorl, with the umbilicus of moderate size.

The umbilicus is shallow, with a low rounded wall and an abruptly rounded umbilical shoulder. The whorls are compressed, the flanks flattened and subparallel, with a rounded venter in intercostal section, the greatest breadth being low on the flanks. The greatest breadth in intercostal section is at the umbilical bulla, where present, with a breadth to height ratio (*Wb* : *Wh*) of 0·83.

There are 7–8 well-defined, conical to comma-shaped umbilical bullae per whorl. These give rise to single ribs, with one or two other ribs more tenuously connected by mere striae. The ribs are quite low, rounded and crowded, gently flexed and slightly prorsiradiate. There are small, conical inner ventrolateral tubercles at the smallest diameter visible, but these are rapidly effaced, although their position is marked by a broadening, strengthening and projection of the rib, which passes across the venter with a slight broadening at clavate outer ventrolateral and siphonal tubercles, which decline over the later parts of the body chamber. One or two ribs are intercalated between the long ribs, arising on the lower or middle flank, to give a total of *c.* 28 ribs on the outer whorl.

Body chamber modifications, indicating the specimens to be adult, include a weakening of the flank ribs, a disappearance of the umbilical bullae and projection of the ribs on the venter into distinct chevrons.

The last few sutures of the holotype are approximated and rather simple.

DIMENSIONS. Percentage figures in brackets.

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
Anabatsifaka specimen (after Collignon)	17·0 (100)	9·0 (53)	8·0 (47)	1·13	5·0 (29)
Holotype	24·1 (100)	7·8 (32)	9·3 (39)	0·83	7·2 (30)

DISCUSSION. The holotype was originally referred to '*Protacanthoceras*' *tropicum* (Stoliczka), which we believe to be a juvenile *Thomelites* (p. 101). The holotype of *tropicum* retains siphonal tubercles to a much greater size than *P. imperatoris* and lacks the obviously mature body chamber ornament; these alone suffice to differentiate the two species. Differences from *P. bunburianum* are also obvious and include much stronger clavate ventral tuberculation and a higher, compressed whorl section in the latter. Perhaps the closest species is *Protacanthoceras involutum* Thomel (1972 : 100; pl. 32, figs 5–8) from the Cenomanian of Peille, Alpes-Maritimes, the dimensions of whose holotype and only known specimen are as follows (after Thomel):

D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
26·4 (100)	80 (30)	12·5 (47)	0·64	5·6 (21)

The specimen is a little distorted by compaction but shows the following features which distinguish it from *P. imperatoris*: strong inner ventrolateral tubercles, retention of all tubercles to a later stage in development and a stronger projection of ribs across the ventrolateral shoulder.

OCCURRENCE. The holotype is said to be from Collignon's Middle Cenomanian Zone of *Euomphaloceras euomphalum*, but the same locality has yielded *Pseudocalycoceras harpax* (Stoliczka) and varieties, *Lotzeites aberrans madagascariensis* Collignon, *Calycoceras cottreaui* Collignon, *Eucalycoceras spathi* Collignon and other species suggesting rather an Upper Cenomanian horizon.

Other species previously referred to *Protacanthoceras*

'Acanthoceras' cuspidum Stephenson
(Figs 56, 59C)

1952 *Acanthoceras cuspidum* Stephenson : 203; pl. 50, figs 1–4.
1971 *Protacanthoceras cuspidum* (Stephenson) Kennedy : 122.

TYPES. The holotype, by original designation, is USNM 105974, from the Templeton Member of the Woodbine Formation, gullies south of the old Sherman Road, 2·8 miles east of Whitsboro, Grayson County, Texas. Two paratypes, USNM 18971, from the same horizon and locality as the holotype, and USNM 14092, from the Templeton Member of the Woodbine Formation, bluff south of the Missouri–Kansas–Texas Railroad, 1 mile north and 1·85 miles east of Sadler, Grayson County, Texas.

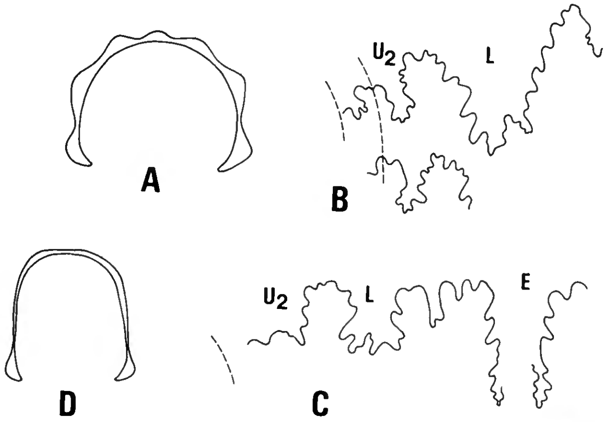

Fig. 59 59A–B, *Acanthoceras* aff. *cuspidum* Stephenson, BM(NH) C82005. 59A, whorl section, × 2. 59B, partial sutures, × 4. 59C, *Acanthoceras cuspidum* Stephenson, suture of USNM 105974, × 4. 59D, *Protacanthoceras imperatoris* sp. nov. Whorl section of holotype, × 2.

DISCUSSION. Stephenson's *Acanthoceras cuspidum* closely resembles strongly-ribbed and tuberculate variants of *Protacanthoceras bunburianum* and also some variants of *P. tuberculatum*. For these reasons we had been inclined to regard the species as a North American example of the genus. Examination of the type specimens has shown that the similarity of ornament is superficial only. They show no signs of reaching or even approaching maturity, whilst the sutures (Fig. 59C) are distinct from those of any *Protacanthoceras* we have seen. These features indicate that *cuspidum* is a juvenile of some other genus.

There are some comparisons to be made with the genus *Dunveganoceras* Warren & Stelck (1940); particularly striking is the asymmetry of the outer ventrolateral clavi in profile, with steep front and gently inclined back faces, whilst there are basic sutural similarities (Cobban 1953 : pl. 10, figs 1–6). We would suggest that *'Mammites' bellsanus* Stephenson (1952 : 202; pl. 50, figs 1–4), which also comes from the Templeton Member, may be a *Dunveganoceras*, which lends some support to the placement of *cuspidum* in that genus.

OCCURRENCE. The species is only known from the type occurrence in Texas. It is extremely difficult to place this stratigraphically in terms of the north-west European sequence, but the Templeton Member is certainly older than the *gracile* Zone. The occurrence of a *Eucalycoceras* of the *pentagonum* (Jukes-Browne) group (USGS collns, Denver, *ex* J. P. Conlin coll.) in the Templeton Member, and the rare occurrence of *Metengonoceras dumbli* (Cragin) in the Upper Cenomanian of Sarthe provide evidence that the unit is approximately equivalent to the *naviculare* Zone and of middle late Cenomanian age. The occurrence of a specimen in Division C of the Cenomanian Limestone, described below as *'Acanthoceras'* aff. *cuspidum*, lends support to this view.

'Acanthoceras' aff. ***cuspidum*** Stephenson
(Figs 55, 59A, B)

compare: 1952 *Acanthoceras cuspidum* Stephenson : 203; pl. 50, figs 1–4.

MATERIAL. One specimen only, BM(NH) C82005, from the high *Calycoceras naviculare* Zone remanié phosphatic fauna at the base of Division C of the Cenomanian Limestone, Pinhay Bay, Devon.

DESCRIPTION. The specimen is a glauconitized phosphatic internal mould, with most of the ventral region of the outer whorl lacking. The last third of the outer whorl is body chamber and the last few septa are neither crowded, approximated nor simplified, indicating the specimen to be immature.

The coiling is very evolute, less than a quarter of the previous whorl being covered, the lower ventrolateral tubercles of which are exposed in the umbilicus. The umbilicus is quite large (34% of diameter) and relatively deep, with a high, vertical, rounded wall and abruptly rounded shoulder. The umbilical seam is crenulated to accommodate the tubercles of the previous whorl. The whorl section is depressed, with flattened, gently rounded flanks, a rounded ventrolateral shoulder and venter, the whorl breadth to height ratio being 1·22, and the greatest breadth at a point below mid-flank. The costal section is polygonal, the greatest breadth being at the umbilical bullae, with a breadth to height ratio of 1·30. There are ten umbilical bullae which vary greatly in strength, from mere swellings at the juncture of two ribs to prominent conical protruberences. They give rise to pairs of ribs (or rarely a single one), which are generally broad, prorsi- or rectiradiate and straight, and which in turn bear strong conical to subspinose inner ventrolateral tubercles.

The ventral ornament is highly distinctive, a low broad swelling crossing the venter bearing very strong, sharp, elongate outer ventrolateral and siphonal clavi. The siphonal row are longer than the ventrolateral and all clavi have a striking asymmetry in profile with a very steep adoral face.

There are only *c.* 16 ribs on the outer whorl.

The suture (Fig. 59B) is incompletely visible, but appears to have been relatively little subdivided. L/U_2 is markedly asymmetric; U_2 is small and rather narrow, whilst the largest of the auxiliaries is also asymmetric.

DIMENSIONS. Percentage figures in brackets; the maximum diameter of the specimen is 28 mm.

		D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
BM(NH) C82005	costal	21·1 (100)	10·5 (50)	8·1 (38)	1·30	7·2 (34)
	intercostal	21·1 (100)	9·3 (44)	7·6 (36)	1·22	7·2 (34)

DISCUSSION. The affinities of this specimen are somewhat cryptic. The sparse ribbing and coarse ornament recall the *Protacanthoceras tuberculatum* group (Figs 14–17) and, to a degree, the contemporary *P. tuberculatum cyclopeum* (Fig. 45). None of these, however, shows the same style of ventral ornament with elongate clavi, and this alone serves to distinguish the specimen from that species. This ornament and the asymmetric profile of the clavi strongly recall the coarsely ornamented variants of *P. bunburianum*, but none of these show the depressed whorl section, strong spinose umbilical and ventrolateral bullae nor the same retention of ornament. In these respects the specimen more closely resembles the North American '*Acanthoceras*' *cuspidum* Stephenson (Fig. 56); even here there are differences, however, for *cuspidum* has denser, more crowded ribs and bullae, stronger lower ventrolateral tubercles which are produced into spines (possibly a reflection of the presence of shell material) and an umbilicus in which the lower ventrolateral spines are visible on the wall of the succeeding whorl (although again this may be a reflection of the presence of shell material in the American specimens). There are also obvious differences in the suture (compare Figs 59B and C) such as to preclude reference to '*Acanthoceras*' *cuspidum* itself.

OCCURRENCE. As for figured specimen.

Ammonites tropicus Stoliczka
(Figs 4–5, 60A–D)

1865 *Ammonites tropicus* Stoliczka : 78; pl. 43, figs 2, 2a, 2b.
1898 *Acanthoceras tropicum* (Stoliczka) Kossmat : 122.
1925 *Acanthoceras tropicum* (Stoliczka); Diener : 166.
non 1937 *Protacanthoceras tropicum* (Stoliczka); Collignon : 63; pl. 1, figs 1, 1a, 1b.
non 1964 *Protacanthoceras tropicum* (Stoliczka); Collignon : 146; pl. 373, fig. 1623.
1972 *Protacanthoceras tropicum* (Stoliczka); Thomel : 99.

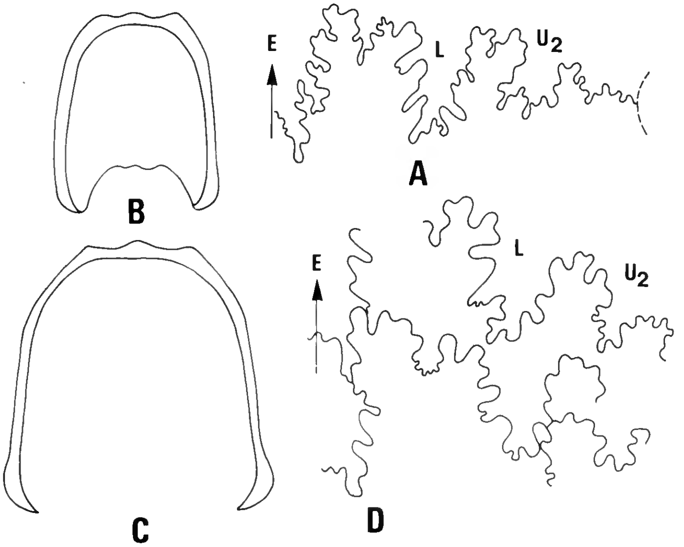

Fig. 60 *Ammonites tropicus* Stoliczka. 60A, suture, × 4, and 60B, whorl section, × 2, of the holotype, after Kossmat. 60C, whorl section, × 2, and 60D, suture, × 4, of BM(NH) C12590.

HOLOTYPE. By monotypy Stoliczka's original specimen from the Utatur Group, north of Odium, southern India.

DISCUSSION. Most authors since Spath's introduction of *Protacanthoceras* have referred *Ammonites tropicus* to this genus and indeed Stoliczka noted how similar his species was to Sharpe's *Ammonites bunburianus*. As the original figures show (Fig. 5a–b), however, the holotype retains all its tubercles to the aperture and at a diameter of 27 mm is still immature. Furthermore the suture (reproduced here as Fig. 60A) has deeply incised and subdivided elements quite distinct from the very simple sutures of typical *Protacanthoceras*, a deep E, a smaller but narrow L and a relatively broad U_2, E/L bifid and deeply incised, L/U_2 small and bifid, with one large and several smaller, poorly-defined auxiliaries on the suspensive lobe.

Other specimens referred to the species (Collignon 1937, 1964) are quite distinctive and have been described above as a new species, *Protacanthoceras imperatoris* (p. 97).

The affinities of *Ammonites tropicus* are much closer to *Thomelites* and we figure here (Fig. 4a–c) a juvenile from the Upper Cenomanian of southern England which is closely related to, if not conspecific with, Stoliczka's species.

Ammonites triserialis J. de C. Sowerby

1836 *Ammonites triserialis* J. de C. Sowerby *in* Fitton : 239, 344; pl. 18, fig. 27.
1863 *Ammonites triserialis* Sowerby; Pictet : 39.
1923 *Protacanthoceras triserialis* (J. de C. Sowerby) Spath : 144.
1925 *Acanthoceras triserialis* (Sowerby *in* Fitton) Diener : 166.
1951 *Protacanthoceras triseriale* (J. de C. Sowerby); Wright & Wright : 29.

1971 *Protacanthoceras triseriale* (J. de C. Sowerby); Kennedy : 99.
1972 *Protacanthoceras triseriale* (Sowerby); Thomel : 99.

Discussion. The name *Ammonites triserialis* was introduced by J. de C. Sowerby in the description of fossils illustrated by Fitton, who (1836 : 239) lists '*A. triserialis* Pl. XVIII, f. 27. Mr. Sowerby's Museum', in a 'List of Fossils from the sands of Blackdown and of some other places in Devonshire'. In his explanation he points out that all the fossils in his list are from 'the Whetstone Pits at *Blackdown*, except those to which a different locality is assigned'. He thus lists a variety of fossils from other localities and indeed horizons, such as *Ammonites hippocastanus* and *varians* from Pinhay. Sowerby's specimen has disappeared but, on the basis of the figure, Spath (1923 : 144) regarded the species as an early *Protacanthoceras* which gave rise to *P. compressum* (Jukes-Browne) and *P. bunburianum* (Sharpe), apparently believing it to be related to the rather depressed, square-whorled *Protacanthoceras* of the *tuberculatum* group from the Middle Cenomanian Chalk Basement Beds of south-west England. Following Spath we both initially suggested (Wright & Wright 1951; Kennedy 1971) that the species was a *Protacanthoceras* and inferred that it came from a Basement Bed of the chalk of south-west England.

Sowerby's specimen bears no resemblance to any of the species here included in *Protacanthoceras*. But for the clear statement in Fitton (1836: table on p. 366) that it came from Blackdown and the unlikelihood of Sowerby or Fitton confusing a phosphatic specimen from the Devon coast with the siliceous preservation for which Blackdown was famous, we should have had no hesitation in treating it as a *Calycoceras* (*Newboldiceras*) from the Cenomanian Bed C of the coast sections. It bears an extremely close resemblance to one of the characteristic 'post-*spinosum*' forms from that horizon, although in the absence of the specimen there must remain slight doubt as to its identity.

Protacanthoceras sp. nov. (?) of Matsumoto, Saito & Fukada
(Figs 53a–b)

1957 *Protacanthoceras* sp. nov. (?); Matsumoto, Saito & Fukada : 39; pl. 14, fig. 3.

Material. The original figured specimen, no. GH 7874, in the collections of Hokkaido University, from the Middle Cenomanian *Trigonia* Sandstone of Katsurazawa, Ikushumbets Valley, Hokkaido (*ex* Nemoto collection).

Discussion. This tiny specimen is immature and bears weak, irregular flank-ribs, rounded inner ventrolateral tubercles and clavate outer ventrolateral tubercles which are stronger than the siphonal row. In our view it is not possible to place it generically with any confidence; it may be a juvenile *Acanthoceras*, or even a *Protacanthoceras* juvenile comparable to the *tuberculatum* group rather than to *P. compressum* (i.e. *bunburianum*) with which Matsumoto, Saito & Fukada compared it.

Occurrence. Middle Cenomanian of Hokkaido, Japan.

Discussion: Evolutionary trends

Most of the material described in this paper comes from diachronous, condensed phosphatic Chalk Basement Beds, the fossils in which are known to have complex histories (Kennedy & Garrison 1975). In spite of this, the various associations of species can be fitted into the biostratigraphic sequence determined in the expanded chalk sequence of south-eastern England and northern France (Kennedy 1969; Juignet & Kennedy 1976) and the broad outline of evolution of *Protacanthoceras* is clear. Within this framework inferences about the relationships of species which occur in the same Basement Bed in the same area have been made on morphological criteria, with, in some cases, clues from differential preservation (e.g. differing numbers of phases of mineralization). Subject to these limitations the evolution of *Protacanthoceras* can be seen as follows (Fig. 61).

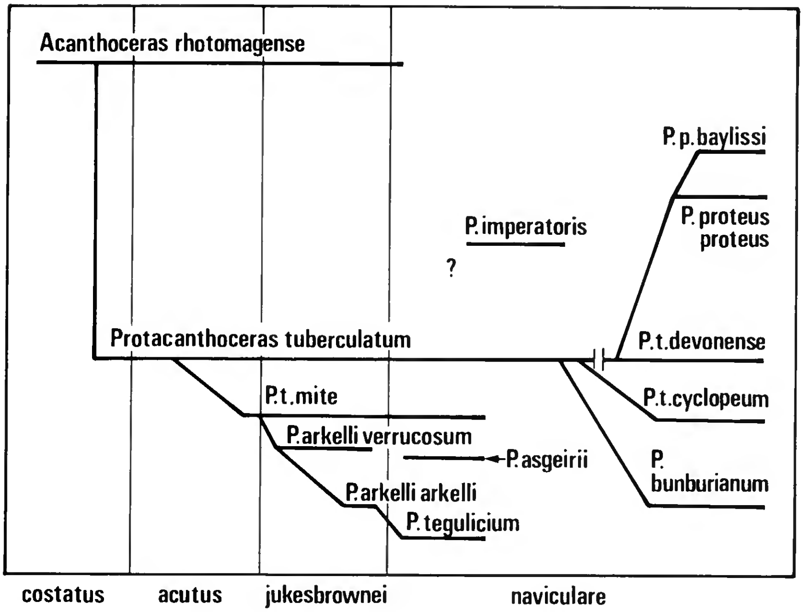

Fig. 61 The phylogeny of *Protacanthoceras* species.

The genus is a paedomorphic derivative of *Acanthoceras rhotomagense*, appearing for the first time in the early Middle Cenomanian. The rootstock of the genus is *Protacanthoceras tuberculatum* Thomel, the nominate subspecies of which survived until the mid Upper Cenomanian. During late Middle Cenomanian time a slender, feebly-ornamented subspecies, *P. tuberculatum mite*, evolved and gave rise to the compressed, weakly-ornamented *P. arkelli*, which shows very striking ontogenetic changes, involving loss of all ventral ornament in middle growth. Rare examples of an intermediate form, *P. arkelli verrucosum*, are known. The nuclei of *P. arkelli* are constricted and lack siphonal and outer ventrolateral tubercles, being miniatures of the early Upper Cenomanian *Protacanthoceras tegulicium*, which is interpreted as a paedomorphic derivative of *arkelli*. The innermost whorls of early Upper Cenomanian *P. tuberculatum* are also a miniature of the middle growth stage of the diminutive *P. asgeirri*, which is likewise regarded as a paedomorphic offshoot of the *tuberculatum* stock.

The latest *Protacanthoceras*, from the mid Upper Cenomanian, probably derive from the *tuberculatum* group. *Protacanthoceras tuberculatum cyclopeum*, the largest form, is the product of evolutionary size increase, whilst typical *P. tuberculatum devonense* is a product of evolutionary size decrease. Both have essentially the same style of ornament as *P. tuberculatum tuberculatum*.

Some variants of *P. tuberculatum devonense* show a weakening of ventral tuberculation and a rounding of the whorls, which strongly suggests that this subspecies is the origin of *Protacanthoceras proteus proteus* and *P. p. baylissi*.

P. bunburianum, type species of the genus, stands separated from its contemporaries by a clear morphological hiatus, but rare compressed late Middle Cenomanian *Protacanthoceras* of the *tuberculatum* group may be close to its ancestral stock.

Protacanthoceras imperatoris cannot be related to any of the stages in the evolutionary sequence described above. This species and a series of interesting *Protacanthoceras*-like micromorphs from the Cenomanian of the U.S. western Interior, kindly shown to us by Dr W. A. Cobban, may even be quite independent offshoots of *Acanthoceras* species other than *rhotomagense*, filling the same ecological niche as the European species of *Protacanthoceras* in the Malagasy and U.S. Interior ammonite faunas.

There is a striking resemblance between *Protacanthoceras* and several other genera, although there is insufficient evidence to confirm the relationships suggested below beyond doubt, whilst there is always a tendency to regard any genus studied in depth as the key to the phylogeny of the higher taxonomic group to which it belongs.

Thomelites, which first appears in the early Upper Cenomanian, has many *Protacanthoceras*-like features, especially in tuberculation and rib style, although the sutures (Fig. 23E, p. 81) are more complex than in *Protacanthoceras*. The early, multi-tuberculate stage of Lower Turonian *Nigericeras* (Fig. 10a–b) are similar to the early developmental stages of *Protacanthoceras asgeirri*, magnified several times, although no intermediates are known from the *Sciponoceras gracile* Zone faunas which separate them.

The flank ribbing, body chamber ornament and suture of *Protacanthoceras p. proteus* closely resemble those of the earliest *Vascoceras*, *V.* (*Vascoceras*) *diartianum* (d'Orbigny), from the succeeding late Cenomanian *Sciponoceras gracile* Zone. Similarly, *P. proteus baylissi*, which is ribbed and bullate and has virtually lost its ventral tubercles, resembles juvenile *Fagesia* in many respects, although it is less markedly depressed and constricted.

Finally, compressed variants of *Protacanthoceras bunburianum* show strong resemblance to *Quitmaniceras brandi*, of Lower Turonian age, which has a tuberculate siphonal keel.

These similarities between the various Upper Cenomanian *Protacanthoceras* fauna and later acanthoceratids are of great interest, but it is unlikely we have found the missing links between Cenomanian and Turonian acanthoceratid faunas.

Our study of *Protacanthoceras* provides good examples of paedomorphosis as an important mechanism in ammonite evolution. The record, restricted admittedly by the nature of the available collections, appears to show speciation in this genus in part as a series of sudden jumps in morphology, that is saltation, and in part, in the case of the *tuberculatum* rootstock, as a clear example of gradual change.

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Ashgill Brachiopoda from the Glyn Ceiriog District, north Wales

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Synopsis

The Ashgill age of the rocks of the Glyn Ceiriog district was first established in 1908 by Groom and Lake, who also reported the large shelly fauna. A more precise age has never been determined and with this objective the fauna has been revised in light of other recent work on the Ashgill. Sixty-seven brachiopod species including four new species, *Platystrophia anomala*, *Strophomena ceiriogensis*, *Katastrophomena dolhirensis* and *Mjoesina marri*, and two new subspecies, *Platystrophia lutkevichi costellata* and *Ravozetina rava prima*, are here described, and referred to sixty genera. It has been possible to date the Glyn Valley Group, comprising the older Dolhir and younger Glyn Formations, as ranging in age from top Cautleyan, through Rawtheyan, to Hirnantian. Close correlation has been established with rocks in the neighbouring inliers of Cyrn-y-brain and Mynydd Cricor, from which brachiopods are also described.

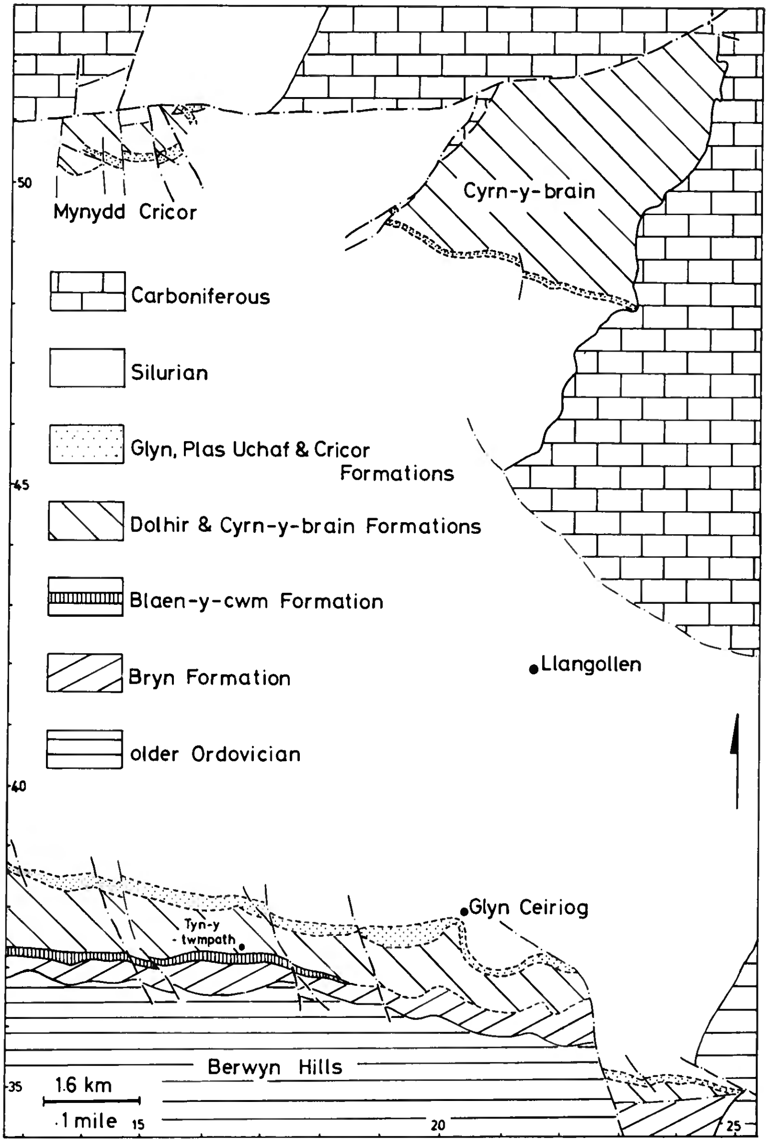


Fig. 1 Geological map of the Llangollen district.

Introduction

The present work comprises a study of the Ashgill brachiopods of the Glyn Ceiriog district, which lies in the north-eastern part of the Berwyn Hills, south of Llangollen, and those collected from the small inliers of Cyrn-y-brain and Mynydd Cricor a short distance to the north (Fig. 1). The earliest known account of the geology of the Glyn Ceiriog district is to be found in Bowmann's paper (1841). Its chief concern is the Silurian rocks of the Vale of Llangollen, but it includes a description of the igneous rocks cropping out along the River Ceiriog. Sedgwick recognized three main divisions in the rocks of the Ceiriog Valley (1845: 14): a lower group, containing some fossils; a middle group consisting of 'a great series of beds full of fossils' which alternate with several bands of volcanic rock; and a thick upper group, whose outcrop is about one mile wide, composed of calcareous slates with two bands of limestone. He concluded (p. 15) that this upper group was stratigraphically far above the horizon of the 'Bala' Limestone (the Cymerig Limestone of modern usage), although at this time he regarded the Rhiwlas Limestone as being older than the 'Bala' Limestone (p. 7). He also recognized that the inliers of Cyrn-y-brain and Cricor Mawr (Mynydd Cricor) were older than surrounding rocks and the same age as those at Glyn Ceiriog. Davies (1872: 300) disagreed with Sedgwick in that he equated the limestone at the base of the Dolhir Formation with the 'Bala' Limestone and the limestone in the Glyn Formation with the Hirnant Limestone.

Groom and Lake published their account of the local geology in 1908 and the succession they produced is still in current use with only minor modifications. Groom and Lake included large faunal lists for the different horizons and it was they who first established an Ashgill age for the two formations on which the present study is focussed. The connection between the Glyn Ceiriog area and the inliers of Mynydd Cricor and Cyrn-y-brain was confirmed by Wills and Smith (1922) and also by Wedd *et al.* (1927).

Stratigraphy

The lithological units referred to in this paper are the same as those used in Wedd *et al.* (1927) and remapping did not reveal the need for any major stratigraphical revision. However, the terminology is brought into line here with the I.U.G.S. code for stratigraphical nomenclature. Thus the Ashgill rocks of the Glyn Ceiriog area belong to the Glyn Valley Group which can be divided into the Dolhir Formation, in which the laterally equivalent, basal, Tyn-y-twmpath and Dolhir Limestone Members can be recognized, and the Glyn Formation, including the Glyn Limestone Member. In both inliers to the north the Cyrn-y-brain Formation is the equivalent of the Dolhir Formation, while the Glyn Formation is represented on Cyrn-y-brain by the Plas Uchaf Formation and by the Cricor Formation on Mynydd Cricor.

In the Ceiriog Valley, the Dolhir Formation consists of about 475 m of cleaved micaceous siltstones and mudstones with subsidiary sandstone and limestone bands, all a characteristic blue colour. It rests unconformably on Bryn Formation siltstones which have been dated as Lower Longvillian (Brenchley 1965: 38, 40) or topmost Soudleyan (Bancroft 1945: 245) in age, and at its base is a 60 m thick series of beds of a distinctly calcareous nature (Dolhir Limestone Member), including a 10 m thick band of limestone which was once quarried at two localities. About 3·5 km to the west, in the valley of Nant Tyn-y-twmpath, no such calcareous beds are to be found, instead the first 70 m of the Dolhir Formation consist of highly cleaved, fissile mudstones (Tyn-y-twmpath Member), and these rest, not on Bryn Formation siltstones but on blue-black pyritous shales of the Blaen-y-cwm Formation. This is reported to contain poorly preserved graptolites (Groom & Lake 1908: 570; Wills & Smith 1922: 183) of a *Pleurograptus linearis* zone age (Wills & Smith 1922: 186). Therefore one hiatus exists between the Blaen-y-cwm Formation and the underlying Bryn Formation and another between the Blaen-y-cwm Formation and the Dolhir Formation, which to the east oversteps the Blaen-y-cwm Formation to rest on the Bryn Formation. (Fig. 2).

The Dolhir Formation contains a large and varied fauna in which brachiopods are the dominant element, but trilobites, ostracodes, bryozoa, gastropods, bivalves, cystoids, corals, crinoids and nautiloids are also present but in lesser numbers. The beds are fossiliferous throughout the formation but a particular band, about 50 m thick, immediately above the Tyn-y-twmpath and Dolhir Limestone Members, is especially rich in organic remains.

The Glyn Formation is composed of about 40 m of fine to coarse grained, buff-coloured sandstones with thin siltstones and a locally developed limestone member (Glyn Limestone) at the base on Mynydd Fron Frys. The formation is conformable on the Dolhir Formation which grades up into it. Fossils are common in the lower part, especially in rottenstone bands and lenses associated with the Glyn Limestone, but towards the top of the formation fossil remains are much rarer and the beds yield only the occasional brachiopod or small solitary coral. Across the whole area the Glyn Formation is conformably overlain by greenish-grey, cleaved mudstones and thin grey sandstones of the Fron Frys Formation. A poorly preserved shelly fauna dates this as being of Lower Llandovery age.

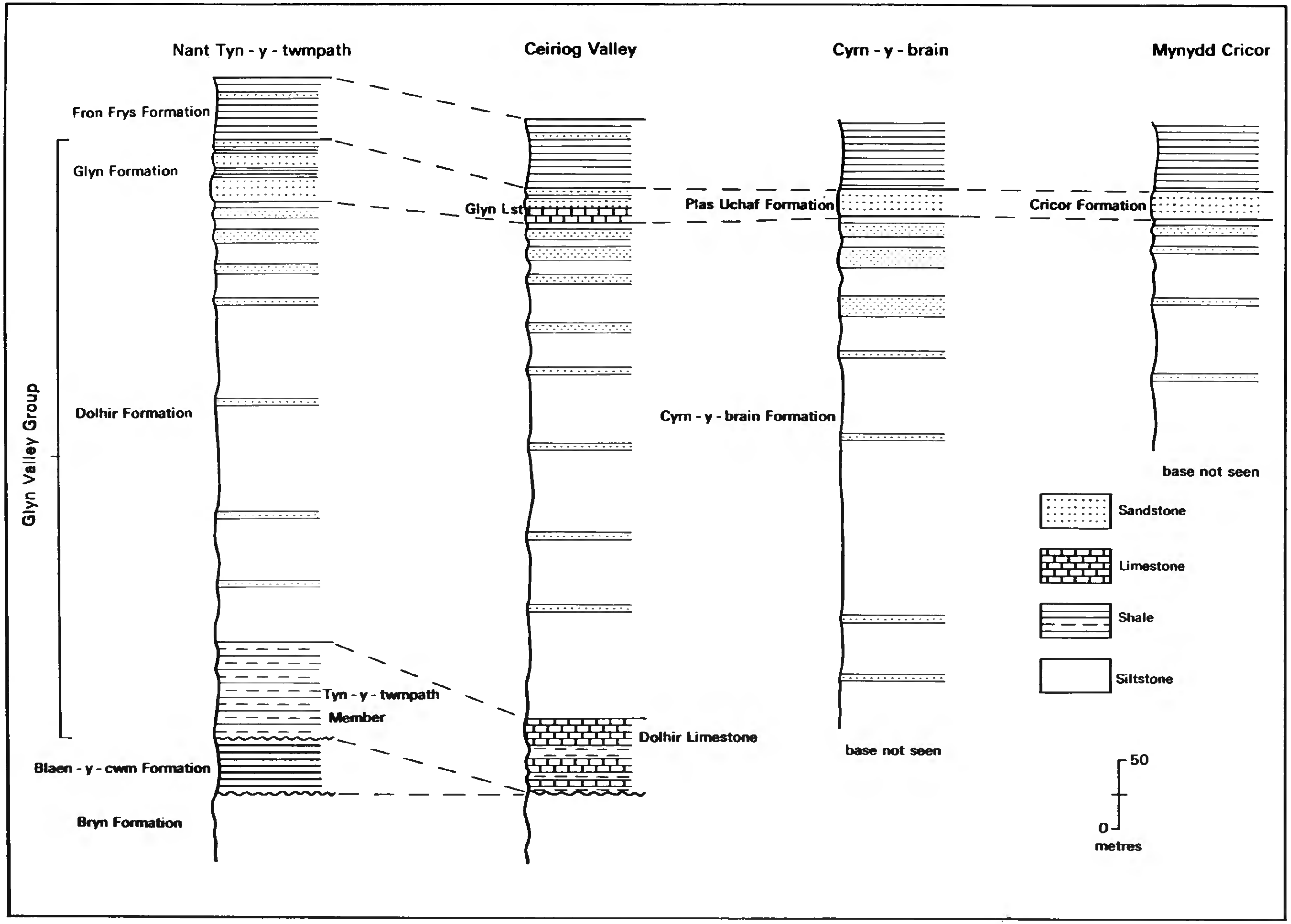


Fig. 2 Chart showing the correlation between the Ashgill formations of the areas studied.

Table 1 The number of pedicle, brachial or conjoined valves recovered from the various localities throughout the succession.

Locality	T			L		D																C							M		G						P
Species	1	2	3	1	2	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	1	2	3	4	5	6	7	1	2	1	2	3	4	5	6	1
Catazyga cf. *headi*	31																																				
Chonetoidea cf. *papillosa*	1								4																												
Glyptorthis cf. *maritima*	3			5		2	4	4	1	2	15			1																							
Katastrophomena dolhirensis		2		8		2	3		6	12	24																										
Kullervo complectens albida	1			1					3		2									1																	
Laticrura cf. *erecta*	1			8		1			12	12	3	3								2																	
Leangella cf. *scissa*	1		1	1			3		5	1	1									1																	
Leptaena cf. *rugosa*	2	1			1	1	7		3	2	26	1		1			5	2		22			5									2					
Lingulella sp. *B.*	1																																				
Nicolella actoniae	5			6			2	3	15	9	2			1			2			1											2		1				
Orthambonites cf. *humilidorsatus*	7			1				1		3	1									1																	
Oxoplecia cf. *plicata*	1					1			3		12									2			1														
Platystrophia anomala	7			6			1		20	20	22	4	4	1							3																
Porambonites sp.	5																																				
Reuschella sp.	7			1						1								1																			
Sampo cf. *ruralis*		1				1			2	1	8	2																			1		1				
Sowerbyella cf. *sladensis*	1	2		1		1	1	1	25	23	8			3	1	2	8	1	8	8	32		4	1	6				6	14	5	34	10	1	2	1	
Spinorthis geniculata	3		1	1																																	
Strophomena ceiriogensis	5	1		1				2		2	12						1	2		1			3	1													
Triplesia cf. *insularis*	5			2			1	1	6	2	39		1			3				8	1										3						
Dolerorthis aff. *intercostata*				2		1	3		4		3		1							1	2								1								
Eremotrema cf. *paucicostellatum*				1			2		7	8	5									1																	
?*Limbimurina* sp.				1																																	
Skenidioides cf. *asteroideus*				1			9	11	26	17	1		1	1	1			1		1											4						
Spiriferide gen. et sp. indet.				1																																	
Catazyga cf. *hicksi*								1			2																										
Christiania sp.									1	4	5		1	1																							
Cremnorthis sp.										2																											
Cryptothyrella crassa incipiens																				1		2	9	19	7	19											
Cyclospira sp.											1																										
Dalmanella cf. *testudinaria*								1			4							3	13		1		1			1				1	1	8	2				

Diambonia cf. *gibbosa*															1	4										7					
Dicoelosia cf. *indenta*	1					20		5				1	2	14	2											1					
Dicoelosia sp.	1				3	5																									
Fardenia scotica												2	3		1		1	1	2												
Gunnarella sp.			1																												
?*Howellites* sp.	6	2				8			3	2																					
Kjaerina sp.			6																												
?*Kozlowskites* sp.					1	1																									
Kullervo sp.															1																
Leptaenid gen et. sp. indet.															1																
Lingulella sp. *A*.		4				3																									
?*Luhaia* sp.															1												1				
Mjoesina marri															4							9									
Paracraniops sp.	2				1	3																									
?*Parastrophina* sp.															2																
Philhedra cf. *grayii*		1				1																									
Plaesiomys porcata		1		2	1	1		1							4	2		1	2				1				2	4			
Plectatrypa cf. *sulevi*														1																	
Portranella sp.		2	2												1			1													
Protozyga cf. *perplexa*						11																									
Ravozetina silvicola prima	1			35	37	2																									
Saukrodictya hibernica			1																												
Triplesiid gen. et sp. indet.															1																
Vellamo cf. *diversa*						1									4			7								1	1	2			
?*Dalmanella* sp.																	3														
Eoplectodonta sp.																		1									10				
Eostropheodonta hirnantensis																			14								1				1
Epitomyonia sp.																			3												
Platystrophia lutkevichi costellata																		7	4												
Plectatrypa cf. *gaspeensis*																		2						2							
Schizophorella cf. *fallax silicis*																		3	1							1		6			
Eodinobolus sp.																												1			
Hesperorthis sp.																											15		1		
Hirnantia sagittifera?																											7	1			3
Ptychopleurella sp.																										2					
Cliftonia sp.																															1

In the inliers to the north, the Dolhir Formation is represented by the coarser grained Cyrn-y-brain Formation, comprising over 500 m of tough, cleaved, blue siltstones and sandstones, the base of which is never exposed. The beds are locally very fossiliferous. On Cyrn-y-brain, the Plas Uchaf Formation, with a total thickness of about 15 m, rests conformably on the Cyrn-y-brain Formation and can be divided into three members. A massive, cleaved, coarse grained sandstone, 6 m thick, is succeeded by 5 m of platey-bedded muddy siltstone which is overlain by brown weathering, dark, blue grey sandy mudstone. Fossils are rare, with only a few brachiopods being recovered from the upper two members.

On Mynydd Cricor, the Cricor Formation is not as distinct lithologically as its equivalents on Cyrn-y-brain and at Glyn Ceiriog. It consists of impersistent bands of fine to coarse sandstone interbedded with bluish mudstones and attains a thickness of about 20 m. The beds yielded only a few unidentifiable brachiopods.

Age and correlation

To apply the fine zonation established at Cautley and Dent (Ingham 1966) is impossible at Glyn Ceiriog, where the fauna remained largely unchanged throughout Ashgill times. The overall size and diversity of the fauna gives it a definite Cautleyan aspect but, as can be seen from Table 1 where the localities are arranged in ascending order, there are subtle changes which may help to indicate which stage or stages are represented. Forms restricted to the lower part of the Dolhir Formation are also best known from the Cautleyan stage in Yorkshire e.g., *Catazyga* (zones 1–3), *Gunnarella* (zone 3), *Porambonites* (zone 3) and *Spinorthis* (zone 4). It seems therefore that the lower part of the Dolhir Formation can be taken as being high Cautleyan (zones 3–4) in age and ranging up into the Rawtheyan in the upper parts. This borne out by the close similarity between the lower Dolhir fauna and that from the Portrane Limestone (Wright, 1963, 1964, Ms) which has also been dated as high Cautleyan (Williams in Williams *et al.* 1972 : 56). Of the 52 genera found in the Dolhir Formation, 30 are found at Portrane and 11 are regarded as conspecific.

The large Ashgill fauna of the Killey Bridge Formation, Pomeroy, dated as low Cautleyan (Mitchell, 1977), has many genera in common with the Dolhir Formation but at the same time many of the characteristic forms found at Glyn Ceiriog are absent from the Irish deposits e.g., *Fardenia*, *Katastrophomena* and *Laticrura*, and it is felt that the Killey Bridge Formation with its strong Caradoc affinities is slightly older than the Dolhir Formation.

The Rawtheyan aspect of the Dolhir fauna is confirmed by comparison with the Rhiwlas Limestone of Bala, now regarded as being early Rawtheyan (zone 5) in age (Bassett in Williams *et al.* 1972 : 25). Of the 17 genera recorded from this by Bassett *et al.* (1966 : 263, 4), 12 occur at Glyn Ceiriog. This is substantiated by comparisons with other areas in Wales from which Rawtheyan faunas have been recognized, such as the Bodeidda Mudstones and Deganwy Mudstones of Conway, north Wales (Elles, 1909; Bassett in Williams *et al.* 1972 : 22) and the Slade and Redhill Mudstone Formation of Haverfordwest, south Wales (Reed, 1905; Cocks & Price, 1975). However in many cases the faunas are in need of revision as they have not been studied for some time (Fig. 3).

Ingham's detailed zonation of the Ashgill in the Cautley and Dent districts is based on trilobite assemblages, in particular the species of *Tretaspis* and their evolution. However, at Glyn Ceiriog the most common *Tretaspis* found occurred in the lower part of the Dolhir Formation and is close to *T. hadelandica brachystichus* Ingham, a form best known from zones 5 and 6 at Cautley but which has also been recorded from as low as zone 2. A *Tretaspis* of the *T. moeldenensis* group was recovered from the Tyn-y-twmpath Member, but preservation was insufficient for precise identification and dating. However, *T. moeldenensis* Cave has been positively identified from a locality within the Tyn-y-twmpath Member 11 km west of Glyn Ceiriog (Price, 1977 : 769, 772), which suggests a correlation with the Cautleyan Sholeshook Limestone of south Wales. A *Tretaspis*, regarded by Ingham (1970 : 43) to be conspecific with *T. latilimba brøggeri* Størmer, has been recorded from high up in the Dolhir Formation near Cynwyd, about 15 km west of Glyn Ceiriog, indicating a high Rawtheyan age for those beds.

The only other commonly occurring trilobite in the Dolhir Formation is *Flexicalymeme*

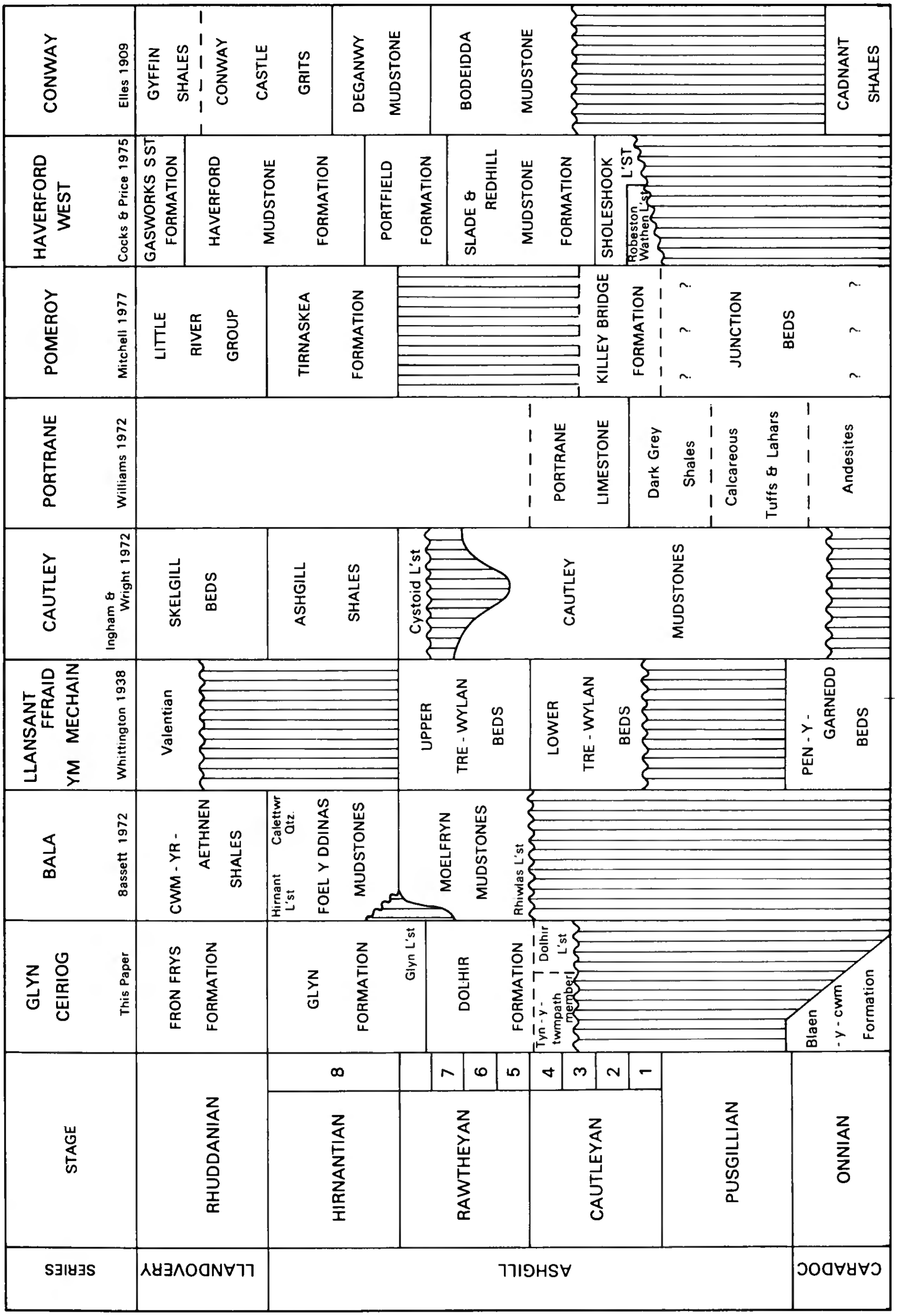


Fig. 3 Correlation of the Glyn Ceiriog succession with others in the British Isles.

quadrata (King) which may indicate a Rawtheyan age, because it occurs in the Upper Tre-wylan Beds of Llansantffraid ym Mechain (Whittington, 1938). These succeed the *P. parabola* and *D. drummuckensis* zones, both of which are considered to be Cautleyan (Ingham, 1966 : 494 and Price, 1973 : 539). The remaining trilobites from Glyn Ceiriog are not sufficiently well preserved to be of use in correlation or age determinations.

The fauna of the Glyn Formation is a continuation of that from the Dolhir Formation although it is much reduced in size. It contains elements of the widespread *Hirnantia* fauna: *Dalmanella* cf. *testudinaria* (Dalman), *Eostropheodonta hirnantensis* (M'Coy) and *Hirnantia sagittifera*? (M'Coy) and these, coupled with a stratigraphical position just below Lower Llandovery shales, might suggest a Hirnantian age for the formation: however, the diversity of the fauna and the presence of *Flexicalymene quadrata* at the base of the formation indicates a slightly older age.

The fauna of the Cyrn-y-brain Formation is typified by forms found only in the higher part of the Dolhir and Glyn Formations. If the preceding age determinations are to be accepted, then a Rawtheyan age is indicated for that part of the formation from which fossils have been collected. The presence of *Cryptothyrella crassa incipiens* (Williams), *Eostropheodonta hirnantensis* and *Plectatrypa* cf. *gaspeensis* Cooper at the top of the formation suggest a very high Rawtheyan or even Hirnantian age when compared to the Cautley and Dent succession, where such forms are known only from the Ashgill Shales (zone 8).

The three species so far recovered from the Plas Uchaf Formation, *Cliftonia* sp., *Hirnantia sagittifera*? and *Eostropheodonta hirnantensis*, are all members of the *Hirnantia* fauna and, with the formation coming between beds of Rawtheyan and Lower Llandovery ages, an Hirnantian age is concluded for the formation, which is also suggested by the restricted nature of the fauna.

Fossil localities

Tyn-y-twmpath Member: most of the fauna from this horizon was collected at locality T1 (Grid Ref: SJ 167374), in the stream bank 100 m north of Tyn-y-twmpath farmhouse, but some fossils were also recovered from T2 (Grid Ref: SJ 179369), a small exposure where the lane crosses the stream 600 m east-south-east of Tyn-y-celyn and T3 (Grid Ref: SJ 173372), a bank behind the house at Tyn-y-celyn (Fig. 4).

Dolhir Limestone Member: fossils were found 40 m below the main limestone band at locality L1 (Grid Ref: SJ 202367), in a bank marked by a line of trees 200 m south-south-east of Ddôl-hir; blocks of limestone were taken for etching from old quarries at L2 (Grid Ref: SJ 203369), by the roadside 200 m south-east of Ddôl-hir and L3 (Grid Ref: SJ 212364), south of the lane 120 m west of Cefngoed (Fig. 4).

Dolhir Formation: by far the most richly fossiliferous part of the formation lies immediately above the level of the basal members. About 1m above the limestone are localities D1 (Grid Ref: SJ 197367), among the roots of some trees 100 m south of Plas Einion and D2 (Grid Ref: SJ 199368), a small cliff 150 m east of Plas Einion; a little higher, about 16 m above the limestone is D3 (Grid Ref: SJ 198368), 50 m east of Plas Einion. 25–30 m above the limestone is D4 (Grid Ref: SJ 194367) on a ridge by the lane from Plas Einion to Aberwheel, 330 m west of Plas Einion and about 20 m higher are localities D5 (Grid Ref: SJ 193368) along the same ridge but 300 m east of Aberwheel, D6 (Grid Ref: SJ 203369) by the roadside 160 m east of Ddôl-hir and D7 (Grid Ref: SJ205368), a small exposure 300 m east of Ddôl-hir. A few specimens were obtained from D8 (Grid Ref: SJ 212365), a low cliff 160 m north-west of Cefngoed.

The fauna from the upper parts of the formation is much less diversified than at lower horizons and the number of individuals is less. There are eight main localities; D9 (Grid Ref: SJ 171375), where the lane crosses the stream 400 m north-north-west of Tyn-y-celyn, D10 (Grid Ref: SJ 155376), a low cliff by the lane 100 m north of Plas Nantyr, D11 (Grid Ref: SJ 151382), in the stream bank 800 m north of Plas Nantyr and a little higher in the sequence D12 (Grid Ref: SJ 174374), a small excavation by the side of the lane 260 m north of Tyn-y-celyn, D13 (Grid Ref: SJ 199374), a steep bank by the road 160 m west of Soar Chapel in Glyn Ceiriog village, D14 (Grid Ref: SJ 211368), a very small exposure on top of the hill 460 m south-west of Fron Frys farm.

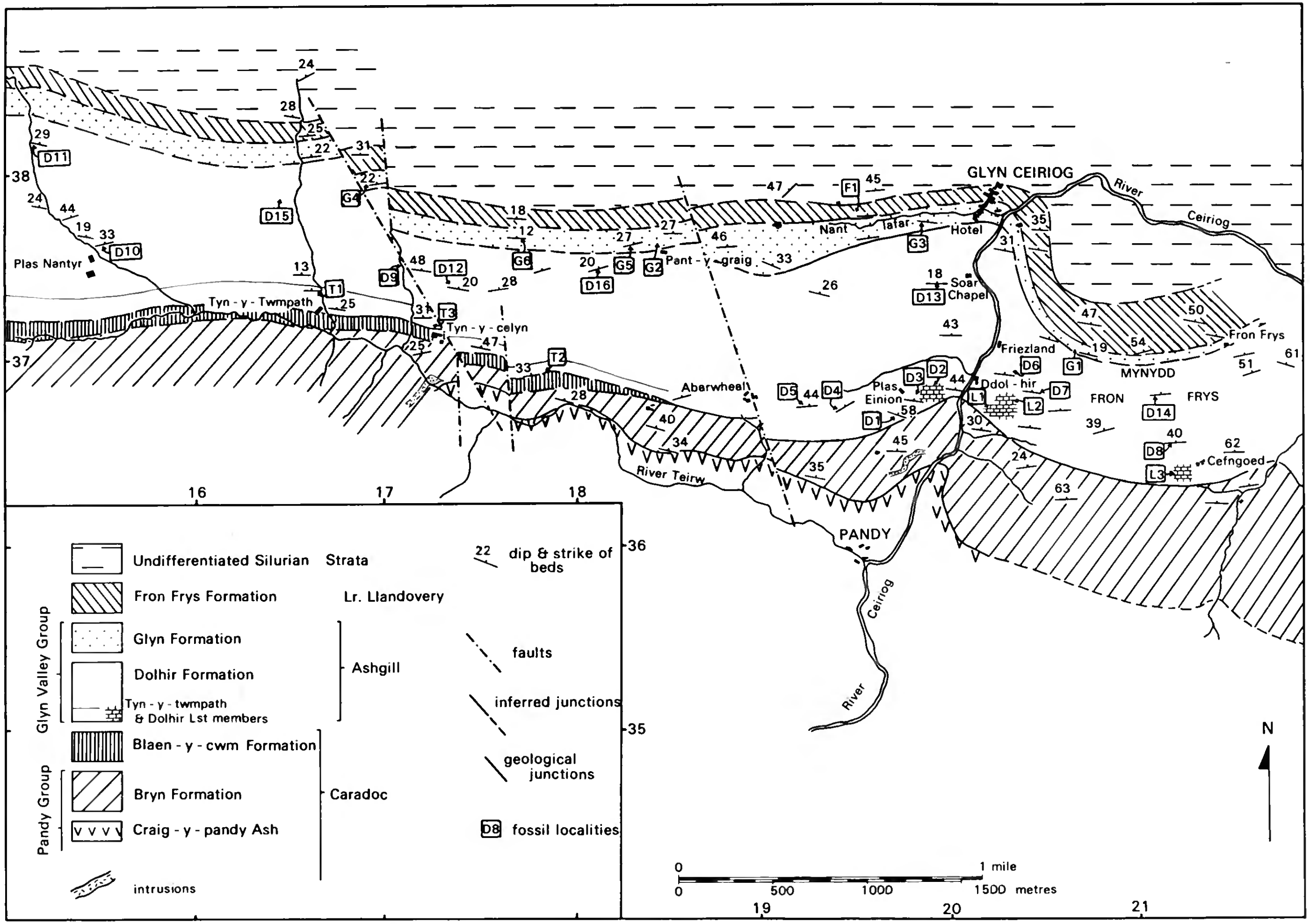


Fig. 4 Geological Map of the area around Glyn Ceiriog.

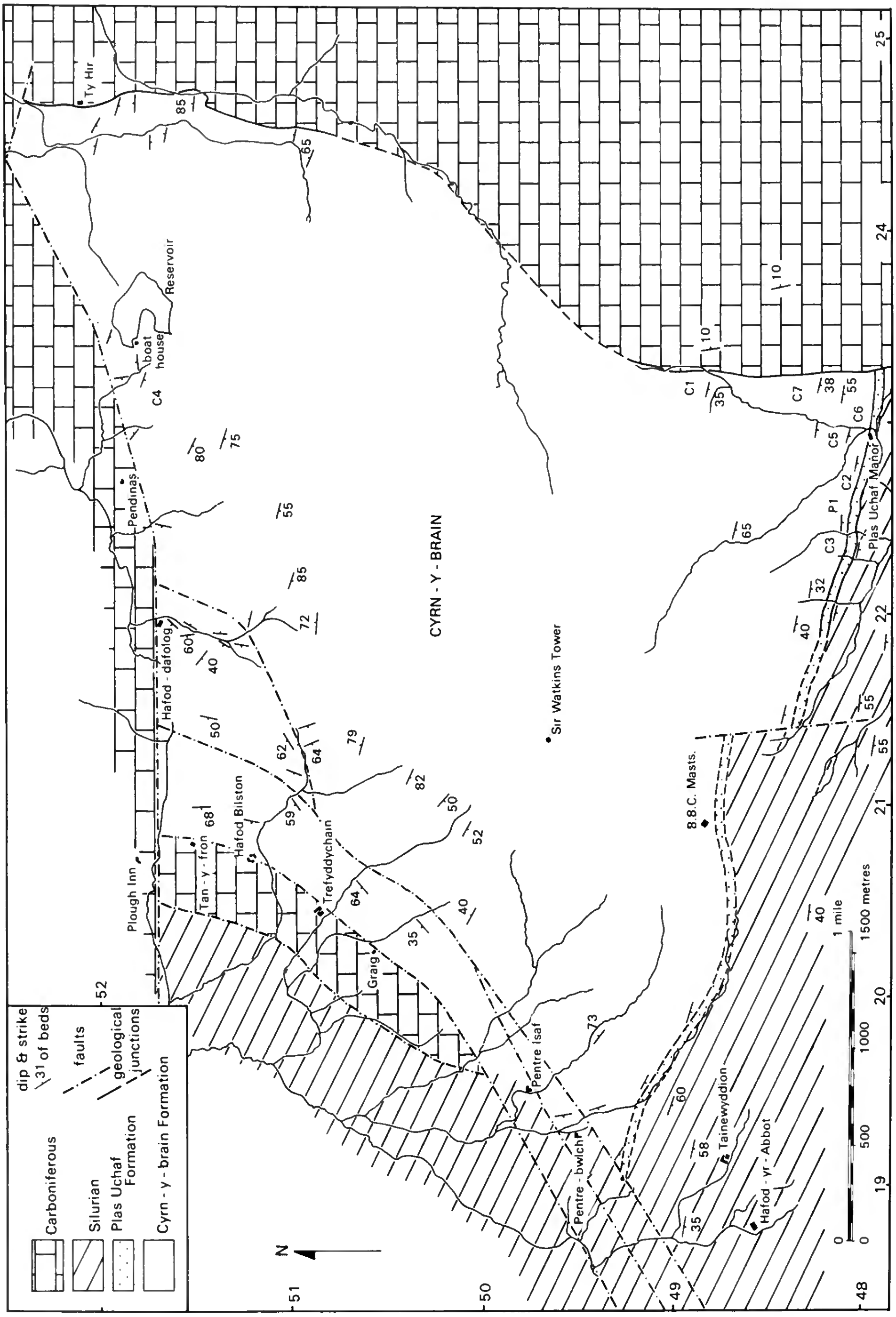


Fig. 5 Geological Map of the Cyrn-y-brain Inlier.

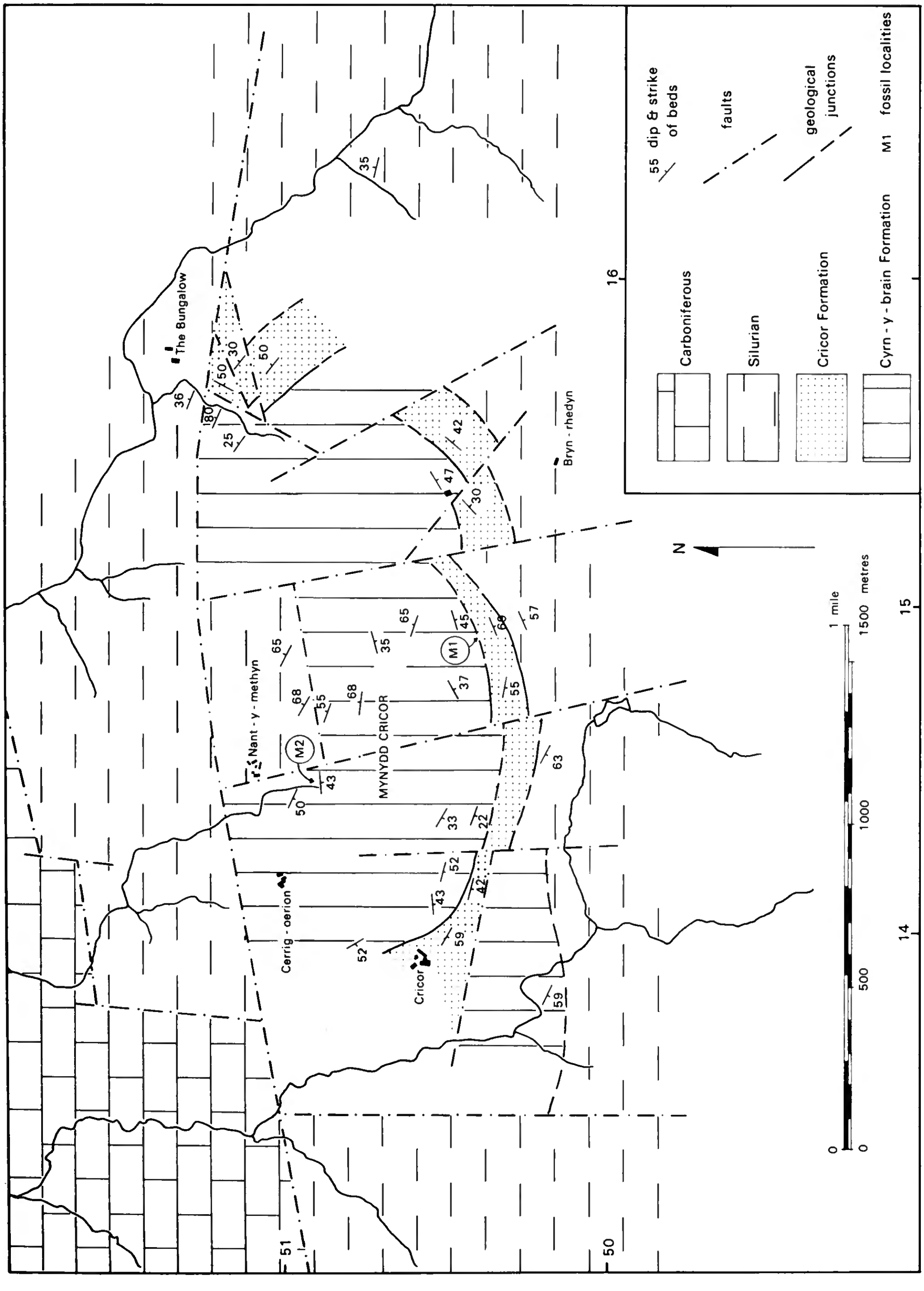


Fig. 6 Geological Map of the Mynydd Cricor Inlier.

The top 120 m of the formation are not well exposed but two localities provided a good sample of the fauna; D15 (Grid Ref: SJ 165378), an excavation by the side of the lane 600 m north of Tyn-y-twmpath and D16 (Grid Ref: SJ 181375), a small excavation by the road junction 360 m west of Pant-y-graig. (Fig. 4).

Glyn Formation: fossils were collected from the Glyn Limestone Member at locality G1 (Grid Ref: SJ 207370), an old quarry at the top of the hill, 400 m east of Friezland, and from the rest of the formation at localities G2 (Grid Ref: SJ 185376), a cliff behind the house at Pant-y-graig, G3 (Grid Ref: SJ 199377), in the southern bank of Nant Lafar by the old railway incline, 300 m west of the Glyn Valley Hotel, G4 (Grid Ref: SJ 169379), 750 m north-north-east of Tyn-y-twmpath, G5 (Grid Ref: SJ 184376), 150m west-north-west of Panty-y-graig, and G6 (Grid Ref: SJ 177376), 700 m north-east of Tyn-y-celyn (Fig. 4.)

Cyrn-y-brain Formation: most of the collections were made in the uppermost part of the formation exposed on the southern slopes of Cyrn-y-brain. The principal localities are C1 (Grid Ref: SJ 233488), in the stream banks 860 m north-north-east of Plas Uchaf Manor, C2 (Grid Ref: SJ 228480), by the side of the path 160 m west of Plas Uchaf and C3 (Grid Ref: SJ 224481), where the path crosses the stream 500 m west of the Manor house. One locality in the northern part of the inlier yielded quite a good sample from a similar horizon, C4 (Grid Ref: SJ 232518), by the side of a forestry road 200 m west of the boat house by the reservoir. Smaller collections were made from C5 (Grid Ref: SJ 229481), 100 m north of Plas Uchaf Manor, C6 (Grid Ref: SJ 232482) and C7 (Grid Ref: SJ 232483), respectively 250 m and 350 m north-east of the Manor (Fig. 5.)

The small collection taken from this formation on Mynydd Cricor was recovered mostly from localities M1 (Grid Ref: SJ 149504), 1 km south-east of Cricor farm, and M2 (Grid Ref: SJ 144509), 250 m east of Cerrig-oerion (Fig. 6.)

Plas Uchaf Formation: although this formation proved to be largely unfossiliferous a few specimens were recovered from its upper members around locality P1 (Grid Ref: SJ 225480), 400 m west of Plas Uchaf Manor (Fig. 5.)

Fron Frys Formation: a few specimens of *Plectatrypa* cf. *gaspeensis* Cooper, of Lower Llandovery age, were taken from this formation and included in the description with those recovered from the Cyrn-y-brain Formation. The locality, F1 (Grid Ref: SJ 194378), in the bank by the side of the road, 600 m west of the Glyn Valley Hotel is situated about 20 m above the base of the formation (Fig. 4.)

Systematic Palaeontology

The application of quantitative methods to the faunas from the Glyn Ceiriog district can raise considerable practical difficulties due to the distortion suffered by many of the specimens. This is caused both by post-depositional compaction and by cleavage associated with folding, but is not uniform throughout the different horizons. Those specimens recovered from the more competent Glyn and Cyrn-y-brain Formations have largely escaped distortion and for the purposes of statistical analysis, measurements of size and growth ratios have been taken only on those specimens which show the minimum of distortion, i.e., those specimens in which lines that can be assumed to have been originally at right angles, have remained at right angles or nearly so. However, assessment of those characters that remain more or less unchanged even after shape has been altered can still be made on most specimens, e.g., counts of ribs at a particular growth stage.

The measurements taken on morphological features of the specimens, preserved mostly as internal and external moulds, are the same as those outlined by Mitchell (1977 : 18–19) and the treatment of the data thus obtained was by the standard approach to biometrics of Kermack and Haldane (1950) adapted for use in comparisons of data derived from brachiopods by Williams (1962 : 69–79; 1963 : 333; 1974 : 23–25). All measurements are in millimetres.

Class **INARTICULATA** Huxley, 1869
Order **LINGULIDA** Waagen, 1885
Superfamily **LINGULACEA** Menke, 1828
Family **OBOLIDAE** King, 1846
Subfamily **LINGULELLINAE** Schuchert, 1893

LINGULELLA Salter, 1866

Lingulella sp. A.
Figs 11–15

?1908 *Lingula brevis* Portlock; Groom & Lake: 572.
1922 *Lingula* sp.; Wills & Smith: 191.

MATERIAL AND HORIZON. 2 pairs of conjoined valves, 4 pedicle and 1 brachial valves from the lower part of the Dolhir Formation, 1 m–50 m above the Dolhir Limestone, and 1 pedicle valve from the middle part of the formation.

DESCRIPTION. Biconvex, elongately oval shells, dark brown to black in colour; maximum width equal to less than one-half of valve length. Pedicle valve gently convex in both profiles with gently curved sides and pointed umbo. Brachial valve slightly shorter with rounded umbo. Ornament of fine concentric growth lines; two specimens show fine reticulate pattern reminiscent of *Glossella*. Inner shell layers show very fine radial striation. Internal structures not preserved except for vague trace of median septum posteriorly in one brachial valve.

DIMENSIONS

	length	width
Pedicle valve, BB37164	c. 33	13·5
Conjoined valves, BB37165	27·5	12·8
Pedicle valve, BB37166	23·8	9·3
Conjoined valves, BB37167	c. 19	c. 9
External mould of a brachial valve, BB37168	13·6	7·2

DISCUSSION. Most of the specimens are broken or slightly crushed, but their general form resembles *L. ovata* (M'Coy, 1846), although an unequivocal specific identification is unwarranted.

? ***Lingulella*** sp. B
Figs 16, 17

MATERIAL AND HORIZON. Single pedicle valve, BB37170, from the Tyn-y-twmpath Member at the base of the Dolhir Formation. Length 19·7 mm, width 16·0 mm.

DESCRIPTION. Elongately subcircular pedicle valve, bluish-black in colour, about four-fifths as wide as long; very gently convex in both profiles. Posterior margin indented by pedicle notch one-sixth as long as valve. Ornament of concentric growth lines; inner shell layers with very fine radial striations. One small patch on exterior shows development of short spines. Internal structures not preserved.

DISCUSSION. The generic placing of this specimen is uncertain, but the fine radial striations on inner shell layers are typical of *Lingulella*, although the well developed pedicle notch is better known from the Trematidae. The small spines are similar to those on *Spinilingula* but are not arranged in regular concentric rows, so for the present the specimen is doubtfully left in *Lingulella*.

Family **CRANIOPSIDAE** Williams, 1963

PARACRANIOPS Williams, 1963

Paracraniops sp.
Figs 18–23

?1908 *Crania* (?) sp.; Groom & Lake: 572.

MATERIAL AND HORIZON. Internal and external moulds of 11 specimens from lower part of the Dolhir Formation, 1–50 m above the Dolhir Limestone.

Description. Sub-circular to elongately sub-oval, gently convex pedicle (?) valves over three-quarters as wide as long and one-sixth as deep as long. Apex of valves about one-eighth of valve length from posterior margin; maximum width about mid-valve. Ornament of widely spaced concentric lamellae numbering 8–10 on valves less than 6 mm long. Well developed limbus seen on several specimens.

Ventral interior with medianly situated, slightly raised, shield-shaped platform, about one-half as long as valve, bearing a pair of sub-oval adductor scars, separated at their anterior ends by very faint longitudinal depression in one specimen and a faint ridge in another. Detail obscure in rest of sample. Shell material apparently impunctate.

Dimensions

	length	width
Internal mould of a pedicle valve, BB37172	1·9	1·2
External mould of a pedicle (?) valve, SMA 53.862 . . .	1·5	1·4
External mould of a pedicle (?) valve, BB37173	2·2	1·4
Internal mould of a pedicle valve, BB37174	2·2	1·7
External mould of a pedicle valve, BB37175	2·2	1·7
Internal mould of a pedicle valve, BB37176	2·0	1·3

Discussion. The indifferent preservation of these small specimens makes it difficult to distinguish between brachial and pedicle valves, and those specimens which have been tentatively identified as pedicle valves have only been placed as such after comparisons with photographs of *Paracraniops pararia* Williams, 1962 and *P. macella* Williams, 1963. It would be imprudent to attempt a specific identification with the material available, although the specimens may be separated from *P. macella* on the basis of the terminal location of the apex in that species. Temple (1968 : 11 and 1970 : 10) described an unnamed species of *Paracraniops* which superficially resembles the Glyn Ceiriog form, as does the type species *P. pararia.*

Superfamily **TRIMERELLACEA** Davidson & King, 1872
Family **TRIMERELLIDAE** Davidson & King, 1872

EODINOBOLUS Rowell, 1963

Eodinobolus sp.
Fig. 24

?1908 *Obolella* (?) sp.; Groom & Lake: 572.
?1922 ?*Dinobolus* sp.; Wills & Smith: 191.

Material and horizon. External and internal moulds of a single pair of conjoined valves, BB37178, from the Glyn Formation. Length about 10 mm, width about 9 mm.

Description. Dorsi-biconvex shells of sub-circular outline; both valves about nine-tenths as wide as long, brachial valve over one-sixth as deep as long. Shell surface apparently smooth in early growth stages but ornamented by fairly strong, concentric growth lines anteriorly. Internal structures not preserved.

Discussion. This poorly preserved specimen cannot be compared to any of the known species of *Eodinobolus*, which are mostly from rocks of Caradoc age.

Order **ACROTRETIDA** Kuhn, 1949
Suborder **CRANIIDINA** Waagen, 1885
Superfamily **CRANIACEA** Menke, 1828
Family **CRANIIDAE** Menke, 1828

PHILHEDRA Koken, 1889

***Philhedra* cf. *grayii* (Davidson, 1866)**

Figs 25–27

cf. 1866 *Crania* ? *Grayii* Davidson: 82, pl. 8, figs 22–24.
cf. 1978 *Philhedra grayii* (Davidson) Cocks: 31.

MATERIAL AND HORIZON. Two specimens from the lower part of the Dolhir Formation, 1 m–50 m above the Dolhir Limestone. Both brachial valves, one showing interior and exterior moulds BB37180 (length 2·5 mm, width 3·0 mm), the other a deformed external mould, BB37179.

DESCRIPTION. Brachial valve with sub-circular outline, slightly wider than long. Profile conical, height about seven-tenths of length; umbo about one-third of valve length from posterior margin on well preserved specimen; surface irregular; anterior slope slightly convex, posterior slopes slightly concave; valve profile becoming flattened marginally but width of flattened area varying around circumference. Pair of well defined, sub-circular muscle scars situated just in front of umbo. Punctae well seen over whole of internal surface. Ornament of fairly coarse, round-topped, slightly sinuous ribs, increasing in number by intercalation. Concentric growth-imbrications quite strongly developed in later stages and occasionally forming short, thick 'spines' at intersection with radial ornament.

DISCUSSION. The closest form to the Glyn Ceiriog specimens is that described from Keisley by Temple (1968 : 12). Both forms are characterized by distinctive fairly coarse ribbing which is most like that of the poorly known Wenlock form *Philhedra grayii* (Davidson, 1866) and the author follows Temple in ascribing the Glyn Ceiriog specimens to that species, although when more material becomes available it may be possible to separate them.

Class **ARTICULATA** Huxley, 1869
Order **ORTHIDA** Schuchert & Cooper, 1932
Suborder **ORTHIDINA** Schuchert & Cooper, 1932
Superfamily **ORTHACEA** Woodward, 1852
Family **ORTHIDAE** Woodward, 1852
Subfamily **ORTHINAE** Woodward, 1852
ORTHAMBONITES Pander, 1830

***Orthambonites* cf. *humilidorsatus* Wright, 1964**

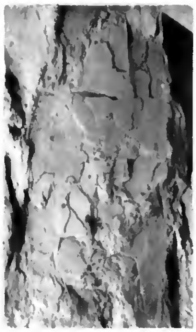
Figs 28–34, 39

1908 *Orthis calligramma* Dalman; Groom & Lake: 572, 577 (pars).
?1922 *Orthis calligramma* (?) Dalman; Wills & Smith: 187, 191 (pars).
cf. 1964 *Orthambonites humilidorsatus* Wright: 160, pl. 1, figs. 1–12.

MATERIAL AND HORIZON. Internal and external moulds of 7 pedicle and 7 brachial valves from the Dolhir Formation.

DESCRIPTION. Ventri-biconvex shells of transversely subquadrate outline with maximum width anterior to hinge-line; cardinal angles obtuse. Pedicle valve over two-thirds as long as wide and about three-tenths as deep as long; evenly convex in both lateral and anterior profiles; interarea curved, apsacline, less than one-tenth as long as valve; delthyrium open. Brachial valve three-fifths as long as wide and one-fifth as deep as long; flatly convex in lateral profile, anterior profile gently sulcate. Interarea very short, flat, anacline; notothyrium open. Ornamentation of 14–16 subangular costae on pedicle valve, 14–17 on brachial valve, and fine concentric fila yielding counts of 15 or 16 per mm, at 2 mm growth stage.

Ventral interior with short, stout teeth supported by receding dental plates; muscle field nine-tenths as long as wide and about one-third as long as valve, adductors slightly shorter than flanking diductors. *Vascula terminalia* seen in one specimen (Fig. 30). Dorsal interior with sockets bounded by short blade-like brachiophores supported only at their proximal ends by secondary shell substance. Oval-shaped cardinal process projecting from notothyrium, passing anteriorly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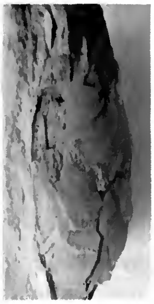
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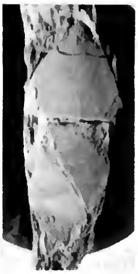
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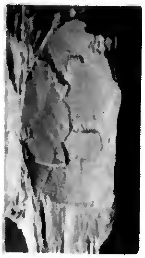
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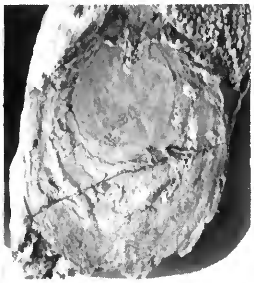
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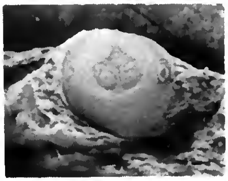
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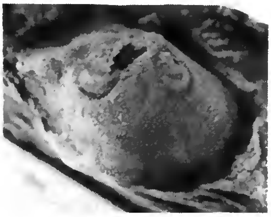
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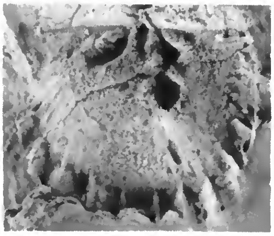
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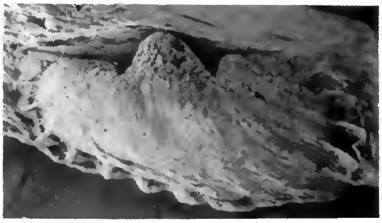
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Figs 11–15 *Lingulella* sp. A. Dolhir Formation: Fig. 11, BB37164, Exterior of a pedicle valve, ×1·5, loc. D6; Fig. 12, BB37165, Exterior of conjoined valves, ×1·6, loc. D2; Fig. 13, BB37166, Exterior of a pedicle valve, ×1·6, loc. D2; Fig. 14, BB37167, Exterior of conjoined valves, ×1·6, loc. D6; Fig. 15, BB37168, External mould of a brachial valve, ×2·1, loc. D2.

into platform; width variable, but always becoming narrower posteriorly. Poorly defined, subquadrate adductor scars about one-half as long as valve, divided longitudinally by median ridge extending anteriorly from notothyrial platform.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB37182	6·8	7·7
Internal mould of a pedicle valve, BB37183	—	11·0
Internal mould of a brachial valve, BB37184	c. 8	c. 11
Internal and external moulds of a pedicle valve, BB37185	3·7	5·6
Internal and external moulds of a brachial valve, BB37187	5·7	10·9

DISCUSSION. The ornament of the Glyn Ceiriog *Orthambonites* (14–16 costae on 2, 1, 1 pedicle valves) bears a close resemblance to that of *O. playfairi* (Reed), *O. cessatus* Williams and *O. humilidorsatus* Wright. *O. cessatus* differs in that it lacks a dorsal sulcus, has a high ventral interarea almost one-quarter as long as valve, and it has long blade-like brachiophores. Thirty-three specimens of *O. playfairi* from Craighead, Girvan have a mean depth : length ratio of 31·8% (var. 18·0); a sample of 6 Glyn Ceiriog valves has a mean of 29·5% (var. 137·34); a 't' test showed that there was no significant difference between them. The outline of the average Welsh pedicle valve tends to be more transverse than the Scottish shells, and a test comparing the a's proved the Glyn Ceiriog species to be significantly wider ($0{\cdot}05 > P > 0{\cdot}02$). However, the deformation in some of the Welsh specimens means that no great importance can be placed on this result; similar tests on the same statistics show that there is no significant difference between the Glyn Ceiriog form and *O. humilidorsatus* from the Portrane Limestone. The cardinalia of these two forms are similar, and Wright used this character to distinguish between the Irish shells and the closely related Estonian *O. lyckholmiensis* (Wysogorski) which also has a much deeper brachial valve.

The following statistical data were obtained for the sample:
Pedicle valves Length (l) : width (w), n = 6; $\bar{l}$ (var. l) = 4·53 (2·355) mm; $\bar{w}$ (var. w) = 6·45 (5·695) mm; r = 0·821; a (var. a) = 1·555 (0·0549).

Subfamily **PRODUCTORTHINAE** Schuchert & Cooper, 1931

NICOLELLA Reed, 1917

Nicolella actoniae (J. de C. Sowerby, 1839)

Figs 35–38, 40, 41

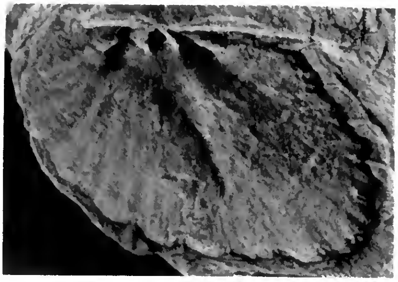
Figs 16–17 *Lingulella* sp. B. Tyn-y-twmpath Member. BB37170, Exterior and interior of a pedicle valve, ×1·7, loc. T1.

Figs 18–23 *Paracraniops* sp. Dolhir Formation: Fig. 18, BB37172, Internal mould of a pedicle valve, ×8·4, loc. D1; Fig. 19, SM.A53.862, External mould of a (?) pedicle valve, ×11·9; Fig. 20, BB37173, Latex cast of the exterior of a (?) Pedicle valve, ×7·3, loc. D4; Fig. 21, BB37174, Internal mould of a pedicle valve, ×5·9, loc. D1; Fig. 22, BB37175, Latex cast of the exterior of a pedicle valve, ×8·2, loc. D1; Fig. 23, BB37176, Internal mould of a pedicle valve, ×10·5, loc. D5.

Fig 24 *Eodinobolus* sp. Glyn Formation: BB37178, Internal mould of conjoined valves, dorsal view, ×2, loc. G3.

Figs 25–27 *Philhedra* cf. *grayii* (Davidson). Dolhir Formation: Fig. 25, BB37179, Fragment of the external mould of a brachial valve, ×6, loc. D2; Fig. 26, BB37180, Internal mould of a brachial valve, ×10·2, loc. D6; Fig. 27, BB37180, Latex cast of a fragment of the exterior of a brachial valve, ×10·2, loc. D6.

Figs 28–30 *Orthambonites* cf. *humilidorsatus* Wright. Tyn-y-twmpath Member: Figs 28–29, BB37182, Internal mould and latex cast of a brachial valve, ×4·9, loc. T1. Dolhir Formation: Fig. 30, BB37183, Internal mould of a pedicle valve, ×4·4, loc. D5.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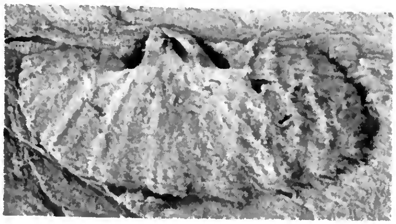
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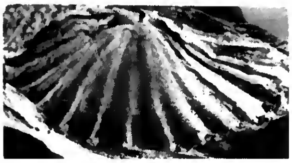
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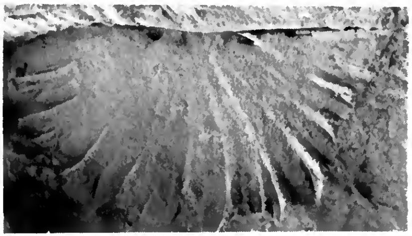
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1839 *Orthis actoniae* J. de C. Sowerby *in* Murchison: 639, pl. 20 fig. 16.
1908 *Orthis actoniae* Sowerby; Groom & Lake: 572, 577.
1917 *Orthis* (*Nicolella*) *actoniae* J. de C. Sowerby; Reed: 860 *pars*, pl. 10, figs 25, 26, non fig. 27.
1922 *Orthis actoniae* Sowerby; Wills & Smith: 191.
1963 *Nicolella actoniae* (J. de C. Sowerby); Williams: 352, pl. 1. figs 15–19.

MATERIAL AND HORIZON. Internal and external moulds of 34 pedicle, 15 brachial and one pair of conjoined valves from throughout the Dolhir Formation and Glyn Formation. Most specimens are deformed to a greater or lesser degree.

DIMENSIONS

	length	width
Internal mould of a pedicle valve, BB37189	c. 12	13·4
Internal and external moulds of a brachial valve, BB37190 . .	12·5	20·8
Internal mould of a brachial valve, BB37193	8·1	14·9
Internal mould of a pedicle valve, BB37194	10·6	14·2

DISCUSSION. In size, shape and style of ornament the Glyn Ceiriog *Nicolella* is very close to *N. actoniae* (Sowerby) and its subspecies *N. actoniae obesa* Williams, 1963, and so a full description is omitted here. Because of the deformation of the Glyn Ceiriog sample a statistical comparison with either of these two (Williams 1963) cannot be taken as reliable, but in 't' tests of valve length : maximum thickness of pedicle valves *Nicolella* from Glyn Ceiriog cannot be distinguished from either *N. actoniae* or *N. actoniae obesa*. In all the tests carried out between the Glyn Ceiriog sample and the other two forms the only significant difference established was between the Glyn Ceiriog species and *N. actoniae obesa*. In this the Glyn Ceiriog form proved to have a relatively shorter brachial valve, ($0{\cdot}05 > P > 0{\cdot}02$), and thus the shells are placed here within *Nicolella actoniae* (s.s).

The following statistical data were obtained for the Glyn Ceiriog sample:
Pedicle valves Length (l) : width (w), $n = 24$; $\bar{l}(\text{var. } l) = 9{\cdot}83\ (14{\cdot}974)$ mm; $\bar{w}(\text{var. } w) = 13{\cdot}39\ (21{\cdot}636)$ mm; $r = 0{\cdot}880$; $a(\text{var. } a) = 1{\cdot}202\ (0{\cdot}0149)$; $\overline{\log_e l}\ (\text{var.} \log_e l) = 2{\cdot}2129\ (0{\cdot}1442)$; $\overline{\log_e w}(\text{var } \log_e w) = 2{\cdot}5376\ (0{\cdot}1138)$; $r_e = 0{\cdot}888$; $\alpha(\text{var. } \alpha) = 0{\cdot}886\ (0{\cdot}00761)$.
Length (l) : thickness (t), $n = 19$; $\bar{l}(\text{var. } l) = 9{\cdot}92\ (19{\cdot}745)$ mm; $\bar{t}(\text{var. } t) = 3{\cdot}25\ (2{\cdot}484)$ mm; $r = 0{\cdot}704$; $a(\text{var. } a) = 0{\cdot}355\ (0{\cdot}00372)$; $\overline{\log_e l}(\text{var. } \log_e l) = 2{\cdot}2032\ (0{\cdot}1828)$; $\overline{\log_e t}(\text{var. } \log_e t) = 1{\cdot}0722\ (0{\cdot}2114)$; $r_e = 0{\cdot}7238$; $\alpha(\text{var. } \alpha) = 1{\cdot}0756\ (0{\cdot}03239)$.
Brachial valves Length (l) : width (w), $n = 14$; $\bar{l}(\text{var. } l) = 6{\cdot}32\ (6{\cdot}910)$ mm; $\bar{w}(\text{var. } w) = 11{\cdot}78\ (19{\cdot}657)$ mm; $r = 0{\cdot}887$; $a(\text{var. } a) = 1{\cdot}687\ (0{\cdot}0507)$; $\overline{\log_e l}(\text{var. } \log_e l) = 1{\cdot}7642\ (0{\cdot}1595)$; $\overline{\log_e w}\ (\text{var. } \log_e w) = 2{\cdot}3999\ (0{\cdot}1324)$; $r_e = 0{\cdot}8941$; $\alpha(\text{var. } \alpha) = 0{\cdot}9113\ (0{\cdot}01387)$.

Figs 31–34, 39 *Orthambonites* cf. *humilidorsatus* Wright. Tyn-y-twmpath Member Fig. 31, BB37184, Internal mould of a brachial valve, ×4·6, loc. T1; Fig. 32, BB37185, Internal mould of a pedicle valve, ×5, loc. T1; Fig. 33, BB37186, Latex cast of the exterior of a pedicle valve, ×5, loc. T1; Fig. 34, BB37187, Internal mould of a brachial valve, ×5, loc. T1; Fig. 39, BB37188, External mould of a brachial valve, ×5, loc. T1.

Figs 35–38, 40–41 *Nicolella actoniae* (Sowerby). Dolhir Formation: Fig. 36, BB37189, Internal mould of a pedicle valve, ×2·2, loc. D5; Fig. 37, BB37193, Internal mould of a brachial valve, ×2·6, loc. D4; Fig. 38, BB37196, Internal mould of a brachial valve, ×2·5, loc. D4. Dolhir Limestone Member: Fig. 35, BB37190, External mould of a brachial valve, ×2·4, loc. L3; Fig. 40, BB37190, Internal mould of a brachial valve, ×2·4, loc. L3. Tyn-y-twmpath Member: Fig. 41, BB37194, Internal mould of a pedicle valve, ×2·5, loc. T1.

Figs 42–47 *Dolerorthis* aff. *intercostata* (Portlock). Dolhir Formation. Figs 42, 45, BB37203, Internal mould and latex cast of a pedicle valve, ×1·4, loc. D4; Figs 43, 44, BB37197, Internal mould and latex cast of a brachial valve, ×2·4, loc. D6; Fig. 46, BB37199, Internal mould of a brachial valve, ×1·7, loc. D15; Fig. 47, BB37198, Latex cast of the exterior of a brachial valve, ×1·7, loc. D15.


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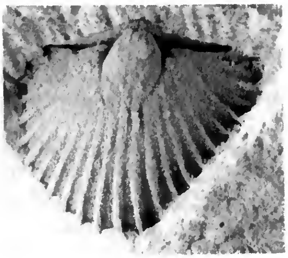
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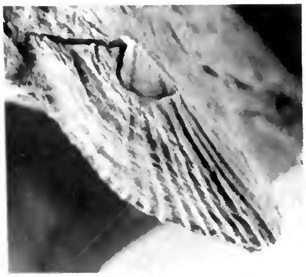
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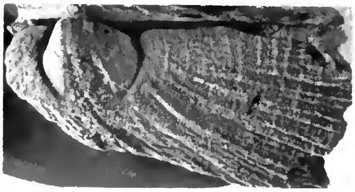
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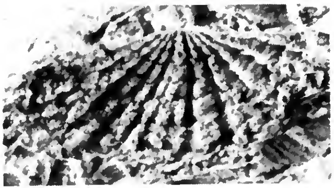
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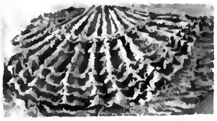
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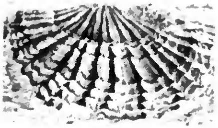
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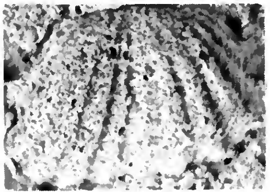
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Family **DOLERORTHIDAE** Öpik, 1934
Subfamily **DOLERORTHINAE** Öpik, 1936

DOLERORTHIS Schuchert & Cooper, 1931

Dolerorthis aff. ***intercostata*** (Portlock, 1843)
Figs 42–49, 53, 54

aff. 1843 *Orthis intercostata* Portlock: 454, pl. 37, fig. 3.
?1908 *Orthis flabellulum* Sowerby; Groom & Lake: 573 (pars).
aff. 1977 *Dolerorthis intercostata* (Portlock); Mitchell: 32, pl. 3, figs 24–27.

MATERIAL AND HORIZON. Specimens distributed throughout the Dolhir Formation with a single specimen from the Mynydd Cricor inlier, a total of 13 pedicle and 7 brachial valves, with additional fragmental material.

DESCRIPTION. Biconvex shells of transversely subquadrate outline, with maximum width at hingeline or just anterior to it, cardinal angles rectangular to obtuse. Pedicle valve almost three-quarters as long as wide, and depth ranging from one-sixth to one-third of valve length, some large valves being resupinate; lateral profile with greatest depth and convexity near umbo, becoming less convex or even concave anteriorly. Anterior profile gently convex. Interarea curved, catacline to apsacline, less than one-fifth as long as valve; delthyrium quite narrow, open. Brachial valve almost four-fifths as long as wide and one-fifth as deep as long; lateral profile evenly convex; anterior profile convex but with faint median sulcus in 6 out of 12 specimens. Interarea flat, anacline to orthocline, about one-seventh as long as valve; notothyrium open. Ornament consisting of rounded to subangular costae and costellae with subparallel sides. Ribs with density of 3 per 2 mm at 10 mm growth stage, crossed by faint fila, with density of 5–7 per mm at 5 mm growth stage, visible more clearly in rib interspaces. 13–16 primary costae at dorsal umbo with up to 5 additional costae along posterior margin on either side. Ventral ornament with median costa developing costella on either side, ribs 2 and 3 producing single external costella; rib 4 with external costella and occasionally an internal one also; rib 5 with costella on either side; commonly rib 6 and rarely rib 7 develop single costella, either internal or external; ribs lateral to 7 normally remain simple costae. Costellae do not usually become as strong as costae but differentiation commonly lost in later growth stages of large shells.

Ventral interior with strong teeth supported by receding dental lamellae; muscle field triangular to subpentagonal, almost as long as wide and three-tenths as long as valve; adductor scars about one-third as wide as whole scar and slightly shorter than diductors. Narrowly divergent trunks of *vascula media* extending anteriorly from in front of adductor scars, with *vascula genitalia* situated posterolaterally to them, are well seen in one specimen (BB37203). Dorsal interior with simple

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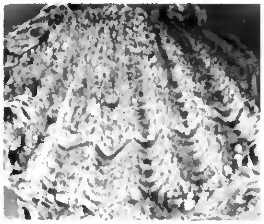
Figs 48–49, 53–54 *Dolerorthis* aff. *intercostata* (Portlock). Dolhir Formation. Fig. 53, BB37204, Internal mould of a brachial valve, ×1·4, loc. D4; Fig. 54, BB37205, Broken internal mould of a pedicle valve, ×1·7, loc. D4. Dolhir Limestone Member. Fig. 48, BB37200, Latex cast of the exterior of a pedicle valve, ×1·7, loc. L3; Fig. 49, BB37200, Internal mould of a pedicle valve, ×1·9, loc. L3.

Figs 50–52, 55 *Hesperorthis* sp. Glyn Formation. Fig. 50, BB37214, Latex cast of the exterior of a pedicle valve, ×2, loc. G2; Figs 51, 55, BB37212, Latex cast and internal mould of a pedicle valve, ×2·4, loc. G2; Fig. 52, BB37215, Internal mould of a pedicle valve, ×2·6, loc. G2.

Figs 56–62, 64 *Glyptorthis* cf. *maritima* Wright. Dolhir Formation: Fig. 56, BB37222, Internal mould of a pedicle valve, ×3·0, loc. D6; Fig. 57, BB37218, Internal mould of a brachial valve, ×3·4, loc. D6; Fig. 58, BB37225, External mould of a brachial valve, ×4·6, loc. D6; Fig. 59, BB37224, Internal mould of a brachial valve, ×3·5, loc. D2; Fig. 60, BB37218, External mould of a brachial valve, ×3·4, loc. D6; Figs. 61, 62, BB37219, External mould and latex cast of a brachial valve, ×3·5, loc. D3; Fig. 64, BB37221, Internal mould of a pedicle valve, ×3·0, loc. D6.

Fig, 63 *Ptychopleurella* sp. Glyn Formation. BB37226, Latex cast of the exterior of a brachial valve, ×5·0, loc. G1.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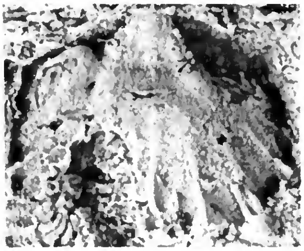
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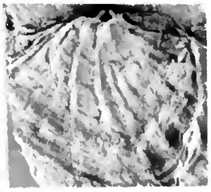
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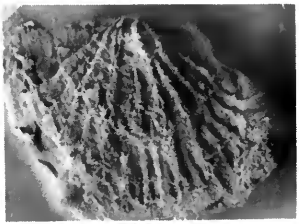
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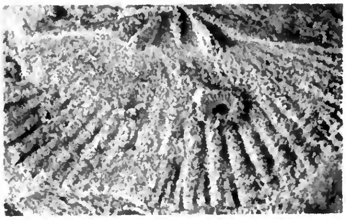
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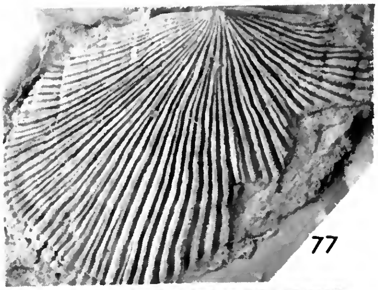
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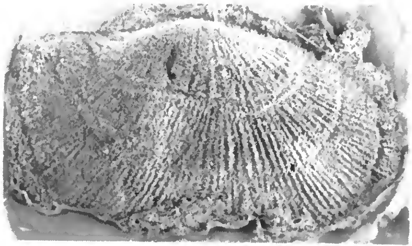
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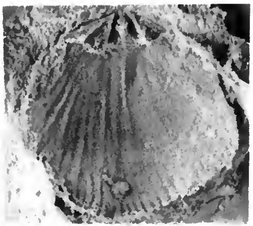
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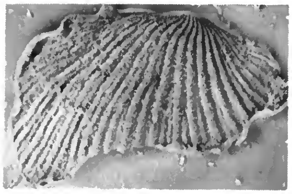
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cardinal process on thickened notothyrial platform, anterior to which is short, low, median ridge extending for three-tenths of valve length. Unsupported brachiophores short, blade-like, may be grooved along inner side. One specimen, BB37204, bears impressions of *vascula genitalia* and *vascula media* in the apocopate condition.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB37197	6·3	13·0
External mould of a brachial valve, BB37198	11·4	19·5
Internal mould of a brachial valve, BB37199	11·2	19·4
Internal mould of a pedicle valve, BB37200	18·0	25·8
External mould of a pedicle valve, BB37200	18·2	26·0
Internal mould of a pedicle valve, BB37203	28·9	32·1
Internal mould of a brachial valve, BB37204	32·4	31·0

DISCUSSION. Some features of this deformed *Dolerorthis* sample are well enough preserved to enable comparison to be made with some known stocks; e.g., the strong dorsal sulcus seen in *D. rankini* (Davidson) and *D. inaequicostata* Wright is lacking in the Glyn Ceiriog shells; the fact that only half of the brachial valves develop a faint median sulcus suggests similarities with *D. duftonensis* (Reed). One striking feature of these Welsh specimens is the resupinate nature of large pedicle valves and in this respect they resemble *D. intercostata* (Portlock) which is also faintly sulcate in the initial growth stages of the brachial valve.

The costae and costellae of the Glyn Ceiriog form are of almost equal strength at the margin of large shells. This condition applies equally to *D. duftonensis s.l.* but in *D. inaequicostata* the costellae are never as prominent as the primary ribs. Only one ventral exterior has the ornament well enough preserved to count the ribs, and this has 16 primaries at the umbo with 5 additional ribs arising along the posterior margin on either side. There are 21 ribs at the 3 mm growth stage, 23 at 5 mm and 39 at 10 mm. The pattern of ribbing on this shell does not differ markedly from that on any of the other forms except *D. tenuicostata* Williams which develops tertiary ribs.

D. duftonensis differs from the Glyn Ceiriog species in having a relatively shorter ventral muscle scar compared to valve length but its subspecies, *D. duftonensis prolixa* Williams is not significantly different in this respect; however, this latter is slightly more finely ribbed and more consistently develops a dorsal sulcus. The resupinate pedicle valve is considered to be an important characteristic of the Glyn Ceiriog species and for this reason it is suggested that it has strong affinities with the *D. intercostata* stock.

Figs 65–66 *Ptychopleurella* sp. Glyn Formation: Fig. 65, BB37227, Latex cast of the exterior of a pedicle valve, ×5·8, loc. G1; Fig. 66, BB37227, Internal mould of a pedicle valve, ×5·8, loc. G1.

Figs 67–73 *Spinorthis geniculata* Wright. Tyn-y-twmpath Member: Fig. 67, BB37231, Internal mould of a brachial valve, ×2·7, loc. T1; Fig. 68, BB37231, External mould of a brachial valve, ×2·7, loc. T1; Fig. 69, BB37234, Internal mould of a brachial valve, ×3·5, loc. T1; Figs. 70, 71, BB37233, External mould and latex cast of brachial valve, ×3·5, loc. T1. Dolhir Limestone Member: Figs. 72, 73, BB37230, External mould and latex cast of a brachial valve, ×3·5, loc. L3.

Figs 74–78, 81 *Plaesiomys porcata* (M'Coy). Cym-y-brain Formation. Fig. 74, BB37236, Latex cast of the interior of a brachial valve, ×4·1, loc. C3; Fig. 77, BB37241, Latex cast of the exterior of a pedicle valve, ×1·6, loc. C2; Fig. 78, BB37245, Latex cast of the exterior of a brachial valve, ×1·9, loc. C1; Fig. 81, BB37239, Internal mould of a pedicle valve, ×1·2, loc. C2. Glyn Formation: Fig. 75, BB37238, Broken internal mould of a pedicle valve, ×2·3, loc. G2; Fig. 76, BB37243, Latex cast of cardinalia, ×1·4, loc. G3.

Figs 79–80, 82–83 *Schizophorella* cf. *fallax silicis* Wright. Cyrn-y-brain Formation: Figs 79, 80 BB37249, Internal mould and latex cast of a brachial valve, ×2·7, ×2·5, loc. C2; Fig. 83, BB37247, Latex cast of the exterior of a pedicle valve, ×1·6, loc. C2. Glyn Formation: Fig. 82, BB37250,

Subfamily **HESPERORTHINAE** Schuchert & Cooper, 1931

HESPERORTHIS Schuchert & Cooper, 1931

Hesperorthis sp.
Figs 50–52, 55

?1908 *Orthis calligramma* Dalman; Groom & Lake: 572, 577 (pars).
?1922 *Orthis calligramma* Dalman; Wills & Smith: 187, 191 (pars).

Material and horizon. Internal and external moulds of 12 pedicle valves (e.g. BB37212, l = 14·3, w = 14·2; BB37214, l = 9·4, w = 11·3; BB37215, l = 13·0, w = 14·1) and 4 brachial valves, all from the Glyn Formation.

Description. Plano-convex shells of transversely subquadrate outline; maximum width along hinge-line or just anterior to it; cardinal angles rectangular to slightly obtuse. Pedicle valve almost nine-tenths as long as wide and nearly one-third as deep as long; moderately convex in both lateral and anterior profiles. Interarea high, curved, apsacline, over one-fifth as long as valve; delthyrium open with apical plate well developed. Brachial valves poorly preserved but about two-thirds as long as wide with broad shallow sulcus arising at umbo; interarea short, flat, anacline; notothyrium open. Ornamentation of rounded costae, 22–24 being recorded for 4, 0, 1 pedicle valves; interspaces also rounded.

Ventral interior with teeth supported by high thin dental plates; muscle field elongate, about four-fifths as wide as long and about one-third as long as valve. Dorsal interior with simple ridge cardinal process; other features not seen.

Discussion. *Hesperorthis* has been recorded from a few localities in Britain in recent years, but the genus has often been listed under *Orthis calligramma* and, until the existing lists have been re-examined, its distribution must remain uncertain. Williams (1962 : 107) described two species from the Girvan area, *H. australis exitis* and *H. craigensis*, neither of which are the same as the Welsh shells, both having finer ornamentation with 30–33 and 26–30 costae respectively. An unnamed species of *Hesperorthis* from Pomeroy (Mitchell, 1977 : 34) is said to resemble *H. australis exitis* and is therefore unlike the Glyn Ceiriog form. However, *Hesperorthis* sp. from the Portrane Limestone (Wright, 1964 : 711) is very like the present specimens, especially one pedicle valve with 22 ribs (Wright 1964 : Pl. 2 figs 8, 9, 14).

Subfamily **GLYPTORTHINAE** Schuchert & Cooper, 1932

GLYPTORTHIS Foerste, 1914

Glyptorthis cf. ***maritima*** Wright, 1964
Figs 56–62, 64

1908 *Orthis crispa* M'Coy: Groom & Lake: 573, 577.
1922 *Orthis crispa* M'Coy: Wills & Smith: 191.
cf. 1964 *Glyptorthis maritima* Wright: 172, pl. 1, figs. 21–29.

Material and horizon. Internal and external moulds of 20 brachial and 15 pedicle valves from the lower part of the Dolhir Formation and the Glyn Formation. A lot of the material is fragmentary and a certain amount of distortion is observed.

Description. Ventri-biconvex shells of transversely subquadrate outline. Pedicle valve about four-fifths as long as wide and one-quarter as deep as long; maximum width anterior to hinge-line; cardinal angles obtuse. Lateral and anterior profiles evenly convex. Interarea gently curved, apsacline; delthyrium open. Young forms with faint, narrow fold which disappears in later growth stages. Brachial valve with sulcus originating at umbo, but becoming shallower and flattening out anteriorly. Interarea short, flat, anacline; notothyrium open. Radial ornament of costae and costellae with total number of ribs at 3 mm ranging from 12–18 (mode 14), and at 5 mm, 16–24 (mode 18). Concentric lamellae well developed, varying from 1–4, but most commonly 2, per mm at 5 mm growth stage.

Ventral interior with subquadrate muscle scar about nine-tenths as wide as long, and one-third as long as valve and situated on low platform; slightly elevated median adductor scars about one-half as wide as complete scar. Teeth strong; dental plates bound muscle platform. *Vascula media* emanating from front of muscle scar. Dorsal interior with blade-like brachiophores bounding notothyrium; low median ridge extending from notothyrial platform to divide poorly defined adductor scars. Cardinal process a strong simple ridge.

DIMENSIONS

	length	width
Internal and external moulds of a brachial valve, BB37218 . .	7·9	—
External mould of a brachial valve, BB37219	4·9	9·0
Internal mould of a pedicle valve, BB37222	c. 11	—
Internal mould of a brachial valve, BB37224	6·1	9·7
External mould of a brachial valve, BB37225	2·9	5·9

DISCUSSION. The distorted and fragmentary specimens from Glyn Ceiriog do not lend themselves readily to a statistical analysis. However, enough information can be gleaned about the ribbing pattern and size of the ventral muscle field to allow comparisons with species bearing a close likeness to the Welsh form. In comparisons with shells of a similar age the closest morphological similarity with the Glyn Ceiriog species lies in the Portrane Limestone *G. maritima*. The contemporary American species *G. pulchra* (Wang, 1949), *G. insculpta* (Hall, 1847). *G. crispata* (Emmons, 1842) and *G. bellarugosa* (Conrad, 1843) all have finer ornament, and all but *G. crispata* have persistent dorsal sulci. Of the British species *G. speciosa* (Reed, 1944), from the Drummuck Group, differs in having a slightly finer ornament, maximum width along the hinge-line and a pronounced ventral fold. *G. balcletchiensis* (Davidson, 1883) has a similar outline to the Glyn Ceiriog form, but has a longer ventral muscle field, finer imbricate ornament and a more persistent dorsal sulcus.

G. maritima has an outline and ornament similar to the Glyn Ceiriog shells and no significant difference was found between the two in the length of the ventral muscle field relative to the length of the valve. However, whilst both forms possess an impersistent dorsal sulcus, it was replaced by a fold in some of the Portrane specimens, a feature not seen in the Glyn Ceiriog sample; also a significant difference was revealed between the two in a comparison of the length of the ventral muscle field relative to its width, the Glyn Ceiriog form was found to have a significantly wider muscle scar ($0{\cdot}002 > P > 0{\cdot}001$).

Therefore it is felt that although the Glyn Ceiriog *Glyptorthis* is close to *G. maritima*, it may not be exactly conspecific with it, and the material available was judged to be too poor for further assessments of the specific character of the shells to be made.

The following statistical data were obtained for the Glyn Ceiriog sample:

(*a*) Length (l) : thickness (d) of pedicle valves; n = 9; $\bar{l}$(var. l) = 6·08 (7·892) mm; $\bar{d}$(var. d) = 1·80 (0·568) mm; r = 0·9185; a(var. a) = (0·0016).

(*b*) Length of pedicle valve (l) : width of pedicle valve (w); n = 11: $\bar{l}$(var. l) = 7·55 (17·661) mm; $\bar{w}$(var. w) = 9·24 (15·515) mm; r = 0·8800; a(var. a) = 0·937 (0·022); $\overline{\log_e l}$(var. $\log_e l$) = 1·8859 (0·02701); $\overline{\log_e w}$(var. $\log_e w$) = 2·1398 (0·1670); r_e = 0·8937; α(var. α) = 0·7862 (0·01382).

(*c*) Length (l) : width (w) of ventral muscle scar; n = 11; $\bar{l}$(var. l) = 2·56 (1·713) mm; $\bar{w}$(var. w) = 2·49 (1·495) mm; r = 0·9735; a(var. a) = 0·9343 (0·00507).

(*d*) Length of ventral muscle scar (m) : valve length (l); n = 9; $\bar{m}$(var. m) = 2·29 (1·671) mm; l(var. l) = 8·29 (18·534) mm; r = 0·8775; a(var. a) = 3·33.

(*e*) Ratio of width of adductor scar : width of complete scar. Seven valves show a mean of 52·2% (var. 105·85) for this statistic.

(*f*) Length (l) : width (w) of brachial valves; n = 14; $\bar{l}$(var. l) = 6·39 (21·26) mm; $\bar{w}$(var. w) = 9·64 (22·27) mm; r = 0·881; a(var. a) = 1·023 (0·01953).


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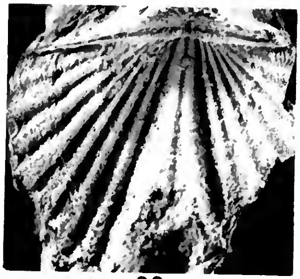
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PTYCHOPLEURELLA Schuchert & Cooper, 1931

Ptychopleurella sp.

Figs 63, 65, 66

1927 *Orthis* aff. *bouchardi* Davidson: Wedd, Smith & Wills: 38, 39.

Material and horizon. Internal and external moulds of a pedicle valve, BB 37227 (length 5·3, width 5·7), and an external mould of a brachial valve, BB 37226 (length c. 4, width 6·2), from the Glyn Limestone Member at the base of the Glyn Formation.

Description. Small subquadrate, biconvex shells with maximum width about mid-valve; cardinal angles obtuse. Pedicle valve about nine-tenths as long as wide and one-quarter as deep as long; both profiles evenly convex. Interarea flat, apsacline, about one-fifth as long as valve; delthyrium open. Brachial valve two-thirds as long as wide and one-third as deep as long. Lateral profile convex; anterior profile convex except for well developed median sulcus which expands anteriorly. Ornamentation of concentric lamellae with density of 3–5 per mm at 3 mm growth stage; occasional strong growth stage present. Radial ornament of simple costae with 11 on pedicle valve—a median rib with 5 on either flank; and 13 on brachial valve, 2 in sulcus with 5 or 6 on flanks.

Ventral interior with teeth supported by very short, receding dental plates; muscle field confined to umbonal cavity and of sub-triangular outline, over three-quarters as long as wide and over one-quarter as long as valve. Dorsal interior unknown.

Discussion. Specific identification of *Ptychopleurella* depends largely on the nature of the ornament, and the present sample is too small to assess variation within the population. However, a close resemblance to *P. twenhofeli* Wright, 1964, from the Portrane Limestone, is seen both in the general form of the shells and in the number of ribs present.

SPINORTHIS Wright, 1964

Spinorthis geniculata Wright, 1964

Figs 67–73

1964 *Spinorthis geniculata* Wright: 185, pl. 5, figs. 1–8, 10–12.

Material and horizon. Five brachial valves preserved as internal and external moulds (e.g. BB37230, l = 6·0, w = 9·6; BB37231, l = 9·6, w = 11·7; BB37233, l = 8·6, w = 11·1) from the lowest part of the Dolhir Formation. (Tyn-y-twmpath Member and its lateral equivalent at the base of the Dolhir Limestone).

Description. Subquadrate valves almost three-quarters as long as wide; lateral profile convex umbonally, becoming flatter anteriorly before being sharply deflected dorsally at between 7–8 mm

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Figs 84–87 *Schizophorella* cf. *fallax silicis* Wright. Cyrn-y-brain Formation: Figs. 84, 85, BB37247, Internal mould and latex cast of a pedicle valve, ×1·6, ×2·3, loc. C2. Glyn Formation: Fig. 86, BB37246, Broken internal mould of a pedicle valve, ×3·1, loc. G3; Fig. 87, BB37251, Internal mould of a brachial valve, ×2·2, loc. G3.

Figs 88–97 *Platystrophia anomala* sp. nov. Dolhir Formation: Figs 88, 89, Holotype, BB37256, External mould and latex cast of a pedicle valve, ×3, ×2·5, loc. D4; Fig. 90, BB37258, External mould of a pedicle valve, ×2·5, loc. D5; Fig. 91, BB37267, Internal mould of a brachial valve, ×3·5, loc. D4; Fig. 92, BB37262, Internal mould of a pedicle valve, ×3·8, loc. D5; Fig. 93, BB37263, Internal mould of a pedicle valve, ×3, loc. D6; Fig. 94, BB37261, Latex cast of the exterior of a brachial valve, ×3·7, loc. D6; Fig. 95, BB37265, Internal mould of a brachial valve, ×3·5, loc. D6; Fig. 96, BB37259, Latex cast of the exterior of a pedicle valve, ×2·8, loc. D7; Fig. 97, BB37257, Fragment of the external mould of a brachial valve, ×3·5, loc. D5.

Figs 98–99 *Platystrophia lutkevichi costellata* subsp. nov. Cyrn-y-brain Formation: Fig. 98, BB37269), Internal mould of a brachial valve, Holotype, ×1·2, loc. C2; Fig. 99, BB37272, Internal mould of a pedicle valve, ×2·4, loc. C2.

from umbo; anterior profile, before deflection, very gently convex except for broad, shallow median sulcus bounded on either side by a strong costa. Interarea extremely short, almost linear except for median portion. Radial ornament of sharply crested costae and costellae giving a basic pattern of 3 strong costae on either flank with costellae commonly arising by intercalation; a later median costa arises in the sulcus at between 2 mm and 3 mm from umbo. Concentric ornament of strong frills spaced at about 1 mm intervals with fine growth lines occasionally observed. At intersection of radial and concentric ornaments, hollow spines project at a steep angle from the surface of the valve, although they are not well preserved.

Interior of brachial valve with simple cardinal process situated on notothyrial platform from which a broad rounded ridge extends anteriorly to divide adductor muscle field, details of which are obscure. Thin, blade-like brachiophores diverge at 115°–120°; sockets shallow. Pedicle valve interior unknown.

Discussion. These few specimens can be closely compared with *S. geniculata* Wright, 1964. Although the deflection cannot be seen well in the Glyn Ceiriog shells, it occurs at about the same growth stage, i.e. at 7·4 mm from the umbo as compared to 7·15 mm in the Portrane form.

The mean width of the sulcus 3 mm from the umbo is 1·6 mm in 4 Glyn Ceiriog valves compared with 1·5 mm for 21 valves of *S. geniculata* from Portrane and the development of ribs in the sulcus is similar. The basic ribbing pattern is also the same for both samples; at the 5 mm growth stage the Glyn Ceiriog forms give total rib counts of 11, 12, 13, 13, 13 on 5 valves while the Portrane species has 11, 12, 13, 15, 15 ribs on 5 valves, which on a Rank Sum Test show no significant difference. On the basis of the brachial valves therefore, the Glyn Ceiriog shells may be regarded as being conspecific with the Irish specimens.

Family **PLAESIOMYIDAE** Schuchert, 1913

Subfamily **PLAESIOMYINAE** Schuchert, 1913

PLAESIOMYS Hall & Clarke, 1892

Plaesiomys porcata (M'Coy 1846)

Figs 74–78, 81

1846 *Orthis porcata* M'Coy: 32, pl. 3, fig. 14.
1908 *Orthis porcata* M'Coy: Groom & Lake: 573, 577.
cf. 1922 *Orthis* (*Plaesiomys*) *porcata* M'Coy: Wills & Smith: 191.

Material and horizon. Internal and external moulds of 3 pairs of conjoined valves, 5 brachial valves and 10 pedicle valves from throughout the Dolhir Formation and Glyn Formation.

Description. Dorsi-biconvex to convexo-concave shells of transversely sub-elliptical outline, maximum width anterior to hinge-line. Pedicle valve almost three-quarters as long as wide and one-sixth as deep as long, maximum depth close to umbo. Cardinal angles obtuse. Interarea about one-fifth as long as wide and about one-fifth as long as valve; flat, varying from apsacline to catacline; delthyrium open. Lateral profile varying from very gently convex to slightly concave; anterior profile slightly convex to flat. Brachial valve evenly convex in both profiles with faint sulcus modifying anterior profile in 3 out of 8 specimens. Depth over one-quarter of valve length on average but ranging from one-sixth to one-half. Interarea very short, less than one-tenth of valve length, curved orthocline to slightly apsacline. Ornament of subangular to rounded costae and costellae with about 17 primary costae on pedicle valve increasing to 28–34 ribs by 10 mm stage.

Ventral interior with teeth supported by receding dental plates which continue anteriorly to form low ridge bounding sub-pentagonal muscle field. This is almost as long as wide and extends for just over one-third of valve length. Pedicle callist small, medianly situated adductor scars small, elongately oval and almost enclosed by triangular diductor lobes; lateral diductor lobes well developed.

Dorsal interior with simple brachiophores diverging at about 90° and extending for about one-sixth of valve length, and supported only by secondary shell substance. Notothyrial platform moderately thick with high cardinal process differentiated into narrow shaft and grooved myophore. Low ridge extends anteriorly from platform to bisect slightly impressed adductor field which is just over two-thirds as long as wide. Suboval posterior scars larger than subquadrate anterior pair.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB37236	5·9	11·0
Internal mould of a pedicle valve, BB37238	c. 17	c. 22
Internal mould of a pedicle valve, BB37239	20·2	25·5
External mould of a pedicle valve, BB37241	27·0	c. 33
Internal mould of a brachial valve, BB37243	26·7	33·0
External mould of a brachial valve, BB37245	16·0	28·0

DISCUSSION. *Plaesiomys porcata* (M'Coy, 1846) is a widespread form in British Ashgill rocks, and the specimens described here are very close to topotype specimens except for the occasional development of a faint sulcus in the brachial valve. An important feature of the Plaesiomyidae is the ventral muscle field and in this respect there was no significant difference between the Welsh stock and topotype *P. porcata* from the Portrane Limestone (Wright 1964 : 188) on comparison of length : width ratios of the muscle scar. The two forms are also similar in the length : width ratios of the pedicle valves, although the Glyn Ceiriog sample is relatively shallower with a mean depth : length ratio of 17·6% (var. 24·19) for 11 valves, while 4 Portrane valves show the ratios 22, 23, 24 and 27%, but the difference is not significant. The broken nature of the material makes reliable data on the ribbing of the Glyn Ceiriog specimens difficult to obtain, but a density of 2–4 ribs per 2 mm was observed on 1, 3, 1 pedicle valves measured medianly 5 mm from the umbo. Three brachial valves give total counts of 28, 34, 37 ribs at the 7·5 mm growth stage. Corresponding measurements on *P. porcata* show another close similarity between the two forms.

Family **PLECTORTHIDAE** Schuchert & Le Vene, 1929
Subfamily **PLECTORTHINAE** Schuchert & Le Vene, 1929

SCHIZOPHORELLA Reed, 1917

Schizophorella cf. ***fallax*** (Salter, 1846) ***silicis*** Wright, 1964

Figs 79, 80, 82–87

1927 *Orthis* (*Platystrophia*) *spiriferoides*, M'Coy: Wedd, Smith & Wills: 38 (pars).
cf. 1964 *Schizophorella fallax silicis* Wright: 198, pl. 5, figs 9, 13–19, 22, 23, pl. 6, fig. 1.

MATERIAL AND HORIZON. Internal and external moulds of 2 brachial and 5 pedicle valves from the Glyn Formation, and 3 brachial and 3 pedicle valves from the Cyrn-y-brain Formation.

DESCRIPTION. Biconvex shells of rounded to transversely elliptical outline; cardinal angles obtuse, rounded; hinge-line width almost three-quarters of maximum valve width. Pedicle valve over seven-tenths as long as wide and just over one-quarter as deep as long; lateral profile convex, anterior profile convex, indented medianly by gently rounded sulcus originating at about 7 mm from umbo; anteriorly sulcus may form tongue-like dorsal projection. Interarea gently curved, apsacline, about one-quarter as long as valve; delthyrium open. Brachial valve about seven-tenths as long as wide and almost two-fifths as deep as long with broad median fold originating about 7 mm from umbo.

Ventral interior with small teeth supported by strong dental plates which converge towards valve floor and whose anterior continuance delimits lateral edges of elongate, oval muscle field. This measures over one-half as wide as long and about one-half as long as valve. Median adductor scar elevated on ridge; diductor scars partially raised from valve floor on parts of dental lamellae adjacent to muscle field. Anterior edge of muscle field indented medianly where diductor lobes extend beyond adductor ridge. Low, narrow ridge extends for short way in front of muscle field. Lightly impressed mantle canals seen to cover almost entire inner surface of one large pedicle valve (BB37247) (Fig. 7).


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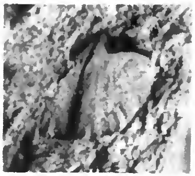
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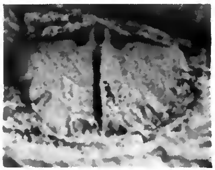
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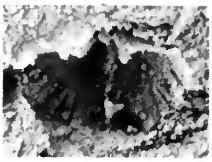
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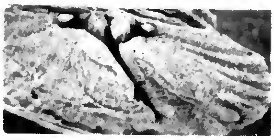
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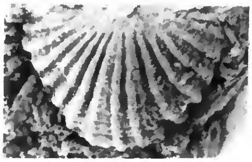
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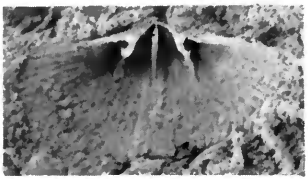
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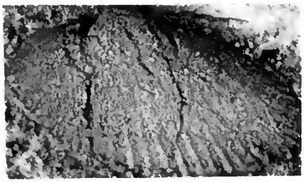
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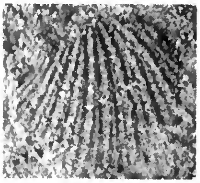
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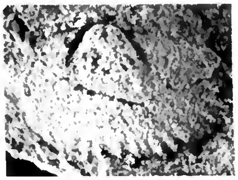
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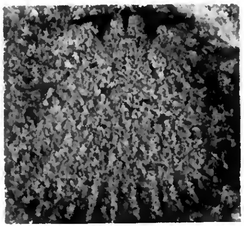
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Figs 100–102 *Platystrophia lutkevichi costellata* subsp. nov. Cyrn-y-brain Formation: Fig. 100, Holotype, BB37269, Latex cast of the exterior of a brachial valve, × 1·7, loc. C2; Fig. 101, BB37271, Internal mould of a brachial valve, × 2·1, loc. C2; Fig. 102, BB27273, Internal mould of a pedicle valve, × 2·5, loc. C3.

Dorsal interior with low notothyrial platform with cardinal process differentiated into crenulated myophore and short, thick shaft. Brachiophores widely divergent, blade-like, supported posteriorly by plates which pass into notothyrial platform. Sockets defined by fulcral plates. Poorly defined median ridge extends anteriorly from notothyrial platform for about one-third of valve length; less marked in large specimens. Indistinct, weakly impressed adductor muscle scar about one-third as long as valve.

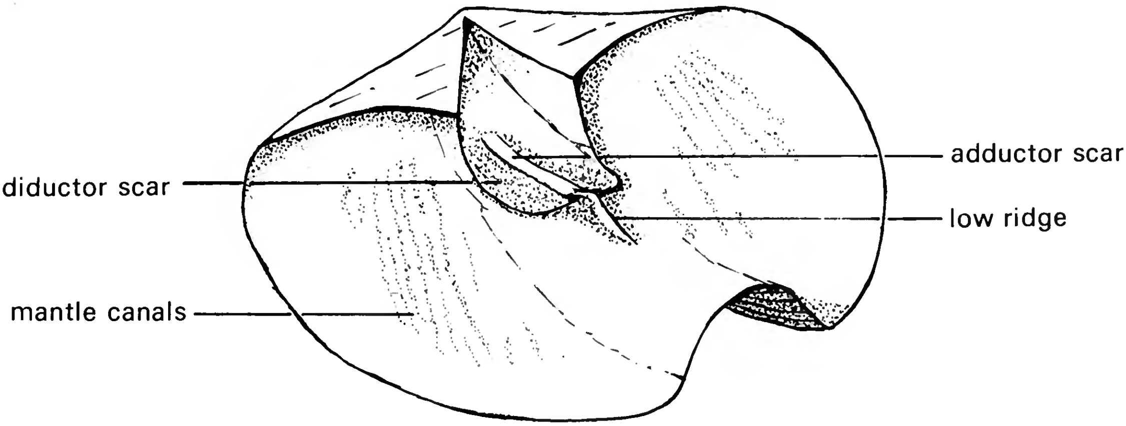

Fig. 7 Diagrammatic view of the ventral interior of *Schizophorella* cf. *fallax silicis*.

DIMENSIONS

	length	width
Internal mould of a pedicle valve, BB37246	11·4	—
Internal mould of a pedicle valve, BB37247	17·5	22·4
External mould of a pedicle valve, BB37247	17·6	22·6
Internal mould of a brachial valve, BB37249	10·8	11·3
External mould of a pedicle valve, BB37250	—	c. 14
Internal mould of a brachial valve, BB37251	20·8	20·0

DISCUSSION. The only species so far assigned to the genus are *S. fallax* (Salter, 1846), the subspecies *S. fallax silicis* Wright, 1964, and the doubtfully placed *S. kasachstanica* Rukavishnikova,

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Figs 103–105 *Cremnorthis* sp. Fig. 103, BB37275, Internal mould of a brachial valve, ×28, loc. D5; Fig. 104, 105, BB37276, Internal mould and latex cast of a brachial valve, ×18·0, loc. D5.

Figs 106–118 *Skenidioides* cf. *asteroideus* (Reed). Dolhir Formation: Fig. 116, BB37277, Internal mould of a brachial valve, ×4·8, loc. D5; Fig. 111, BB37278, Internal mould of a brachial valve, ×4·6, loc. D4; Fig. 117, BB37279, Internal mould of a pedicle valve, ×4·6, loc. D5; Fig. 110, BB37280, Latex cast of the exterior of a pedicle valve, ×4·9, loc. D5; Fig. 114, BB37284, Internal mould of a pedicle valve, ×2·8, loc. D5; Figs. 107, 108, BB37281, Internal mould and latex cast of a pedicle valve, ×4·0, loc, D5; Fig. 113, BB37282, Internal mould of a pedicle valve, ×6·2, loc. D4; Fig. 112, BB37288, Latex cast of the exterior of a pedicle valve, ×4·1, loc. D6; Fig. 109, BB37285, Internal mould of a brachial valve, ×8·2, loc. D4; Fig. 115, BB37291, Latex cast of the exterior of a brachial valve, ×3·8, loc. D15; Fig. 106, BB37290, Internal mould of a brachial valve, ×3·6, loc. D5; Fig. 118, BB37289, Latex cast of the exterior of a pedicle valve, ×3·8, loc. D4.

Figs 119–125 *Hirnantia sagittifera* ? (M'Coy). Plas Uchaf Formation: Figs 119–120, BB37292, Internal mould and latex cast of a brachial valve, ×5·9, loc. P1. Glyn Formation: Fig. 121, BB37298, Internal mould of a pedicle valve, ×3·6, loc. G3; Fig. 125, BB37295, Internal mould of a brachial valve, ×5·0, loc. G2; Fig. 122, BB37293, Internal mould of a brachial valve, ×5·3, loc. G2; Fig. 123, BB37293, Latex cast of the exterior of a brachial valve, ×5·3, loc. G2; Fig. 124, BB37297, Internal mould of a pedicle valve, ×5·0, loc. G2.

1956 from Kazakhstan, which lacks the dorsal median ridge, fulcral plates and convergent supporting plates that are characteristic of *Schizophorella fallax*. The principal difference between *S. fallax fallax* and *S. fallax silicis* is that the latter possesses a narrower more elongate ventral muscle field and a stronger dorsal median ridge. Mitchell (1977 : 46) reinvestigated the species and showed that *S. fallax silicis* has slightly coarser ribbing, but concluded from a very small sample that the difference in stature of the dorsal median ridges is of little importance.

In the small sample described here no external moulds are well enough preserved for a comparison of ornaments to be made but the ventral muscle scar on the Welsh species has similar relative dimensions to that of *S. fallax silicis*. Following Mitchell, a low taxonomic weighting is here given to the nature of the dorsal median ridge in the Glyn Ceiriog species, and much more importance to the form of the ventral muscle field; the specimens are accordingly regarded as being close to the Portrane subspecies.

Subfamily **PLATYSTROPHIINAE** Schuchert & Cooper, 1929

PLATYSTROPHIA King, 1859

Platystrophia anomala sp. nov.
Figs 88–97

1908 *Platystrophia biforata* Schlotheim: Groom & Lake: 573.

Diagnosis. A small *Platystrophia* most commonly with a single persistent median costa in the ventral sulcus, although an additional costa or two may develop in larger specimens. It differs from known species in that the second and third ribs in the sulcus do not necessarily appear even in quite large specimens.

Material and horizon. Internal and external moulds of 42 brachial and 49 pedicle valves from localities throughout the Dolhir Formation. Large specimens are mostly fragmentary but smaller ones are quite well preserved although some have been distorted by cleavage.

Description. Strongly dorsi-biconvex shells of subrectangular outline; maximum width slightly anterior to hinge-line. Ventral interarea short, flat to slightly curved, apsacline, less than one-tenth of valve length; that of brachial valve shorter, about three-fifths as long as ventral interarea, curved, anacline. Ventral sulcus deep with flat sides and floor, maximum width at anterior margin about one-third of valve width; corresponding dorsal fold high, flat-topped. Ornamentation of 5–8 strong angular costae on flanks of 9, 11, 12, 8 pedicle valves respectively at 5 mm growth stage; the number may increase to 10 in large shells by development of additional costae along posterior margin. Sulcus with single median costa umbonally; additional sulcal ribs not developed in most specimens but extra ribs may be intercalated after 4 mm growth stage. A similar development is seen on dorsal fold with up to four ribs developed by branching of two primaries. Surface of shell covered in tiny pustules.

Pedicle valve interior with moderately strong teeth and slightly ventrally convergent dental plates whose anterior ends bound elongate, suboval muscle field. This is about two-fifths as long as valve and situated on thickened platform of secondary shell. Adductor scar occupies floor of platform, which tapers posteriorly and diductor lobes are attached to inner sides of dental plates From anterior ends of dental plates pair of slightly divergent, low, sinuous ridges extend. these enclose small oval areas on either side of muscle platform which may possibly be attachment areas for adjustor muscles. On either side of muscle field, outside dental plates, are pair of arcs of pustules, presumably delimiting inner edge of *vascula genitalia*. These structures are seen in several specimens but particularly BB37262 (Fig. 92) (Fig. 8). Brachial valve interior with stout tusk-like brachiophores and small shallow sockets defined by fulcral plates. Cardinal process simple low ridge, rising from fairly thick notothyrial platform. Quadripartite adductor scars with posterior pair smaller than anterior. Impressions of *vascula genitalia* seen outside muscle field in several specimens.

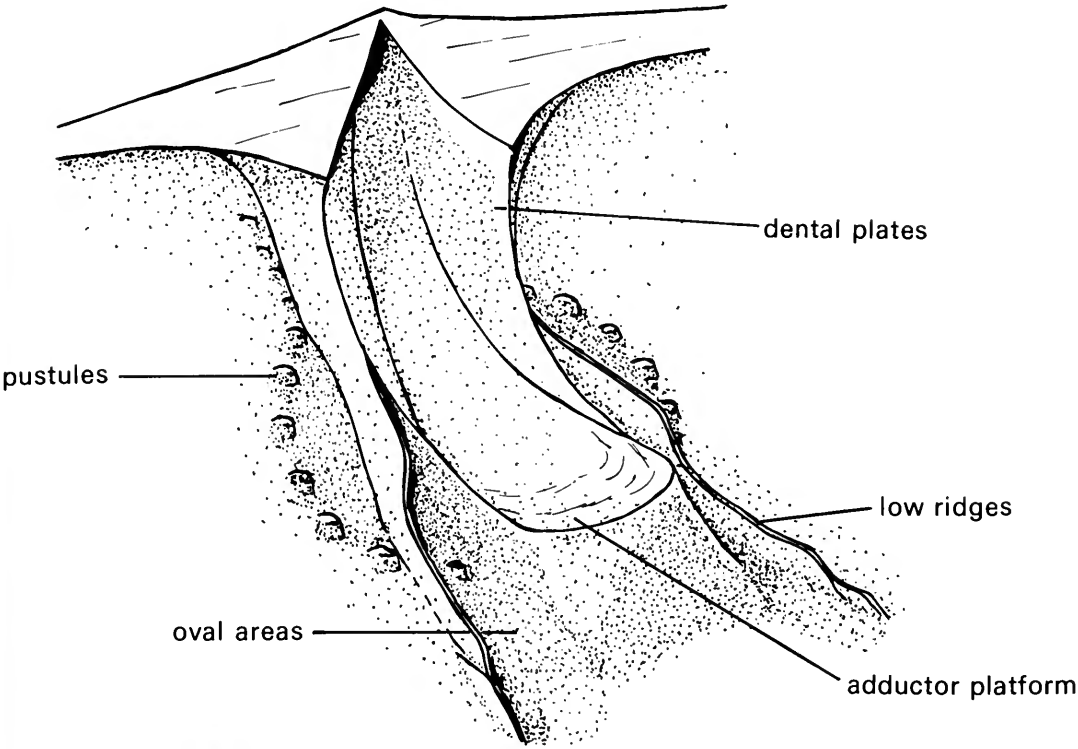

Fig. 8 Diagrammatic view of the ventral interior of *Platystrophia anomala* sp. nov.

TYPE MATERIAL

	length	width
External mould of a pedicle valve, holotype, BB37256 . . .	—	c. 15
External mould of a pedicle valve, BB37258	—	c. 13
External mould of a pedicle valve, BB37259	—	20·0
External mould of a brachial valve, BB37260	8·0	14·8
External mould of a brachial valve, BB37261	7·3	9·8
Internal mould of a pedicle valve, BB37263	—	17·6

DISCUSSION. Several authors have attempted to establish a logical way to aid identification of *Platystrophia* species. Cumings (1903) divided the genus into three species groups on the basis of the number of ribs in the ventral sulcus of early growth stages, and termed unicostate, bicostate, and tricostate (Schuchert & Cooper 1932 : 67). McEwan (1920) elaborated upon earlier work, and subdivided the biplicate (bicostate) group into four subgroups based on the development of further ribs in the sulcus after the initial pair.

Williams (1962 : 126 and 1963 : 371) and Wright (1964 : 206) both pointed out the artificial nature of the 'pigeon-hole' classification, because specimens which would belong to different species groups can be found within a single population sample. Under McEwan's classification the Glyn Ceiriog *Platystrophia* belongs to the unicostate group but those specimens which do develop extra ribs in the sulcus could be placed in the tricostate group. All variations within the sample are found in a single horizon so there is no question of an evolutionary sequence being involved. Cumings (1903 : 11) states that practically any group of *Platystrophia* may produce an occasional unicostate individual but in the Glyn Ceiriog sample 1–3 costae are present in the sulcus of 15, 4 and 0 pedicle valves at the 5 mm growth stage so the unicostate condition is dominant. The sample shows that 4 out of 19 pedicle valves have two ribs in the sulcus at the 5 mm growth stage and that by 6 mm a third rib may be intercalated and at that growth stage 3 out of 15 valves have three ribs.

The unicostate condition serves to distinguish the Glyn Ceiriog specimens from contemporary species such as *P. scotica*, *P. fissicostata*, *P. camerata* and *P. lutkevichi*, all of which belong to the bicostate group, and *P. molaris* which is a tricostate form. The shells which most closely resemble this Welsh species are members of the tricostate group, especially the 'high fold' variety in which the fold has become compressed and the lateral ribs tend to disappear. However, the fold on the Dolhir specimens is not compressed and the lateral ribs remain as strong as the median costae, thus the Glyn Ceiriog *Platystrophia* is regarded as a separate species.

Platystrophia lutkevichi Alichova ***costellata*** subsp. nov.

Figs. 98–102

1922 *Orthis* (*Platystrophia*) *biforata* Schlotheim; Wills & Smith: 191.
1922 *Orthis* (*P.*) *biforata* var. *fissicostata* M'Coy; Wills & Smith: 191 (pars).

DIAGNOSIS. *Platystrophia* differing from *P. lutkevichi* Alichova in developing costellate ornament on flanks of valves.

MATERIAL AND HORIZON. Internal and external moulds of 5 pedicle and 6 brachial valves from near the top of the Cyrn-y-brain Formation, 5–12 metres below junction with the Plas Uchaf Formation.

DESCRIPTION. Strongly dorsi-biconvex shells of subrectangular outline; maximum width near hinge-line, cardinal angles rectangular or roundedly obtuse. Pedicle valve over two-thirds as long as wide and one-third as deep as long. Lateral profile convex; anterior profile convex on flanks with broad, flat median sulcus about one-half as wide as maximum valve width, at anterior margin. Interarea short, curved, apsacline; delthyrium open. Brachial valve four-fifths as long as wide and over two-fifths as deep as long. Strongly convex in lateral profile; anterior profile with high, steep sided, flat-topped fold separating convex flanks. Interarea short, curved, anacline; notothyrium open. Ornament of 6–9 subangular costae on flanks of 1, 3, 0, 2 brachial valves respectively at 5 mm growth stage; these may increase by branching at about 10 mm growth stage. Sulcus with 2 initial costae but further ribs are intercalated by 5 mm growth stage; fold initially with 3 ribs which may branch by 5 mm growth stage.

Ventral interior with strong teeth supported by slightly convergent dental plates whose anterior ends bound elongate, suboval muscle field, three-fifths as long as wide, two-fifths as long as valve and situated on thickened platform of secondary shell. Dorsal interior with strong tusk-like brachiophores and simple, ridge-like cardinal process on thickened notothyrial platform, with very abrupt anterior edge. Subquadrate muscle field, with posterior scars smaller than anterior, divided longitudinally by narrow median furrow. Strongly impressed ribbing obscures mantle canals.

TYPE MATERIAL

	length	width
Internal mould of a brachial valve, holotype, BB37269 . . .	28·0	36·2
Internal mould of a brachial valve, BB37271	16·4	18·9
Internal mould of a pedicle valve, BB37272	18·3	—
Internal mould of a pedicle valve, BB37273	11·6	c. 16

DISCUSSION. These fairly large specimens are all members of the bicostate species group and can be divided into subgroups, A, C and D according to McEwan's classification, again exposing the weakness of such a subdivision. The sample shows that by the 5mm growth stage 1 out of 5 specimens has 3 ribs in the sulcus, and by the 10mm growth stage 3 out of 5 specimens have 4 ribs, 1 out of 5 has 5 ribs and 1 out of 5 has 6 ribs. On the fold at the 5mm growth stage, 6 out of 6 specimens still have 3 ribs, and by the 10 mm growth stage 3 out of 6 have 3 ribs, 2 out of 6 have 5 ribs and 1 out of 6 has 6 ribs. One large specimen has 7 ribs on the fold at 20 mm and another has 8 ribs at 15 mm. A similar variation in rib development was described in the *Platystrophia* from the Portrane Limestone by Wright (1964 : 207) but the Cyrn-y-brain specimens differ in that 6 out of 11 specimens are seen to develop costellae on the flanks. This costellate condition is developed on shells within the same size range as the Portrane specimens and also serves to distinguish the Welsh form from other known subspecies of *P. lutkevichi*, i.e. *P. lutkevichi lutkevichi* Alichova, 1963 and *P. lutkevichi satura* Oraspold, 1959, which it resembles in most other respects. *P. camerata* Twenhofel 1928 is a costellate form but has a rounded rather than high, flat-topped fold. *P. fissicostata* (M'Coy, 1852 : 193) is described as having 6–15 lateral ribs which branch irregularly into two or four, however, the figured specimens (Davidson, 1864; pl. 38 figs 17, 19, not figs 15, 16: see Cocks 1978 : 197) show no such branching ribs on the flanks, and it has been said that M'Coy's original material contained a large quantity of *Oxoplecia* as well as various species of *Platystrophia* (Wright 1964 : 208).

Family **CREMNORTHIDAE** Williams, 1963

Subfamily **CREMNORTHINAE** Williams, 1963

CREMNORTHIS Williams, 1963

Cremnorthis sp.

Figs 103–105

Material and horizon. Internal moulds of two tiny brachial valves, BB37275–6, from the same locality in the lower part of the Dolhir Formation, 50 m above the Tyn-y-twmpath Member. Lengths 0·9 and 1·0, widths 1·2 and 1·4 respectively.

Description. Moderately convex, subrectangular brachial valves almost three-quarters as long as wide and about one-fifth as deep as long; maximum width anterior to hinge-line, cardinal angles obtuse. Interarea flat, anacline, about one-tenth as long as valve. Interior with broad, bulbous cardinal process passing anteriorly into low, thin median septum which extends almost to valve margin. Stout brachiophores supported by thin, slightly divergent bases; fulcral plates well developed. Exterior unknown but internal impressions indicate about 18 ribs at 1 mm growth stage. Pedicle valve unknown.

Discussion. *Cremnorthis* is poorly known from the Ashgill, the only previous record being from the Killey Bridge Formation of Pomeroy (Mitchell 1977 : 47). Both these samples are too small to allow specific identification to be made, although the species are apparently different from the *C. parva* Williams and *C. uhakuana* Hints stocks. The internal impression of the ornament shows the Glyn Ceiriog form to be more coarsely ribbed than *C. uhakuana* which has 30 ribs at the 1 mm growth stage on the brachial valve. The differences with the type species, *C. parva*, are less noticeable but the cardinalia of the Glyn Ceiriog form are apparently less robust although this may be due to the small size of the present specimens and more material is needed before a statistical comparison can be carried out.

Family **SCENIDIIDAE** Kozlowski, 1929

SKENIDIOIDES Schuchert & Cooper, 1931

Skenidioides cf. ***asteroideus*** (Reed 1917)

Figs 106–118

?1908 *Rhynchonella* cf. *Lewisi* Davidson; Groom & Lake: 577.
cf. 1917 *Scenidium Lewisi* Davidson, var. *asteroidea* Reed: 921, pl. 22, figs 1–3.

Material and horizon. Internal and external moulds of 22 brachial and 50 pedicle valves from throughout the Dolhir Formation and from the Glyn Limestone Member at the base of the Glyn Formation.

Description. Ventri-biconvex shells of triangular to subpentagonal outline with maximum width along hinge-line; cardinal angles acute to rectangular. Pedicle valve almost four-fifths as long as wide; posterior edges of valve form straight-sided obtuse angle at umbo. Lateral profile subpyramidal to strongly convex; anterior profile convex, flattened slightly laterally but with weakly developed median fold in large specimens. Interarea well developed, just over two-fifths as long as valve, curved or flatfly apsacline. Brachial valve gently convex; median sulcus broad, gently rounded. Ornamentation of even, sub-rounded ribs, ventral fold with fascile of 2–4 ribs by 3 mm distance from umbo in 8/9 specimens, the other having a solitary median rib. External costellae developed by this growth stage in most specimens to give total rib counts of 12–21. Brachial valve with internal costellae only, one costella per sector, also developed by 3 mm growth stage.

Ventral interior with spondylium about one-third as long as valve; short, thick supporting septum variably developed. Dorsal cardinalia with simple cardinal process; well developed sockets bounded by slightly curved fulcral plates; brachiophore bases converge on to median septum which extends for almost seven-tenths of valve length. Faint adductor muscle field, about as long as wide, bisected longitudinally by median septum.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB37277	3·1	4·8
Internal mould of a brachial valve, BB37278	3·8	5·6
Internal mould of a pedicle valve, BB37279	5·8	6·8
External mould of a pedicle valve, BB37280	5·8	6·9
Internal mould of a pedicle valve, BB37281	8·0	8·6
Internal mould of a pedicle valve, BB37282	3·3	4·5
Internal mould of a pedicle valve, BB37284	8·5	8·7

DISCUSSION. One important consideration used in the differentiation of species of *Skenidioides* is the number of ribs on the pedicle valve. The Glyn Ceiriog species has 12–21 ribs at the 3 mm growth stage on 1, 4, 3, 6, 3, 4, 1, 4, 1, 1 pedicle valves respectively. It can be most closely compared to *S. asteroideus* (Reed, 1917), *S. costatus* Cooper, 1956 and *S. scoliodus* Temple, 1968, all of which have rib counts within the same range as that for the Glyn Ceiriog form.

S. costatus, with 13–21 ribs, is very similar in appearance to the present specimens but possesses a strong median costa which forms a prominent fold, and from Cooper's figured specimens (1956 : pl. 97D, figs 38–48) it would appear to have a more alate outline although no data are available to test this. However, Williams (1963 : 375) describes *S.* cf. *costatus*, from the Caradoc of the Bala district, which does not differ significantly from the Glyn Ceiriog form in comparisons of length : width of the pedicle valves. *S. scoliodus* has 12–20 ribs, but differs from the Glyn Ceiriog species in having a pronounced median rib and on comparisons of length : width of pedicle valves the Keisley form is significantly wider ($0{\cdot}002 > P > 0{\cdot}001$). No figures are available for Reed's material, but a similar comparison with *S. cf asteroideus* from the Portrane Limestone

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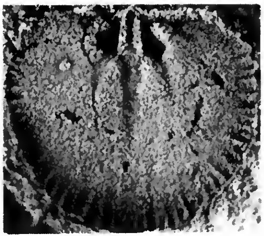
Figs 126–127, 132–133, 137, 140–142, 146–147, 149 *Dalmanella* cf. *testudinaria* (Dalman). Glyn Formation. Figs 126, 127, BB37299, Internal mould and latex cast of a brachial valve, ×3·9, loc. G3; Fig. 141, BB37302, Internal mould of a pedicle valve, ×3·4, loc. G2. Dolhir Formation: Fig. 132, BB37305, Internal mould of a brachial valve, ×6, loc. D14; Fig. 133, BB37300, Latex cast of the exterior of a brachial valve, ×5·3, loc. D14; Fig. 137, BB37301, Internal mould of a brachial valve, ×3·8, loc. D14; Fig. 140, BB37306, Latex cast of the exterior of a brachial valve, ×5·3, loc. D14; Fig. 142, BB37304, Internal mould of a pedicle valve, ×5·2, loc. D14; Fig. 146, BB37308, Internal mould of a brachial valve, ×4, loc. D6; Fig. 147, BB37303, Latex cast of the exterior of a pedicle valve, ×5, loc. D14; Fig. 149, BB37307, Internal mould of a brachial valve, ×5·4, loc. D6.

Figs 138–139, 143–145, 148, 150 ?*Dalmanella* sp. Cyrn-y-brain Formation: Figs 138, 139, BB37317, Internal mould and latex cast of a brachial valve, ×3·5, ×3·1, loc. C1; Figs 143, 144, BB37315, Internal mould and latex cast of a brachial valve, ×3·3, loc. C1; Fig. 145, BB37315, Latex cast of the exterior of a brachial valve, ×3·3, loc. C1; Figs. 148, 150, BB37318, Latex cast and internal mould of a brachial valve, ×3·5, ×4, loc. C1.

Figs 128–131, 134–136, 151 ?*Howellites* sp. Dolhir Formation: Figs 128, 129, BB37320, Internal mould and latex cast of a brachial valve, ×4·3, loc. D10; Figs 130, 131, BB37319, Internal mould and latex cast of a brachial valve, ×4·1, ×4, loc. D2; Figs 134, 135, BB37323, Internal mould and latex cast of a pedicle valve, ×2·3, ×2·4, loc. D2; Fig. 136, BB37321, Latex cast of the exterior of a brachial valve, ×3·6, loc. D1; Fig. 151, BB37322, Latex cast of the exterior of a brachial valve, ×4·3, loc. D2.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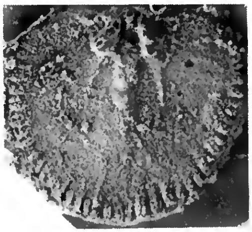
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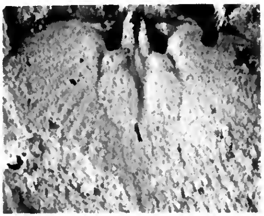
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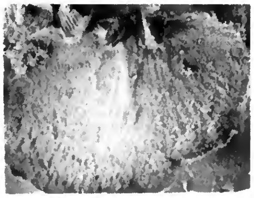
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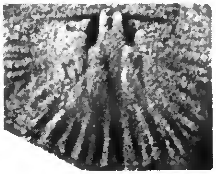
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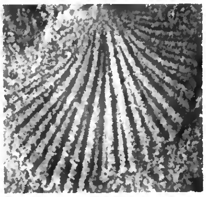
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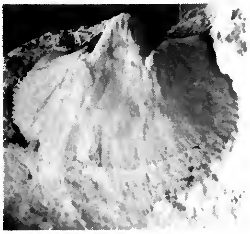
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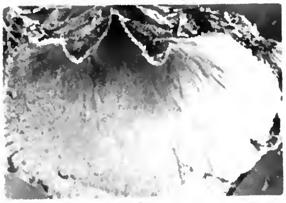
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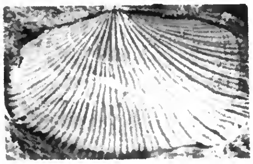
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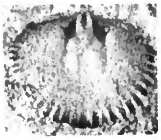
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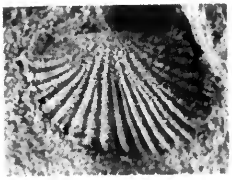
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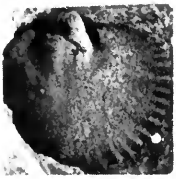
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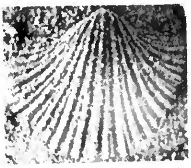
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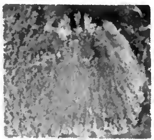
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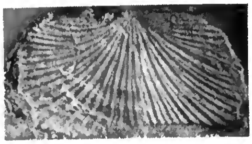
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(Wright, 1964 : 212) shows that there is no significant difference between it and the Glyn Ceiriog form. The Portrane form also has a nearly identical ornament to the Welsh species, with 11–19 ribs on 1, 4, 4, 4, 3, 2, 6, 1, 1 pedicle valves respectively at the 2 mm growth stage. Thus the Glyn Ceiriog *Skenidioides* is regarded as being very closely related to *S.* cf. *asteroideus.*

The following data were obtained for the sample:
Length (l) : *width* (w) *of pedicle valve:* $n = 29$; $\bar{l}$(var. l) = 5·38 (3·773) mm; $\bar{w}$(var. w) = 6·93 (4·456) mm; r = 0·873; a(var. a) = 1·086 (0·00963).

Superfamily **ENTELETACEA** Waagen, 1884
Family **SCHIZOPHORIIDAE** Schuchert & Le Vene, 1929
Subfamily **DRABOVIINAE** Havlíček, 1950

HIRNANTIA Lamont, 1935

Hirnantia sagittifera (M'Coy, 1851)?
Figs 119–125

?1851 *Orthis sagittifera* M'Coy: 398.
1908 *Orthis* cf. *sagittifera* M'Coy; Groom & Lake: 573.
1922 *Orthis* (*Heterorthis*?) *sagittifera* M'Coy; Wills & Smith: 74.

MATERIAL AND HORIZON. Internal and external moulds of 4 pedicle and 7 brachial valves from the Plas Uchaf Formation and the Glyn Formation.

DESCRIPTION. Ventribiconvex shells of subcircular to transversely subelliptical outline; maximum width about mid-valve; cardinal angles obtuse. Pedicle valve over seven-tenths as long as wide and over one-quarter as deep as long; evenly convex in both profiles. Interarea curved, apsacline; delthyrium narrow, open; small pedicle callist present in some specimens. Brachial valve about seven-tenths as long as wide and almost one-fifth as deep as long; moderately convex in both profiles but anterior profile modified by broad, shallow, anteriorly expanding sulcus. Interarea short, flat, anacline; notothyrium open. Ornamentation of fine subangular costae and costellae with density of about 3 ribs/mm at 5 mm growth stage on brachial valve.

Ventral interior with strong teeth supported by widely divergent dental plates (about 70°). Poorly defined, cordate muscle field about five-sixths as long as wide and one-half as long as valve with diductor scars extending slightly beyond adductors. Dorsal interior with cardinal process differentiated into bilobed myophore and slender shaft, extending for about one-quarter of valve length; brachiophores with bases diverging anteriorly at about 50°; sockets defined by fulcral plates. Notothyrial platform not developed to any extent. Faintly impressed adductor muscle field about seven-tenths as long as wide and less than one-half as long as valve, consisting of two pairs of subcircular scars on either side of slight median thickening of valve floor.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB37292	—	8·3
External mould of a brachial valve, BB37293	3·6	5·0
Internal mould of a brachial valve, BB37295	5·9	6·5
Internal mould of a pedicle valve, BB37298	7·8	12·1

DISCUSSION. *Hirnantia sagittifera* (M'Coy, 1851) is a widespread species in the uppermost Ashgill of the British Isles, Europe and North Africa: as a member of the nearly ubiquitous *Hirnantia* fauna, and from previous authors' descriptions, it would appear to be a fairly variable species. For example, Temple (1965 : 395) describes ventri-biconvex, transversely elongated shells with a short, bilobed cardinal process and fulcral plates, but Bergström (1968 : 11) describes biconvex shells with a simple cardinal process and without fulcral plates, while Williams (1951 : 97) describes subcircular dorsi-biconvex shells with a simple cardinal process and fulcral plates. The Glyn Ceiriog and Plas Uchaf specimens fall within the range of variation concerning shell shape and nature of cardinalia covered by other descriptions, being subcircular to transversely elliptical ventri-biconvex with a bilobed cardinal process and having fulcral plates. Some difficulty was encountered, with small specimens in particular, in distinguishing them from certain species of *Pionodema* and *Salopina*.

Family **DALMANELLIDAE** Schuchert, 1913

From the work of Williams and Wright (1963) on the '*Orthis testudinaria* Dalman' group it is evident that generic assignment in this group is primarily based on the details of the cardinalia and ventral muscle field.

Thus only the best specimens may be used, as even slight crushing hazards the generic identification of any individual specimen. In this account of the dalmanellids of Glyn Ceiriog, and the Dolhir Formation in particular, only those specimens which show the least effects of tectonic distortion have been considered. Because of this, the sample sizes quoted in descriptions represent only a fraction of the total sample recovered from the various Ashgill strata, where the dalmenellids by far out-number any other group of brachiopods.

DALMANELLA Hall & Clarke, 1892

Dalmanella cf. ***testudinaria*** (Dalman, 1828)

Figs 126–127, 132–133, 137, 140–142, 146–147, 149

cf. 1828 *Orthis testudinaria* Dalman: 115, 117, pl. 2, fig. 4.
1908 *Orthis testudinaria* Dalman; Groom & Lake: 573.
1922 *Orthis* (*Dalmanella*) cf. *testudinaria* Dalman; Wills & Smith: 187, 191.

MATERIAL AND HORIZON. Internal and external moulds of 12 pedicle and 21 brachial valves from the Dolhir Formation, Glyn Formation and Cyrn-y-brain Formation.

DESCRIPTION. Ventri-biconvex shells of sub-circular outline with maximum width anterior to hinge-line; cardinal angles rounded, obtuse. Pedicle valve almost nine-tenths as long as wide, hinge-line almost four-fifths of maximum valve width; thickness averaging over one-third of valve length. Lateral profile with maximum convexity near umbo; anterior profile with median portion more convex than flanks. Interarea curved, apsacline, about one-seventh as long as wide and one-eighth as long as valve; delthyrium open, pedicle callist present. Brachial valve over four-fifths as long as wide and one-tenth as deep as long; gently convex in both profiles, anterior profile modified by shallow median sulcus which expands anteriorly. Interarea short, anacline, less than one-tenth as long as wide; notothyrium open. Costellate ornament with 4–5 ribs per mm at 2 mm anterior to dorsal umbo.

Ventral interior with stout teeth supported by strong dental plates which continue forward to define muscle field four-fifths as wide as long and over two-fifths as long as valve. Median adductor scar slightly shorter than bounding diductor lobes and occupying almost one-third of total width of scar. Crural fossettes present on inner surfaces of teeth. Dorsal interior with cardinalia extending for one-quarter of valve length, comprising bilobed (?) cardinal process with weakly developed shaft on low notothyrial platform; tops of brachiophores diverging anteriorly at less than 60°, bases diverging along valve floor at slightly, but not significantly, smaller angle. Fulcral plates and crural pits variably developed. Subquadrate adductor field about two-fifths as long as valve, with posterior pair of scars smaller than anterior; low median ridge divides muscle field longitudinally.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB37299	7·8	8·8
External mould of a brachial valve, BB37300	2·8	3·1
Internal mould of a brachial valve, BB37301	2·8	3·2
Internal mould of a pedicle valve, BB37302	6·2	7·0
External mould of a pedicle valve, BB37303	4·5	5·0
Internal mould of a brachial valve, BB37305	3·2	4·3
External mould of a brachial valve, BB37306	2·5	3·2

DISCUSSION. The Glyn Ceiriog *Dalmanella* has its closest relatives in *D. testudinaria* (Dalman, 1828) and *D. portranensis* Wright, 1964. A comparison of the data for the Welsh shells with that for both the Irish and Swedish species reveals that, although the Glyn Ceiriog valves are smaller, there is no significant difference in the shape of either the brachial or pedicle valves of any of the three forms. However, a similar comparison shows that *D. portranensis* is significantly deeper ($0{\cdot}01 > P > 0{\cdot}002$) in ventral profile than the Glyn Ceiriog *Dalmanella*.

Although the more important rib relationships cannot be properly studied on the available Glyn Ceiriog exteriors, which are poorly preserved especially in the early growth stages, the density of 3–4 ribs per mm, measured at 5 mm anterior to the dorsal umbo, is not significantly different from that in the other two forms.

The cardinalia of the Glyn Ceiriog valves extends further forward, relative to the valve length, than in *D. testudinaria*, with the percentage ratios of length being *D. testudinaria*, 5 valves—16, 19, 19, 20, 20% and Glyn Ceiriog *Dalmanella*, 10 valves—18, 20, 21, 23, 24, 25, 25, 26, 26, 26%.

A Rank Sum Test on these data shows a significant difference ($P < 0{\cdot}001$) between the two samples. The figures for the Glyn Ceiriog *Dalmanella* are practically identical to those given by Wright (1964 : 222) for *D. portranensis*.

The posterior edges of the brachiophores of 10 Welsh specimens have a mean angle of divergence of 57·5° (var. 56·94) while their bases diverge at a mean angle of 51·0° (var. 37·78). No significant difference was found in these attributes between this sample and that for *D. testudinaria* but the brachiophore bases of *D. portranensis*, which produced values of 58·5° (var. 43·4) were found to be significantly more divergent ($0{\cdot}05 > P > 0{\cdot}02$).

The dorsal adductor muscle field is similarly disposed in all three forms, with the anterior scars being larger than the posterior pair, but that of the Welsh species extends for a significantly greater proportion of valve length than that of the other species ($0{\cdot}05 > P > 0{\cdot}02$). Comparisons of the ventral muscle fields show that, although the Glyn Ceiriog form is apparently closer to *D. portranensis*, it is not significantly different from either the Irish or Swedish species.

The sample of Glyn Ceiriog *Dalmanella* appears to be intermediate between *D. portranensis*, from which it differs in having more narrowly divergent brachiophore bases and a shallower pedicle valve, and *D. testudinaria* which has significantly shorter cardinalia. However, it is considered that the sample is inadequate and the erection of a new species or subspecies would not be justified, therefore the specimens are best left as being comparable to *D. testudinaria* which is the closer of the two related forms, differing significantly in only the one character whereas *D. portranensis* differs in two characters.

The data for *D. testudinaria* are taken from Williams & Wright (1963 : 30, 31).

The following statistical data have been obtained for the sample.

Pedicle Valves

Length (l) : width (w), $n = 12$; $\bar{l}$(var. l) = 4·51 (1·446) mm; $\bar{w}$(var. w) = 5·18 (2·052) mm; $r = 0{\cdot}95$; a(var. a) = 1·191 (0·0139); $\overline{\log_e l}$(var. $\log_e$l) = 1·47) (0·0687); $\overline{\log_e w}$(var. $\log_e$w) = 1·61 (0·0736); $r_e = 0{\cdot}951$; α(var. α) = 1·035 (0·0102).

Length (l) : thickness (d), $n = 12$; $\bar{l}$(var. l) = 4·51 (1·446) mm; $\bar{d}$(var. d) = 1·57 (0·212) mm; $r = 0{\cdot}743$; a(var. a) = 0·382 (0·00653); $\overline{\log_e l}$(var. $\log_e$l) = 1·47 (0·0687); $\overline{\log_e d}$(var. $\log_e$d) = 0·41 (0·083); $r_e = 0{\cdot}751$; α(var. α) = 1·096 (0·0523).

Length : width of muscle field, 8 valves—67, 74, 75, 78, 79, 90, 90, 93%

Length of muscle field : length of valve, 8 valves—32, 38, 40, 40, 42, 43, 44, 44%

Brachial Valves

Length (l) : width (w), $n = 15$; $\bar{l}$(var. l) = 4·31 (2·322) mm; $\bar{w}$(var. w) = 5·24 (2·571) mm; $r = 0{\cdot}866$; a(var. a) = 1·052 (0·0213); $\overline{\log_e l}$(var. $\log_e$l)= 1·4 (0·118); $\overline{\log_e w}$($\log_e$w) = 1·61 (0·090); $r_e = 0{\cdot}873$; α(var. α) = 0·872 (0·0139).

Length : width of interarea, 7 valves—7, 8, 9. 9, 10, 10, 16%

Length : width of muscle field, 10 valves—61, 62, 62, 63, 65, 65, 67, 67, 68%.

Length of muscle field : length of valve, 10 valves—55, 57, 60, 61, 62, 62, 64, 64, 67, 68%.

?***Dalmanella*** sp.

Figs 138, 139, 143–145, 148, 150

MATERIAL AND HORIZON. Internal and external moulds of 3 brachial valves from the Cyrn-y-brain Formation. Internal dimensions; BB37315, l = 6·0, w = 5·5; BB37317 l = 6·2, w = 5·0; BB37318, l = 5·5, w = 5·4.

DESCRIPTION. Brachial valve elongately subcircular, maximum width about nine-tenths of valve length, situated about mid-valve; cardinal angles obtuse; hinge-line about three-fifths of maximum width; depth almost one-fifth of valve length. Both profiles evenly convex except for narrow median sulcus indenting anterior profile. Interarea flat, anacline, about one-fifth as long as wide and one-tenth as long as valve; notothyrium open. Ornament with 5 subangular costae and costellae per mm, 2 mm anteromedianly from umbo.

Ventral interior unknown. Dorsal interior with cardinalia extending for less than one-fifth of valve length; stout, undifferentiated cardinal process situated on greatly thickened notothyrial platform; posterior edges of brachiophores diverge anteriorly at about 55° and their bases at about 50°. Small sockets bounded by brachiophores and fulcral plates; crural pits very shallow. Adductor muscle field poorly defined but extending for about three-fifths of valve length and divided longitudinally by strong median ridge extending from notothyrial platform.

DISCUSSION. This distinctive species is characterized by its fairly deep brachial valve with its narrow sulcus which does not expand appreciably toward the anterior margin and it is also rather unusual in being longer than wide. Internally it differs from *Dalmanella* cf. *testudinaria* in having shorter cardinalia and a much thicker notothyrial platform. It bears a close resemblance to '*Dalmanella*' *biconvexa* Williams, 1951 from the basal Lower Llandovery of Haverfordwest, but the Cyrn-y-brain sample is too small for a statistical comparison to be carried out. The convexity of the brachial valve and short hinge-line suggests affinity with *Cryptothyris* (Bancroft, 1945) but this is best known from the Caradoc and more material is required before these specimens can be unequivocally assigned to that genus.

HOWELLITES Bancroft, 1945

?***Howellites*** sp.

Figs 128–131, 134–136, 151

1908 *Orthis elegantula* Dalman; Groom & Lake: 527, 577.
1922 *Orthis* (*Dalmanella*) *elegantula* (?) Dalman; Wills & Smith 187, 191.

MATERIAL AND HORIZON. Internal and external moulds of 19 pedicle and 21 brachial valves from the lower and middle parts of the Dolhir Formation.

DESCRIPTION. Ventri-biconvex shells of subcircular outline with maximum width anterior to hinge-line; cardinal angles rounded, obtuse. Pedicle valve over nine-tenths as long as wide and more than one-third as deep as long; hinge-line about nine-tenths as wide as valve; strongly convex in both profiles. Interarea strongly curved, apsacline, about one-fifth as long as valve, one specimen shows grooves diverging from umbo; delthyrium open, pedicle callist present. Brachial valve three-quarters as long as wide and one-tenth as deep as long; gently convex in both profiles with shallow, anteriorly expanding, median sulcus indenting anterior profile. Interarea very short, anacline; notothyrium open. Ornament of fine costae and costellae with density of 6–7 ribs per mm at 2 mm anteromedianly on brachial valves.

Ventral interior with strong teeth supported by thick dental plates bearing crural fossettes on inner surfaces. Muscle field approaching nine-tenths as long as wide and over one-third as long as valve; median adductor scar not enclosed by slightly longer diductors and occupying about one-third of total width of scar. Thick trunks of *vascula media* slightly divergent from anterior ends of diductor lobes. Dorsal cardinalia extending for almost one-quarter of valve length. comprising a differentiated bilobed and crenulated cardinal process on low notothyrial platform; tops of brachiophores diverge at about 56°, whereas bases diverge at 70°. Fulcral plates, in the strict sense, not normally developed but sockets usually supported by thickening of secondary shell; crural pits, if present, are normally very shallow.

Quadripartite adductor muscle field almost as long as wide and two-fifths as long as valve, usually defined by low ridges; subelliptical anterior pair larger than posterior pair. Broad median ridge extending from notothyrial platform bisects muscle field longitudinally.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB37319	6·6	13·2
Internal mould of a brachial valve, BB37320	6·7	7·2
External mould of a brachial valve, BB37321	5·5	8·9
External mould of a brachial valve, BB37322	4·2	6·9
Internal mould of a pedicle valve, BB37323	11·5	13·2

DISCUSSION. The generic assignment of these specimens has been the cause of some difficulty. The form of the cardinalia, in which the brachiophore bases are more widely divergent than the tops, the external ornament and the interior of the pedicle valve all suggest close affinities with three genera, *Resserella* Bancroft, 1928, *Dedzetina* Havlíček, 1950 and *Howellites* Bancroft, 1945, but differences and similarities can be found with each of these. Walmsley and Boucot (1971 : 495) state that the oldest undoubted *Resserella* species are of late *Llandovery* (C_3–C_6) age but they describe *R. sefinensis*, from beds of C_1 age, and they regard *Dedzetina* from the Ashgill of Bohemia as an ancestral form to *Resserella*. *Howellites* is best known from the Caradoc but unnamed species have been recorded from the Ashgill of the Cautley and Dent districts (Ingham, 1966 : 498) and Bala (Bassett, Whittington and Williams, 1966 : 263).

Howellites can be distinguished from *Resserella* and *Dedzetina* by its deeper, more strongly convex brachial valve, and sub-equal pairs of dorsal adductor scars. *Dedzetina* is distinguished from *Resserella* by its gently convex brachial valve with hypercline interarea and dorsal adductor muscle field in which the anterior scars are larger than the posterior pair, the reverse of the situation in *Resserella* (Walmsley and Boucot, 1971 : 50). However, the specimens figured by Walmsley and Boucot (1971 : pl. 91, figs. 1–4) as *Dedzetina macrostomoides* show the posterior scars to be larger than the anterior and, as pointed out by Sheehan (1973 : 62), the size differential is probably a variable feature.

The Glyn Ceiriog genus has a gently convex brachial valve and an adductor muscle field with posterior scars smaller than anterior, and in these respects resembles *Dedzetina* (as defined by Walmsley and Boucot, 1971 : 519) but differs in that the dorsal interarea is invariably anacline, like *Resserella* and *Howellites*. A form very similar to the Glyn Ceiriog shells, except for its more transverse pedicle valve, is *Resserella llandoveriana* Williams, 1951 from Meifod (Temple, 1970 : 22), but this species has been rejected from *Resserella* by Walmsley and Boucot (1971 : 495) although no alternative identification has been given.

If *Resserella* is confined to the Silurian, as is now generally accepted, then the present Ordovician specimens must be placed either in *Dedzetina* or *Howellites* and the form of the dorsal interarea seems to preclude attribution to *Dedzetina*. Hence the Glyn Ceiriog shells are placed in *Howellites*, but with strong reservations because the quite strong curvature of the ventral umbo and the form of the dorsal muscle field are more suggestive of the Resserellinae.

The problems encountered with the present specimens serve to highlight the difficulty in distinguishing between certain genera of the Dalmanellidae, particularly those extant during Ashgill times, because they lie on the border between the better-known Caradoc and Silurian stocks. Despite recent work on this family, much remains to be done to link up Ordovician and Silurian forms and on the variation within any given genus. *Dedzetina* is a poorly known genus with few described species, and its connection with older forms is unknown. The attitude of the dorsal interarea may turn out to be a variable feature and the genus may be closely related to *Howellites*. Such a study will require more material than is at present available, and certainly material that is better preserved than that available from Glyn Ceiriog.

The following data were obtained for the sample:

Pedicle Valves

Length (l) : width (w), n = 6; $\bar{l}$(var. l) = 6·2 (7·308) mm; $\bar{w}$(var. w) = 6·52 (11·366) mm; r = 0·998; a(var. a) = 1·247 (0·00168).

Length (l) : width of interarea (w), $n = 6$; $\bar{l}$(var. l) = 1·3 (0·408) mm; $\bar{w}$(var. w) = 6·78 (4·638) mm; r = 0·923; a(var. a) = 3·371 (0·4194); $\overline{\log_e l}$(var. $\log_e l$) = 0·15 (0·216); $\overline{\log_e w}$(var. $\log_e w$) = 1·87 (0·096); r_e(0·935); α(var. α) = 0·666 (0·014).
Width : length of muscle field, 6 valves—65, 76, 80, 83, 93, 94%.
Length of muscle field : length of valve, 5 valves—25, 29, 29, 34, 40%.
Brachial Valves
Length (l) : width (w), $n = 17$; $\bar{l}$(var. l) = 5·04 (1·145) mm; $\bar{w}$(var. w) = 6·61 (1·742) mm; r = 0·657; a(var. a) = 1·234 (0·0576); $\overline{\log_e l}$(var. $\log_e l$) = 1·60 (0·044); $\overline{\log_e w}$(var. $\log_e w$) = 1·87 (0·039); r_e = 0·668; α(var. α) = 0·941 (0·0327).
Length of valve (l) : length of cardinalia (c), $n = 13$; $\bar{l}$(var. l) = 5·08 (1·126) mm; $\bar{c}$(var. c) = 1·18 (0·05) mm; r = 0·758; a(var. a) = 0·211 (0·00172); $\overline{\log_e l}$(var. $\log_e l$) = 1·60 (0·043); $\overline{\log_e c}$(var. $\log_e c$) = 0·15 (0·036); r_e = 0·772; α(var. α) = 0·914 (0·03072).
Length of valve (l) : length of muscle field (m), $n = 12$; $\bar{l}$(var. l) = 5·02 (1·163) mm; $\bar{m}$(var. m) = 3·15 (0·554) mm; r = 0·907; a(var. a) = 0·690 (0·0084); $\overline{\log_e l}$(var. $\log_e l$) = 1·59 (0·045); $\overline{\log_e m}$ (var. $\log_e m$) = 1·1 (0·054); r_e = 0·911; α(var. α) = 1·095 (0·02032).
Width : length of muscle field, 10 valves—51, 60, 63, 63, 64, 64, 66, 67, 67, 77%.
Length of muscle field : length of valve, 10 valves—52, 58, 59, 59, 61, 62, 63, 64, 64, 67%.

EREMOTREMA Cooper, 1956

Eremotrema cf. ***paucicostellatum*** Mitchell, 1977

Figs 152–160

cf. 1977 *Eremotrema paucicostellatum* Mitchell: 59, pl. 10, figs 10–14.

MATERIAL AND HORIZON. Twelve brachial valves and 10 pedicle valves from the lower part of the Dolhir Formation, and 1 pedicle valve from high up in the same formation. Most of the specimens are well preserved although some have suffered some crushing.

DESCRIPTION. Ventri-biconvex shells of subcircular outline with maximum width at or near mid-valve. Pedicle valve over nine-tenths as long as wide and one-fifth as deep as long; both profiles evenly convex; interarea slightly curved, apsacline, one-seventh as long as valve; delthyrium open. Brachial valve about nine-tenths as long as wide, and over one-tenth as deep as long; anterior profile gently convex on flanks with shallow median sulcus arising at umbo; interarea short, flat, anacline. Ornament of coarse angular costae and costellae yielding total counts of 14–20 ribs at 2 mm growth stage on 1, 0, 2, 1, 3, 0, 2 pedicle valves: internal and external costellae both developed by this stage.

Ventral interior with stout teeth supported by short receding dental plates. Sub-pentagonal muscle field about as wide as long and just over one-third as long as valve.

Dorsal interior with cardinal process differentiated into high, inflated, trilobed myophore, filling notothyrium, and short flattened shaft; widely divergent brachiophores supported by thickened bases converging on to median ridge and posteriorly supporting sockets; cardinalia nearly three-fifths as long as wide and extending anteriorly for one-fifth of valve length. Adductor muscle field about three-quarters as long as wide and divided by short thick ridge extending anteriorly from notothyrial platform for one-half of valve length.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB37327	10·5	14·3
Internal mould of a brachial valve, BB37328	10·5	11·5
External mould of a brachial valve, BB37329	7·1	9·8
External mould of a pedicle valve, BB37330	7·5	10·0
Internal mould of a brachial valve, BB37331	c. 10	12·2
Internal mould of a pedicle valve, BB37332	6·3	9·2
Internal mould of a pedicle valve, BB37337	11·9	12·8


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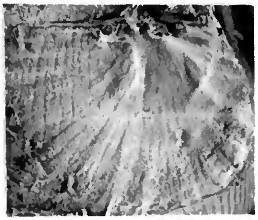
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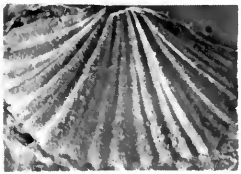
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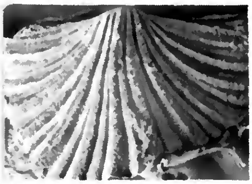
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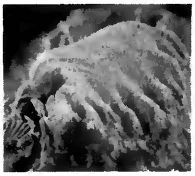
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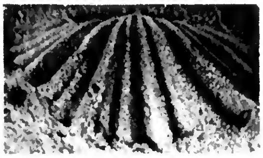
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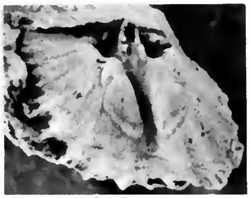
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Figs 152–160 *Eremotrema* cf. *paucicostellatum* Mitchell. Dolhir Formation: Figs 152–3, BB37327, Internal mould and latex cast of a brachial valve, ×2·4, loc. D5; Fig. 155, BB37329, Latex cast of the exterior of a brachial valve, ×3·1, loc. D4; Figs 156–7, BB37328, Internal mould and latex cast of a brachial valve, ×3·8, loc. D2; Fig. 158, BB37330, Internal cast of the exterior of a pedicle valve, ×3·3, loc. D4; Fig. 159, BB37331, Internal mould of a deformed brachial valve, ×3·0, Discussion. Only three species of *Eremotrema* have previously been described: *E. biconvexum* Cooper, 1956, *E. gracile* (Reed, 1917, emended Williams, 1962), and *E. paucicostellatum* Mitchell, 1977. Of the three, the Glyn Ceiriog species compares most closely with the last, having a similarly coarse ornament. Eight Glyn Ceiriog brachial valves yield total rib counts of 16, 18, 20, 20, 20, 20, 22, 22, ribs respectively at the 2 mm growth stage compared with 22 and 26 ribs on 3 and 1 brachial valves of *E. paucicostellatum* from Pomeroy. A density of 2 and 3 ribs per mm was observed on 7 and 2 Welsh pedicle valves respectively, measured 5 mm anteromedianly from the umbo. A single Pomeroy specimen had a density of 2 ribs per mm at the same stage. Another feature which distinguishes *E. paucicostellatum* from the two older species is its short, transverse cardinalia. Although the samples are too small for statistical comparisons, the cardinalia of the Glyn Ceiriog specimens do, on average, appear to be longer than for *E. paucicostellatum*. Other differences occur in the depth of the pedicle valve and relative length of the brachial valve, but these may be partly a result of the crushing suffered by some Glyn Ceiriog specimens. Thus the Welsh species and *E. paucicostellatum* are very similar in ornament but display some differences in shell shape.

RAVOZETINA Havlíček, 1974

Ravozetina silvicola (Temple, 1970) ***prima*** subsp. nov.

Figs 161–173

Diagnosis. Strongly ventri-biconvex *Ravozetina* with low fold on pedicle valve and well developed sulcus on brachial valve. Ribbing relatively simple, without development of third order costellae.

Material and horizon. Internal and external moulds of 37 pedicle and 47 brachial valves from the lower part of the Dolhir Formation, 25–50 m above the Dolhir Limestone.

Description. Small ventri-biconvex shells of transversely subquadrate outline; maximum width commonly anterior to hinge-line; cardinal angles rounded, obtuse. Pedicle valve over four-fifths as long as wide and over one-third as deep as long; lateral profile strongly convex, anterior profile with median maximum convexity reflecting low fold. Interarea short, about one-eighth as long as valve, curved, apsacline; delthyrium open. Brachial valve almost three-quarters as long as wide and over one-fifth as deep as long; lateral profile convex, anterior profile with convex flanks separated by well developed median sulcus which expands anteriorly; anterior commissure gently sulcate. Interarea very short, less than one-tenth as long as valve, flat, anacline; notothyrium open but almost entirely filled by cardinal process. Ornamentation of strong angular costae and costellae numbering 12–18 ribs at 2 mm growth stage on 10 pedicle valves. Ventral fold occupied by 3 primary costae; median one branching to produce costella on either side, lateral costae with external costellae developing at about 1·5 mm. On each flank 2 or 3 primary costae each produce one external costella and occasional internal costellae; capillae may develop in rib interspaces. Dorsal sulcus occupied by pair of narrow submedian costae which may produce internal costella in late growth stages. Sulcus bounded by pair of strong costae which branch internally; outside these 2 primary costae produce internal costellae and the occasional external costella. Prominent

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loc. D5; Fig. 160, BB37332, Internal mould of a pedicle valve, ×4·6, loc. D6. Dolhir Limestone Member: Fig. 154, BB37337, Internal mould of a pedicle valve, ×2·5, loc. L3.

Figs 161–173 *Ravozetina silvicola prima* subsp. nov. Dolhir Formation: Figs 161–2, BB37341, Internal mould and latex cast of a pedicle valve, ×7·5, ×7·4, loc. D5; Fig. 163, Lateral view of the same specimen, ×6·5, loc. D5; Fig. 164, BB37340, Latex cast of the exterior of a pedicle valve, ×6·9, loc. D5; Figs. 165–6, Holotype, BB37338, Internal mould and latex cast of a brachial valve, ×7·0, ×8·0, loc. D4; Fig. 167, BB37338, Latex cast of the exterior of the holotype, ×7·5, loc. D4; Fig. 168, BB37347, Internal mould of a pedicle valve, ×7·5, loc. D5; Figs 169–70, BB37343, Internal mould and latex cast of a brachial valve, ×6·9, loc. D4; Fig. 171, BB37344, Latex cast of the exterior of conjoined valves, ×6·3, loc. D4; Fig. 173, BB37341, Latex cast of the exterior of a pedicle valve, ×5·9, loc. D5; Fig. 172, BB37345, Latex cast of the exterior of a brachial valve, ×7·1, loc. D5.

growth lines seen on some specimens. Shell substance punctate; punctae seen all over internal and external surfaces.

Ventral interior with strong teeth supported by divergent, receding dental plates with occasional crural fossettes. Thick pedicle callist; muscle field lightly impressed, more or less confined to umbonal chamber, about as long as wide and about one-third as long as valve. Slightly raised adductor tract nearly two-fifths as wide as whole scar and only slightly shorter than diductors. Floor of valve slopes away steeply in front of muscle field, so that muscles are situated on thickened platform. *Vascula media* diverge from antero lateral corners of this platform. Dorsal interior with cardinalia extending for one-fifth of valve length and consisting of stout, undifferentiated, rarely bilobed or crenulated, cardinal process situated on thickened notothyrial platform. Shallow sockets bounded by fulcral plates and short, sturdy brachiophores with bases more divergent than tops. Crural pits not developed. Adductor muscle field five-sixths as long as wide and two-fifths as long as valve; bisected longitudinally by thick, rounded ridge extending from notothyrial platform; scars on either side divided by faint diagonal ridge so that posterior scar is smaller than anterior.

TYPE MATERIAL

	length	width
Internal mould of a brachial valve, holotype, BB37338	3·0	4·6
External mould of a brachial valve, holotype, BB37338	3·1	4·7
External mould of a pedicle valve, BB37340	3·0	3·7
Internal mould of a pedicle valve, BB37341	3·1	4·5
External mould of a pedicle valve, BB37341	3·2	4·6
Internal mould of a brachial valve, BB37343	4·1	—
External mould of conjoined valves, BB37344	—	4·8
External mould of a brachial valve, BB37345	—	4·5
Internal mould of a pedicle valve, BB37347	3·3	—

DISCUSSION. This small, distinctive species closely resembles *Ravozetina rava* (Marek & Havlíček, 1967) from the Kosov Formation (Upper Ashgill) of Czechoslovakia and *R. silvicola* (Temple, 1970) from the Lower Llandovery of Meifod, Wales. The latter was originally described as a subspecies of *R. rava* but subsequently assigned as a separate species by Havlíček (1977 : 145). The two forms are distinguished from one another by the stronger fold and sulcus and greater convexity of the valves of *R. silvicola*; this also has a more 'humped' ventral internal mould and stronger coarser ribbing. The Dolhir Formation specimens are more like *R. silvicola* but differ principally in their deeper pedicle valves. A 't'-test comparing length: depth data for 32 Glyn Ceiriog and 9 Meifod pedicle valves revealed that the Dolhir specimens are significantly deeper ($P < 0{\cdot}001$). A similar test showed that the ventral interarea of the Dolhir form is significantly shorter than that of *R. silvicola* ($P < 0{\cdot}001$).

Further, the Glyn Ceiriog shells are not seen to develop third order costellae which Temple records on brachial valves of his species (1970 : 21). A brachial valve has the following costellae:

Right side—1ā 2ā 3ā 4ā
Left side—2ā 3ā 3ā 4ā

This development is reflected in the pedicle valve.

Nevertheless, the general appearance of these two Welsh forms shows that they are morphologically very similar.

The following statistical data were obtained for the sample:

Pedicle Valves

Length (l) : width (w); n = 33; $\bar{l}$(var. l) = 3·24 (0·888) mm; $\bar{w}$(var. w) = 3·83 (0·777) mm; r = 0·578; a(var. a) = 0·935 (0·01878).

Length (l) : thickness (t), n = 32; $\bar{l}$(var. l) = 3·23 (0·918) mm; $\bar{t}$(var. t) = 1·22 (0·118) mm; r = 0·617; a(var. a) = 0·935 (0·00265).

Length (l) : length of interarea (h), n = 10; $\bar{l}$(var. l) = 3·57 (0·909) mm; $\bar{h}$(var. h) = 0·48 (0·024) mm; r = 0·913; a(var. a) = 0·162 (0·00054).

Length (l) : length of muscle scars (m), n = 20; $\bar{l}$(var. l) = 3·46 (0·903) mm; $\bar{m}$(var. m) = 1·12 (0·0792) mm; r = 0·764; a(var. a) = 0·296 (0·00202).

Brachial Valves

Length (l) : width (w), n = 38; $\bar{l}$(var. l) = 2·8 (0·619) mm; $\bar{w}$(var. w) = 3·79 (1·022) mm; r = 0·761; a(var. a) = 1·285 (0·0193).

Length of muscle field (l) : width of muscle field (w), n = 12; $\bar{l}$(var. l) = 1·31 (0·0863) mm; $\bar{w}$(var. w) = 1·52 (0·0924) mm; r = 0·864; a(var. a) = 1·035 (0·0272).

PORTRANELLA Wright, 1964

Portranella sp.

Figs 174–180

MATERIAL AND HORIZON. Moulds of 4 brachial valves and 1 pedicle valve from the Dolhir Formation, and 1 brachial valve from high up in the Cyrn-y-brain Formation.

DESCRIPTION. Ventri-biconvex shells of sub-rounded to transversely subelliptical outline, with maximum width anterior to hinge-line. Pedicle valve about three-quarters as long as wide and one-third as deep as long. Lateral profile with maximum convexity at umbo, which is slightly incurved; anterior profile moderately convex. Interarea short, curved, apsacline; delthyrium open. Brachial valve two-thirds as long as wide, gently convex with median sulcus moderately deep posteriorly but shallowing towards anterior margin. Interarea very short, anacline, cardinal process lobes protruding slightly from open notothyrium. Ornament of strong angular costae and costellae with brachial valve having 11 or 12 primary costae, median pair arising slightly later; branching first occurs in sector 1 with 1a rising quite early.

Ventral interior unknown. Dorsal interior with short, stout brachiophores whose divergent bases bound sockets. Trilobed myophore rising directly from thickened notothyrial platform; lateral lobes extend over posterior ends of brachiophores; no traces of shaft. Low rounded median ridge extending from notothyrial platform to about mid-valve. Few specimens show suggestion of faint punctation.

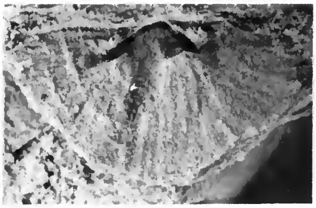
FIGURED SPECIMENS

	length	width
External mould of a brachial valve, BB37350	4·0	4·3
Internal mould of a brachial valve, BB37353	4·1	5·8
Internal mould of a brachial valve, BB37354	2·4	3·7
External mould of a pedicle valve, BB37355	4·9	6·4
Internal mould of a brachial valve, BB37356	6·2	10·2

DISCUSSION. With such a small sample it is difficult to make a complete comparison with the only species in the genus, *P. angulocostellata* Wright, 1964, from the Portrane Limestone. Both forms have similar dimensions, for example the Glyn Ceiriog pedicle valve has a thickness which is 35% of valve length, compared with 32, 33 and 39% of 3 Portrane specimens, 4 Glyn Ceiriog brachial valves have length : width ratios of 53, 61, 65, and 72% compared with 64, 44 and 75% for 3 Portrane valves.

The single Welsh pedicle valve has a density of 4 ribs per 2 mm at 5 mm growth stage; the Irish species has 3, 4 ribs per 2 mm on 3, 3 valves respectively. On the brachial valve the Glyn Ceiriog specimen has 3 ribs in the sulcus and 4 or 5 on the flanks at 3 mm growth stage while the Portrane valves have 2, 4 or 5 ribs in the sulcus and 6, 7 or 8 on the flanks at the same stage. The main difference in the ribbing of the two forms is the insertion of the costellae; in the Portrane specimens $4a^{\circ}$ appears first, followed by $4\bar{a}$ and then $3\bar{a}$, whereas in the Glyn Ceiriog specimen $3\bar{a}$ is preceded only by $1\bar{a}$. So although the two forms are closely comparable there are some differences which may be significant if larger samples were available.

Wright (1964 : 168) placed *Portranella* in the Orthidiellidae partly on the apparent impunctate nature of the shell substance. However, a few of the Glyn Ceiriog specimens, those found in finer sediment, show what may prove to be a fine punctation especially along the internal impression of the ribs (see BB37354). This is not as well developed as the punctation seen in other stocks occurring in the Dolhir Formation with *Portranella*, but if indeed the specimens are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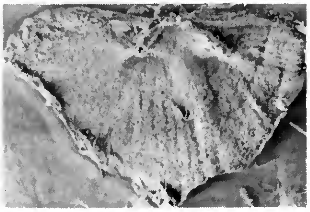
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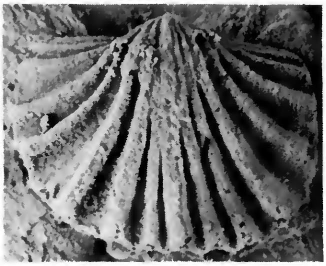
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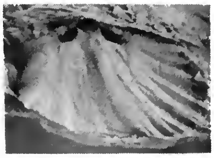
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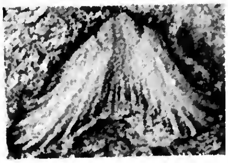
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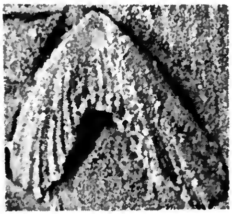
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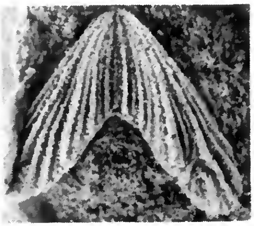
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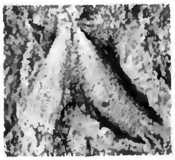
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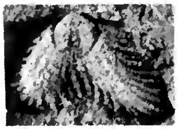
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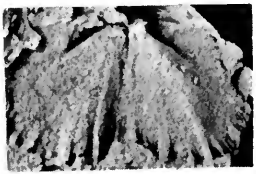
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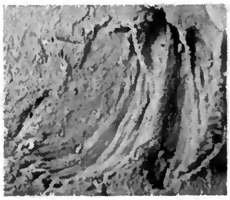
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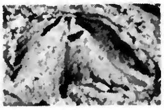
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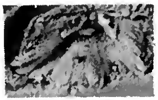
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Figs 174–180 *Portranella* sp. Dolhir Formation: Figs 174, 175, BB37356, Internal mould and latex cast of a brachial valve, ×4·3, loc. D15; Fig. 176, BB37355, Latex cast of the exterior of a pedicle valve, ×5·8, loc. D2; Fig. 177, BB37350, Latex cast of the exterior of a brachial valve, ×8·0, loc. D3; Figs 178, 179, BB37354, Internal mould and latex cast of a brachial valve, ×8·6, loc. D3; Fig. 180, BB37353, Internal mould of a brachial valve, ×4·0, loc. D5.

punctate then the genus must be removed from the Orthidiellidae and is accordingly transferred to the Dalmanellidae.

Family **DICAELOSIIDAE** Cloud, 1948

DICOELOSIA King, 1850

Dicoelosia cf. ***indenta*** (Cooper, 1930)

Figs 181–191

1908 *Orthis biloba* Linnaeus: Groom & Lake: 572, 577.
cf. 1930 *Bilobites indentus* Cooper: 269, pl. 1, fig. 4.

MATERIAL AND HORIZON. Internal and external moulds of 17 brachial and 38 pedicle valves from throughout the Dolhir Formation and Glyn Formation.

DESCRIPTION. Concavo-convex shells with deeply invaginated anterior margin. Pedicle valve nearly nine-tenths as long as wide with mid-line length just over two-thirds of maximum valve length. Valve shallow with approximately even depth throughout its length; thickness less than one-third of valve length ('depth' and 'thickness' as defined by Wright, 1968 : 305). Outer flanks steeply sloping and slightly concave outwards; lobes narrow, rounded, diverging at about 55°. Hinge line just over two-fifths as wide as shell, cardinal extremities obtuse, with small ears. Interarea gently curved, apsacline, up to one-half as long as wide and one-fifth as long as valve; delthyrium open. Sulcus originating at umbo, gently rounded, typically about 1·1 mm wide at 2 mm growth stage; contained ribs not as strongly developed as on lobes. Brachial valve about seven-tenths as long as wide, very shallow with overall concave profile but flat or slightly convex umbonally. Interarea short, flat, anacline; notothyrium open. Shallow, gently curved sulcus originating at umbo, slightly broader than ventral sulcus, about 1·5 mm wide at 2 mm growth stage; again contained ribs weakly developed. Ornamentation of fine costae and costellae, 5, 6, 7 per mm on 7, 4, 3 brachial valves respectively at 2 mm anterolaterally from umbo, over crest of lobe. Fine punctae spread over shell surface.

Ventral interior with teeth supported by almost vertical, narrowly divergent dental plates which continue forward to bound cordate muscle field. This is slightly longer than wide and just over one-quarter as long as valve, with diductor scars extending slightly beyond, but not enclosing, raised median adductor scar. Dorsal interior with blade-like brachiophores diverging at about 70°; cardinal process with relatively long, slender shaft on unthickened notothyrial floor, with small ? myophore preserved at posterior end. Details of musculature and mantle canal system obscure. No evidence of dorsal ridges. Punctae prominent on embayments along margins of valve interiors but rarely seen on eminences; internal punctae much coarser than those seen on exterior of shells.

Figs 181–191 *Dicoelosia* cf. *indenta* Cooper. Dolhir Formation: Figs 181, 182, BB37357, Internal mould and latex cast of a pedicle valve, ×5·1, loc. D14; Fig. 183, BB37358, Internal mould of a brachial valve, ×4·1, loc. D14; Fig. 184, BB37366, Internal mould of a pedicle valve, ×5·2, loc. D14; Fig. 185, BB37360, Internal mould of a pedicle valve, ×5·2, loc. D14; Fig. 186, BB37361, Latex cast of the exterior of a pedicle valve, ×5·2, loc. D14; Fig. 187, BB37362, Latex cast of the exterior of a brachial valve, ×5·5, loc. D14; Fig. 188, BB37363, Internal mould of a pedicle valve, ×5·9, loc. D14; Fig. 189, BB37359, Internal mould of a brachial valve, ×4·9, loc. D14; Fig. 190, BB37367, Internal mould of a pedicle valve, ×5·0, loc. D14; Fig. 191, BB37364, Internal mould of a pedicle valve, ×5·3, loc. D14.

Figs 192–197 *Dicoelosia* sp. Dolhir Formation: Fig. 192, BB37371, Internal mould of a brachial valve, ×6·0, loc. D6; Figs 193, 194, BB37372, Internal mould and latex cast of a pedicle valve, ×4·8, loc. D1; Figs 195, 196, BB37374, Internal mould and latex cast of a brachial valve, ×6·4, loc. D5; Fig. 197, BB37374, Latex cast of the exterior of a brachial valve, ×6·4, loc. D5.

DIMENSIONS

	length	width
Internal mould of a pedicle valve, BB37357	4·7	5·4
Internal mould of a brachial valve, BB37358	5·8	6·5
Internal mould of a brachial valve, BB37359	3·1	3·5
Internal mould of a pedicle valve, BB37360	5·1	5·4
External mould of a pedicle valve, BB37361	5·1	5·5
External mould of a brachial valve, BB37362	4·9	5·3
Internal mould of a pedicle valve, BB37363	3·5	3·7

DISCUSSION. This species of *Dicoelosia* is characterized by narrow, fairly widely divergent lobes, deep emargination, concave brachial valve and faint ribbing in the dorsal sulcus. These would place it in the '*D. jonesridgensis*' group (Wright, 1968*a* : 281) along with *D. indenta* (Cooper, 1930). No statistical data are available for *D. jonesridgensis* Ross & Dutro, 1966 but it differs from the Glyn Ceiriog species in having a more strongly concave brachial valve, a single prominent rib on the crests of the lobes of each valve and in the development of dorsal ridges internally.

The type sample of *D. indenta* is inadequate to give sufficient data for a statistical comparison, but data are available for the sample from the Boda Limestone, (Ashgill) of Dalarna, Sweden which is regarded as being conspecific by Wright (1968*a* : 304). A comparison by 't' test of the maximum length : width of the pedicle valves shows no significant difference between the Dalarna and Glyn Ceiriog forms. The same is true for comparisons of maximum length : thickness of pedicle valves and maximum length : width of brachial valves. However, a marked difference is the absence from the Welsh form of the characteristic dorsal ridge seen in *D. indenta* (Wright 1968*a* : 276). Temple (1970 : 27) describes *D.* cf. *indenta* from Meifod which also lacks a dorsal ridge and is similar to the Glyn Ceiriog species in length : width of the valves and in the relative length of the ventral muscle field. However, it appears to be relatively thicker and has more widely divergent lobes, although this may be a result of the smaller mean size of the Meifod specimens (see Wright 1968*a* : 265).

D. cf. *indenta* from the Keisley Limestone is superficially like the species under discussion but the sample is inadequate for a statistical comparison. Therefore, while the Glyn Ceiriog *Dicoelosia* may not be identical to *D. indenta*, it is considered to be closely allied to it. It is interesting to note that the specimens in which the dorsal ridges have not been recognized have been preserved as natural moulds.

The following statistical data have been obtained from the sample:

Maximum length (l) : maximum width (w) of pedicle valves, n = 34; $\bar{l}$(var. l) = 3·78 (1·394) mm; $\bar{w}$(var. w) = 4·24 (2·303) mm; r = 0·713; a(var. a) = 1·285 (0·02535); $\overline{\log_e l}$(var. $\log_e l$) = 1·283 (0·09313); $\overline{\log_e w}$(var. $\log_e w$) = 1·386 (0·1202); r_e = 0·726; α(var. α) = 1·136 (0·01908).

Maximum length (l) : mid-line length (m) of pedicle valves, n = 34; $\bar{l}$(var. l) = 3·78 (1·394) mm; $\bar{m}$(var. m) = 2·6 (0·523) mm; r = 0·865; a(var. a) = 0·613 (0·00295); $\overline{\log_e l}$(var. $\log_e l$) = 1·283 (0·0913); $\overline{\log_e m}$(var. $\log_e m$) = 0·918 (0·07455); r_e = 0·871; α(var. α) = 0·895 (0·00605).

Maximum length (l) : thickness (t) of pedicle valves, n = 24; $\bar{l}$(var. l) = 3·96 (1·619) mm; $\bar{t}$(var. t) = 1·12 (0·116) mm; r = 0·692; a(var. a) = 0·268 (0·0017); $\overline{\log_e l}$(var. $\log_e l$) = 1·328 (0·09804); $\overline{\log_e t}$(var. $\log_e t$) = 0·066 (0·08906); r_e = 0·702; α(var. α) = 0·953 (0·02093).

Maximum valve length (l) : length of ventral muscle scar (s), n = 20; $\bar{l}$(var. l) = 4·03 (1·118) mm; $\bar{s}$(var. s) = 1·05 (0·107) mm; r = 0·713; a(var. a) = 0·309 (0·00261); $\overline{\log_e l}$(var. $\log_e l$) = 1·36 (0·0664); $\overline{\log_e s}$(var. $\log_e s$) = 0·0025 (0·0925); r_e = 0·721; α(var. α) = 1·18 (0·03712).

Maximum length (l) : maximum width (w) of brachial valves, n = 17; $\bar{l}$(var. l) = 2·96 (0·461) mm; $\bar{w}$(var. w) = 4·32 (1·929) mm; r = 0·673; a(var. a) = 2·045 (0·1524); $\overline{\log_e l}$(var. $\log_e l$) = 1·061 (0·051); $\overline{\log_e w}$(var. $\log_e w$) = 1·414 (0·0982); r_e = 0·683; α(var. α) = 1·387 (0·06846).

Maximum length (l) : mid-line (m) of brachial valves, n = 17; $\bar{l}$(var. l) = 2·96 (0·461) mm; $\bar{m}$(var. m) = 1·96 (0·386) mm; r = 0·686; a(var. a) = 0·915 (0·02953); $\overline{\log_e l}$(var. $\log_e l$) = 1·061 (0·051); $\overline{\log_e m}$(var. $\log_e m$) = 0·624 (0·0957); r_e = 0·698; α(var. α) = 1·37 (0·06451).

Width of dorsal sulcus at 2 mm growth stage (s), n = 17; $\bar{s}$(var. s) = 1·53 (0·1747) mm.

Width of ventral sulcus at 2 mm growth stage (s), n = 33; $\bar{s}$(var. s) = 1·12 (0·0632) mm.

Dicoelosia sp.

Figs 192–197

Material and horizon. Internal and external moulds of 2 brachial valves (BB37371, l = 3·3, w = 5·7; BB37374, l = 1·8, w = 3·3) and 7 pedicle valves (including BB37372, l = 4·9, w = 5·3) from the lower part of the Dolhir Formation, 1–50 m above the Dolhir Limestone. Occurs along with *D.* cf. *indenta.*

Description. Ventri-biconvex shells with moderate invagination of anterior margin. Pedicle valve about nine-tenths as long as wide, with mid-line length almost seven-tenths of maximum valve length; thickness just over one-quarter of maximum valve length. Lobes broad, rounded, diverging at about 65°. Hinge-line just over one-half as wide as shell, cardinal extremities obtuse. Sulcus, originating at umbo, deep, narrow, about 0·9 mm wide at 2 mm growth stage. Interarea slightly curved, apsacline; delthyrium open. Brachial valve three-fifths as long as wide, shallow, with slightly convex lateral profile; posterolateral areas concave. Interarea very short, flat, anacline; notothyrium open. Shallow, gently rounded sulcus originating at umbo fairly broad, about 1·4 mm wide at 2 mm growth stage; contained ribs less strongly developed than those on lobes. Ornament of fine costae and costellae.

Ventral interior with teeth supported by erect, narrowly divergent dental lamellae which define muscle field. This about four-fifths as wide as long and less than one-third as long as valve; diductor scars slightly longer than raised median adductor scar. Dorsal interior with blade-like brachiophores diverging at about 115°; bases slightly divergent on to valve floor. Short cardinal process differentiated into bulbous myophore and short shaft. No evidence of dorsal ridges and details of musculature obscure. Punctae not well seen.

Discussion. This species is characterized by its transverse outline, convex brachial valve, broad, widely divergent lobes, and moderate emargination; the pedicle valve is reminiscent of *Epitomyonia* but the brachial valve is typical of *Dicoelosia.* These attributes of the species place it in the '*D. lata*' group (Wright, 1968*a* : 281) but it differs from *D. inghami* Wright, 1968 by having a convex brachial valve and a narrower ventral sulcus. It resembles *D. lata* Wright, 1964 and *D. simulata* Mitchell, 1977, but until more material becomes available and a statistical analysis of the species can be carried out, its exact affinities cannot be properly assessed.

EPITOMYONIA Wright, 1968

Epitomyonia sp.

Figs 198–202

Material and horizon. An internal mould of a pedicle valve, BB37373 (l = 6·0, w = 8·4) and internal and external moulds of 2 brachial valves (BB37377, l = 4·0, w = 4·3; BB37379, l = 5·0, w = 5·5) from the top of the Cyrn-y-brain Formation, 5 metres below junction with Plas Uchaf Formation.

Description. Concavo-convex shells of subquadrate outline; maximum width about mid-valve; cardinal angles obtuse. Pedicle valve about seven-tenths as long as wide and almost three-fifths as deep as long. Lateral profile strongly convex; anterior profile also strongly convex but with shallow median sulcus which becomes broader anteriorly. Interarea not seen. Brachial valve nine-tenths as long as wide; lateral profile gently convex umbonally but flattening anteriorly to become concave in later growth stages. Flattened posterolateral ears separated from sulcus by relatively narrow convex lobes. Sulcus about 1·3 mm wide at 2 mm growth stage, becoming broader and shallower anteriorly so that invagination of anterior margin is only slight. Interarea very short, flat, anacline. Ornament of subangular costae and branching costellae with about 24 ribs at 3 mm growth stage.

Ventral interior with elongately subquadrate muscle scar bounded laterally by strong ridges which are anterior continuance of dental plates. Median adductor scars raised on thickened ridge which extends as narrow median septum almost to valve margin. Details of teeth and hinge-line obscure. Dorsal interior with cardinal process differentiated into myophore and short, stout


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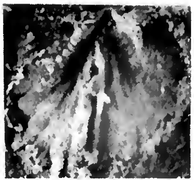
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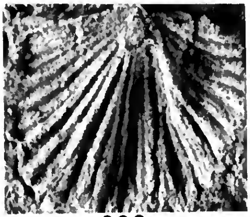
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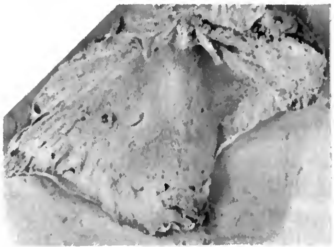
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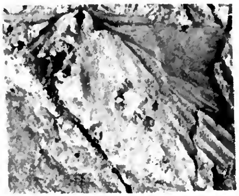
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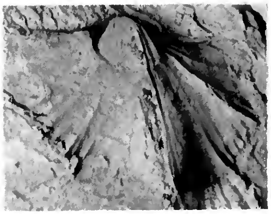
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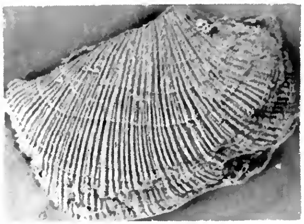
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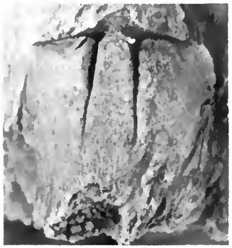
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Figs 198–202 *Epitomyonia* sp. Cyrn-y-brain Formation: Figs 198, 199, BB37373, Internal mould of a pedicle valve, ×4·8, loc. C3; Figs 200, 201, BB37377, Internal mould and latex cast of a brachial valve, ×6·0, loc. C3; Fig. 202, BB37379, Latex cast of the exterior of a brachial valve, ×5·8, loc. C3.

Figs 203–207 *Reuschella* sp. Tyn-y-twmpath Member: Figs 203, 204, BB37380, Internal mould and latex cast of a brachial valve, ×2·0, loc. T1; Fig. 205, BB37381, Internal mould of a pedicle valve, shaft; blade-like brachiophores widely divergent. Median septum rising anterior to cardinal process and extending to shell margin. Details of musculature obscure and no evidence of elevated platform in anterior part of mantle cavity, (Wright, 1968*b* : 130). Punctae well seen over internal surface of valve.

DISCUSSION. The Cyrn-y-brain specimens can apparently be separated from the type species, *E. glypha* Wright 1968, by the deeper pedicle valve, which is three-fifths as deep as long, compared to two-fifths as deep as long for the Swedish species; nor is there the development of an elevated platform in the brachial valve typical of mature specimens of *E. glypha*. It may be that the Cyrn-y-brain specimens are not mature, but they are approximately the same size as Boda Limestone specimens with the platform, although there is a variation in the development of the platform within the Boda sample. The only other record of the genus in Britain is by Temple (1968 : 29) who recovered two pedicle valves from the Lower Llandovery rocks of the Meifod area, but again the sample was too small for statistical comparisons to be made.

Family **HARKNESSELLIDAE** Bancroft, 1928

REUSCHELLA Bancroft, 1928

Reuschella sp.

Figs 203–207

1922 *Orthis* (*Hebertella*) *vespertilio* Sowerby: Wills & Smith: 187.

MATERIAL AND HORIZON. Distorted and fragmentary moulds of 3 pedicle (e.g. BB37381, l = 17·0, w = 34·0; BB37383, l = 13·9, w = 18·6) and 8 brachial (e.g. BB37380, BB37382) valves, from the lower and middle parts of the Dolhir Formation, including the Tyn-y-twmpath Member.

DESCRIPTION. Biconvex shells of transversely sub-rectangular outline about three-fifths as long as wide with maximum width anterior to hinge-line; well developed fold and sulcus arising at ventral and dorsal umbones respectively. Cardinal angles obtuse, rounded in large specimens with suggestions of small ears having been developed in younger forms. Pedicle valve unevenly convex, about one-quarter as deep as long, with sharp, angular median fold. Interarea gently curved, apsacline, about one-tenth as long as valve; delthyrium open. Brachial valve moderately convex in lateral profile, becoming flatter anteriorly; anterior profile, indented by strong sulcus, becoming flat posterolaterally; interarea very short, flat, anacline to orthocline; notothyrium open. Ornament of coarse fascicostellate ribbing, with about 28 angular costae and costellae at the 5 mm growth stage on the brachial valve. At 5 mm growth stage one pedicle valve had a density of 3 ribs per 2 mm immediately external to sector 1.

Ventral interior with teeth supported by strong dental lamellae which continue anteriorly for a short distance to form raised lateral edges to the muscle field. Muscle field broadly triangular about four-fifths as long as wide and about one-third as long as valve, with broad adductor scars, occupying about one-half of total scar width, flanked but not enclosed by diductors. Pedicle callist small. Dorsal interior with stout cardinal process, differentiated into swollen, crenulated myophore and short, thick shaft, situated on thickened notothyrial platform. Brachiophores diverging at about 70°–80°, with grooved inner surfaces; sockets elongate. Crural pits small;

×1·7, loc. T1; Dolhir Formation: Fig. 206, BB37382, Internal mould of a brachial valve, ×2·0, loc. D13. Dolhir Limestone Member: Fig. 207, BB37383, Internal mould of a pedicle valve, ×2·0, loc. L3.

Figs 208–213 *Laticrura* cf. *erecta* Wright. Dolhir Formation: Figs 208, 209, BB37391, Internal mould and latex cast of a pedicle valve, ×2·6, loc. D5; Fig. 210, BB37391, Latex cast of the exterior of a pedicle valve, ×2·6, loc. D5; Fig. 211, BB37393, Internal mould of a brachial valve, ×2·8, loc. D4; Fig. 212, BB37388, Internal mould of a pedicle valve, ×3·7, loc. D5; Fig. 213, BB37394, Internal mould of a brachial valve, ×3·3, loc. D4.

notothyrial platform undercut by posterior end of adductor muscle field. Punctae well seen on inner surfaces of valves.

Discussion. The fragmentary and distorted specimens of this sample cannot be assigned with certainty to any of the known species of *Reuschella*. The ribbing is not well enough preserved to study the relative insertion of the costellae so it cannot be used to place this species in either of Bancroft's two groups (1945 : 239). Most of the described species are of Caradoc age except for *R. inexpectata* Temple, 1968 from Keisley and an unnamed species of *Reuschella* from the Portrane Limestone (Wright, 1964). The former differs from the Glyn Ceiriog species in the absence of crural and adductor pits and more widely divergent brachiophores; the latter differs principally in the size and shape of the ventral muscle field, the Portrane form having a narrower, sub-oval scar, and shorter, more widely divergent brachiophores.

Family **LINOPORELLIDAE** Schuchert & Cooper, 1939

LATICRURA Cooper, 1956

Laticrura cf. ***erecta*** Wright, 1964
Figs 208–217

cf. 1964 *Laticrura erecta* Wright: 233; pl. 10, figs 17, 18; pl. 11 figs 16, 18–21.

Material and horizon. Internal and external moulds of 26 brachial and 16 pedicle valves from throughout the Dolhir Formation.

Description. Transversely sub-oval to subcircular ventri-biconvex shells with hinge-line width about two-thirds of maximum valve width, which is situated about mid-valve; cardinal angles obtuse, rounded. Pedicle valve about five-sixths as long as wide, strongly convex in both profiles. Interarea curved, apsacline, almost one-third as long as wide and one-fifth as long as valve; delthyrium narrow, open. Brachial valve four-fifths as long as wide; gently convex in both profiles with anterior profile indented medianly by variably developed shallow sulcus originating close to umbo. Interarea curved, anacline less than one-tenth as long as valve; notothyrium open. Ornamentation of fine hollow costae and costellae, typically with 4 ribs per mm medianly at 5 mm growth stage on brachial valve. Slightly swollen costellae developed on some specimens.

Ventral interior with teeth supported by very narrowly divergent dental plates whose anterior continuance defines elongately rectangular muscle field about one-half as wide as long and over two-fifths as long as valve; broad median adductor scars flanked by pair of narrow diductors. Pedicle callist developed. Dorsal interior with simple ridge-like cardinal process on notothyrial floor which thickens anteriorly and is bounded by high, almost vertical brachiophore plates. Brachiophores broad and 's' shaped in cross-section; sockets defined by fulcral plates. Strong median septum extends in front of notothyrial platform for about seven-tenths of valve length and may be up to 1 mm in height near posterior end. Pair of lanceolate adductor scars, each about one-half as long as valve, on either side of septum; narrower posterior scars about two-thirds as long as anterior ones. Traces of radiating mantle canals seen on floors of both valves.

Dimensions

	length	width
Internal mould of a pedicle valve, BB37388	—	7·6
Internal and external moulds of a brachial valve, BB37390 . .	9·2	14·1
Internal and external moulds of a pedicle valve, BB37391 . .	12·8	—
Internal mould of a brachial valve, BB37392	11·7	17·3
Internal mould of a brachial valve, BB37394	9·2	10·9
Internal mould of a brachial valve, BB37395	7·1	10·0

Discussion. Of the six species previously assigned to *Laticrura*, the forms which most closely resemble the specimens described here are *L. pionodema* Cooper, 1956 and *L. erecta* Wright, 1964. A comparison of length : width percentage of 11 Welsh brachial valves, mean 79·7 % (var. 26, 83) with Williams' (1962 : 145) figures for the Scottish and American samples of *L. pionodema* shows no significant difference between the two forms. A similar test also shows no significant difference between *L. erecta* and the Glyn Ceiriog species.

An important attribute in differentiating between species of *Laticrura* is the density of the ribbing. 3–5 ribs per mm were observed on 1, 7, 2 and 1, 5, 0 brachial valves of *L. erecta* at 5 mm and 7·5 mm growth stages respectively. Of the two dorsal exteriors sufficiently well preserved in the Glyn Ceiriog sample, one has 4 ribs per mm at both 5 mm and 7·5 mm growth stages, while the other has 4 ribs per mm at 5 mm and 3 ribs per mm at 7·5 mm thus showing a closer affinity of the Welsh species for *L. erecta.*

Cooper (1956) also used the development of an apical plate rather than a pedicle callist, and the definition of a dorsal sulcus to distinguish between species. The Glyn Ceiriog pedicle valves develop a pedicle callist and in this respect resemble *L. pionodema*, whereas *L. erecta* has an apical plate. All three forms have a broad shallow sulcus. Williams (1962 : 145) questions the importance of the difference between a pedicle callist and an apical plate as they serve the same function, and he states that sulcus development seems to be very variable within a *Laticrura* population; accordingly these attributes must be treated cautiously when being used as specific characters.

The Glyn Ceiriog form is apparently intermediate between *L. erecta* and *L. pionodema* but in view of the similarity in their ribbing the Welsh species is considered to be closer to the Portrane form. A test comparing the relative length of the dorsal median septum in the Irish and Welsh forms shows that there is no significant difference between them. Williams (1962 : 144) describes the anterior dorsal adductor scars as being narrower than the posterior pair but in the Glyn Ceiriog specimens it is the posterior pair that are narrower.

Data for a bivariate analysis of length of median septum (s) : length of brachial valve (l), $n = 12$; $\bar{s}(\mathrm{var.}\ s) = 6{\cdot}2\ (4{\cdot}39)$ mm; $\bar{l}(\mathrm{var.}\ l) = 9{\cdot}0\ (9{\cdot}16)$ mm; $r = 0{\cdot}973$; $a(\mathrm{var.}\ a) = 1{\cdot}443$ $(0{\cdot}00502)$.

Family **SAUKRODICTYIDAE** Wright, 1964

SAUKRODICTYA Wright, 1964

Saukrodictya hibernica Wright 1964

Figs 218–221

1964 *Saukrodictya hibernica* Wright: 220; pl. 7, figs 21, 23, 24, 26, 28–30.

MATERIAL AND HORIZON. Internal and external moulds of a well preserved brachial valve, BB37397 (length 4·2, width 6·2), from the lower part of the Dolhir Formation, 50 m above the Dolhir Limestone and 2 fragmentary external moulds from 1 m and 16 m above the limestone.

DESCRIPTION. Strongly sulcate, convex brachial valve of transverse outline. Valve about two-thirds as long as wide, maximum width just anterior to hinge-line; cardinal angles slightly obtuse, angular. Deep, rounded sulcus arising close to umbo, about one-half as wide as valve at anterior margin. Interarea very short, anacline approaching catacline; notothyrium open. External ornament of narrow costae and costellae developed within characteristic honeycomb meshwork.

Dorsal interior with short, stout brachiophores; sockets deep, bounded by short fulcral plates. Simple ridge cardinal process situated on notothyrial platform delimited by convergence of brachiophore plates and extending anteriorly into sub-quadrate adductor muscle field. This is sited on slightly raised platform about one-third as long as valve and bisected longitudinally by faint median ridge.

DISCUSSION. When Wright described the type species of *Saukrodictya hibernica* (1964 : 220) the material he used was sparse and fragmentary but the specimen described here largely confirms his impressions; in fact the Welsh specimen agrees so closely with the description of the Irish form that the two must be regarded as being conspecific, even though the sample is too small to compare them statistically. The Welsh *Saukrodictya philipi* (Davidson, 1883) from the lower Tre-Wylan Beds (Ashgill) of Llansantffraid (Cocks, 1978 : 83) requires further evaluation. The author here follows Temple (1970 : 33) in placing this rare genus within the Enteletacea although the Glyn Ceiriog specimen shows no sign of punctae. The small sample from Meifod clearly shows endo-


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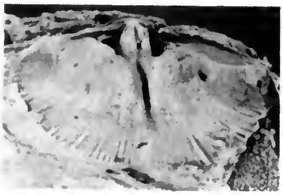
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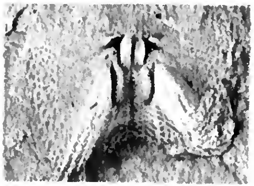
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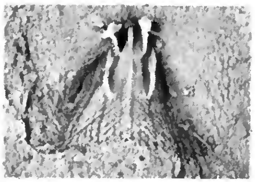
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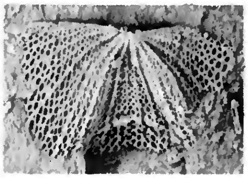
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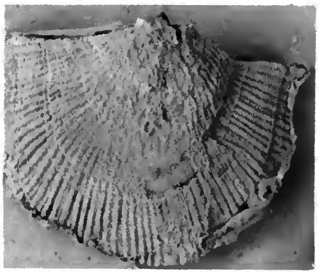
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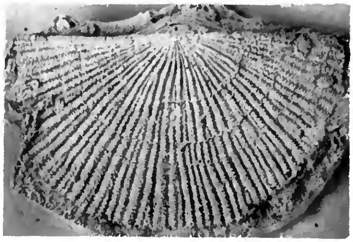
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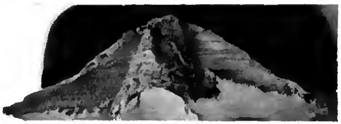
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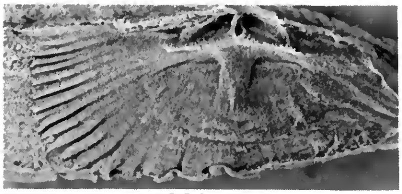
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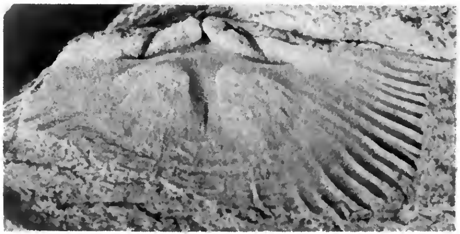
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Figs 214–217 *Laticrura* cf. *erecta* Wright. Dolhir Formation: Figs 214, 215, BB37390, Internal mould and latex cast of a brachial valve, ×2·6, loc. L3; Fig. 216, BB37390, External mould of a brachial valve, ×2·6, loc. L3. Dolhir Formation: Fig. 217, BB37395, Internal mould of a brachial valve, ×3·1, loc. D4.

punctae present on the internal moulds (Temple, 1970 : pl. 7, figs 10, 14, 18) and Wright (1964 : 219) envisaged the possibility of the transfer of the genus from the Orthacea. The Glyn Ceiriog specimen shows the development of short fulcral plates which are not described in the Portrane or Meifod species although in the case of the Irish material this may be a result of preservation.

Suborder **CLITAMBONITIDINA** Öpik, 1934
Superfamily **CLITAMBONITACEA** Winchell & Schuchert, 1893
Family **CLITAMBONITIDAE** Winchell & Schuchert, 1895
Subfamily **CLITAMBONITINAE** Winchell & Schuchert, 1895

VELLAMO Öpik, 1930

Vellamo cf. ***diversa*** (Shaler, 1865)
Figs 222–231

cf. 1865 *Orthisina diversa* Shaler: 67.
1908 *Clitambonites adscendens* Pander; Groom & Lake: 572, 577.
1922 *Clitambonites adscendens* Pander; Wills & Smith: 191.

MATERIAL AND HORIZON. Internal and external moulds of 6 brachial and 9 pedicle valves and 3 pairs of conjoined valves taken from the middle and upper parts of the Dolhir Formation, the Glyn Formation, and from the top of the Cyrn-y-brain Formation.

DESCRIPTION. Ventri-biconvex to plano-convex shells with maximum width usually along hinge-line giving slightly alate appearance. Pedicle valve of pyramidal shape and in some cases distinctly asymmetrical with umbo twisted. Interarea catacline to apsacline with concave to flat, sometimes terraced, profile, over two-fifths as long as wide. Delthyrium about one-third as wide as hinge-line, closed by convex pseudodeltidium perforated by oval foramen.

Brachial valve over three-fifths as long as wide, flat to very gently convex in lateral profile. Convex umbonally and on flanks but concave on posterolateral regions and in broad shallow sulcus which begins at 1 mm growth stage and becomes broader and shallower anteriorly. Interarea very short, about one-tenth of valve length, flat, anacline; notothyrium closed by highly arched chilidium. Ornamentation of even, rounded costae and costellae totalling about 30 and 46 ribs at 5 mm and 10 mm growth stages respectively on pedicle valve. Surface is also ornamented by fine, closely spaced concentric lines but these are never as strong as radial ornament which is only interrupted by growth lines.

Ventral interior with teeth supported by deep, gently curved spondylium simplex. Septum of spondylium extends for almost half of valve length with faint traces of *vascula media* seen, in one specimen to be sub-parallel to it. Dorsal interior with notothyrial cavity divided by short, stout cardinal process; accessory ridges parallel to cardinal process in one specimen; socket ridges widely divergent (about 100°) and about one-sixth as long as wide. Adductor muscle field about one-half as long as wide and just over two-fifths as long as valve, divided longitudinally by rounded median ridge almost two-fifths as wide as long; each half of muscle scar broadly triangular in shape. Thick trunks of *vascula media* are seen to extend from anterolateral corners after crossing anterior half of muscle scars in a few specimens. Anterior and posterior parts of scars are of about equal length.

Figs 218–221 *Saukrodictya hibernica* Wright. Dolhir Formation: Fig. 218, BB37396, Fragment of an external mould, ×4·0, loc. D6; Figs 219, 220, BB37397, Internal mould and latex cast of a brachial valve, ×4·7, loc. D3; Fig. 221, BB37397, Latex cast of the exterior of a brachial valve, ×4·7, loc. D3.

Figs 222–229 *Vellamo* cf. *diversa* (Shaler). Glyn Formation: Figs 222, 225, BB37404, Internal mould of a pedicle valve, ×1·8, ×1·9, loc. G3; Figs 223, 226, 227, BB37404, Latex cast of the exterior of a pedicle valve, ×1·8, ×1·8, ×2·3, loc. G3. Dolhir Formation: Fig. 224, BB37399, Latex cast of the exterior of a brachial valve, ×2·5, loc. D13; Figs 228–9, BB37403, Internal mould and latex cast of a brachial valve, ×4·0, ×3·5, loc. D14.

DIMENSIONS

	length	width
External mould of a brachial valve, BB37399	11·5	18·0
Internal mould of a pedicle valve, BB37400	14·5	24·4
Internal and external moulds of a brachial valve, BB37403	7·5	14·4
Internal and external moulds of a pedicle valve, BB37404	19·6	26·2

DISCUSSION. Some specimens have been tectonically deformed or fragmentary, but the majority, especially those from rottenstone bands, show the major features very well. Deformation may account for some of the asymmetry in the pedicle valves but some twisting of the ventral umbo is well known throughout this genus.

Clitambonites ascendens was recorded from the Dolhir and Glyn Formations by Groom & Lake (1908), and described from further west in the Berwyn Hills by Davidson (1868; 1883) as *Orthisina adscendens*. It was also recorded from the Drummuck Group, Girvan by Reed (1917) and Lamont (1935). However, Öpik, (1930 : 213), stated that the British specimens belonged to the genus *Vellamo* and as *C. adscendens* (Pander) is the type species of *Clitambonites*, the *C. adscendens* of Davidson must be a separate species. Hence the specific characters of this *Vellamo* have not been assessed. Only two other species of the genus have been described from the British Isles, *Clitambonites shallochensis* (Davidson) emend. Reed, which was later placed in synonomy with *V. pyramidalis* (Pahlen) by Öpik (1930 : 213), and *V. sulculata* (Wright) from the Portrane Limestone. Both these differ from the Welsh form in that they are more coarsely ribbed and have a sulcus in the pedicle valve.

The Glyn Ceiriog *Vellamo* is characterized by its apsacline ventral interarea, shallow dorsal sulcus, slightly alate hinge-line and 30 and 46 ribs at 5 mm and 10 mm growth stages respectively. Of the 20 species and 3 subspecies listed by Öpik (1934) the closest to the Welsh form are: *V. verneuili* (Eichwald), *V. leigeri* (Öpik), *V. sauramoi* (Öpik) and *V. wesenbergensis* (Pahlen). The first differs from the Glyn Ceiriog species in having a concave brachial valve, coarser ribbing and a relatively shorter dorsal muscle field in which the posterior scars are always longer and wider than the anterior ones. Also the spondylial septum reaches almost to valve margin. *V. leigeri* has a sulcus in the pedicle valve and a relatively longer dorsal muscle field. *V. sauramoi* is much more coarsely ribbed than the Welsh form and has a longer ventral interarea. *V. wesenbergensis* is very similar to the Glyn Ceiriog species although it does not appear to be alate from Öpik's figures (pl. 10) as is the case with its subspecies, *V. wesenbergensis auriculata*.

Of the American species of *Vellamo*, the one which most closely resembles the Welsh species is *Vellamo diversa*, from the Richmond of Anticosti Island. A small topotypic sample of this species was studied and found to be practically identical to the Glyn Ceiriog form. It was found to have an apsacline ventral interarea, a shallow dorsal sulcus beginning within 1 mm of the umbo, an alate hinge-line, and 30 and 48 ribs respectively at the 5 mm and 10 mm ventral growth stages. The growth ratios of external characters were found to agree closely with those for the Glyn Ceiriog *Vellamo* and any differences were of a minor nature and not statistically significant.

Unfortunately it was not possible to study the interior of the American shells, but in his discussion of *V. wesenbergensis*, Öpik (1934 : 109) points out that one of his specimens (pl. 10, fig. 8) was reminiscent of *V. diversa*. This specimen shows the interior of the brachial valve in which the adductor muscle field is about one-half as long as wide and nearly two-fifths as long as valve. The posterior and anterior parts of the scar are approximately equal in length. Twenhofel (1928) figured the interior of a brachial valve (pl. 23, fig. 11) which shows that the subquadrate anterior adductor scars are slightly larger than the subtriangular posterior pair, although the relative dimensions are similar to Öpik's specimen. However, variation in the muscle field cannot be assessed on the basis of these two figured specimens.

Thus the Welsh, and indeed other British species of *Vellamo* previously described as *Clitambonites adscendens* are closely related to *V. diversa* and *V. wesenbergensis*. This latter was, however, recorded from rocks of the Rakvere (E) stage of Estonia, which is slightly older than the Ashgill horizons from which the British specimens were taken, and the Richmond horizons containing *V. diversa*. Twenhofel (1928 : 200) in his discussion on *C. diversa* said that the nearest European representative was *C. verneuili* and another related species was *C. adscendens*, which differed in size and shape of the ventral interarea and a convex brachial valve. However, *C. verneuili* is different from *V. diversa* (Shaler) but it is not clear to which genus he referred when he mentioned *C. adscendens*. If he meant the British specimens of *Vellamo* then the differences may have been merely the result of variation within the species, but if he actually meant the type species of *Clitambonites*, then the differences were well founded.

Superfamily **GONAMBONITACEA** Schuchert & Cooper, 1931
Family **KULLERVOIDAE** Öpik, 1934
KULLERVO Öpik, 1934
Kullervo complectens (Wiman) ***albida*** (Reed, 1917)
Figs 232–238

1917 *Clitambonites complectens* (Wiman), var. *albida* Reed: 916, pl. 21, figs 19, 20.
1964 *Kullervo complectens albida* (Reed); Wright; 241, pl. 10, figs 3, 10, 13, 15–20.

MATERIAL AND HORIZON. Internal and external moulds of 3 brachial valves (e.g. BB37407, l = 4·3, w = c. 10) and 5 pedicle valves (e.g. BB37405, l = 4·9, w = c. 9; BB37406, l = 4·4; BB37409, l = 8·5) from throughout the Dolhir Formation.

DESCRIPTION. Strongly ventri-biconvex shells with maximum width along hinge-line. Pedicle valve pyramidal with flat to concave posterolateral regions bounded by convex flanks; shallow sulcus, about one-quarter as wide as valve, variably developed. Ventral surface very gently convex in lateral profile; interarea high, curved, apsacline at umbo but becoming catacline near hinge-line, and about one-half as long as wide. Brachial valve alate, with very small umbo, anterior profile gently convex with shallow median sulcus, and flat areas posterolaterally. Length to width ratios of 33% and 42% recorded for two valves. Concentric ridges prominent over whole shell surface and stronger than radial ornamentation in most cases although ribs bounding sulcus show greater prominence in 3 out of 4 pedicle valves. Frequency of concentric ridges per 2 mm of valve length measured anteromedianly from 3 mm growth stage is 3, 5, 5, 6 on four pedicle valves. Concentric ornamentation usually only marking on posterolateral areas of both valves; elsewhere well developed costae and costellae produce a reticulate pattern with concentric ridges. Ventral sulcus delimited on either side by costa much stronger than any other rib in 2 out of 4 specimens; of the remaining specimens one has external costae of similar strength and in the other the sulcus is not seen. Number of ribs in sulcus varies with about 5 in clearly reticulate specimens, but only 2–3 when concentric ridges are dominant. Counts of strong ribs on left flank, external to rib bounding sulcus, show 2–4 ribs on 1, 2, 1 specimens respectively. Total ribs occurring on flank at 3 mm growth stage are 5–7 on 2, 0, 2 valves respectively, these numbers being very much dependent on clear definition of ribs. Dorsal ornamentation similar, with shallow sulcus bounded by strong ribs and a further 2 or 3 external to these.

Ventral interior with spondylium supported by stout median septum; no subsidiary ridges seen. Traces of pinnate vascular markings observed on floor of valve. Dorsal cardinalia consisting of broad, widely divergent socket ridges almost one-third as long as wide; in narrow space between their posterior ends no cardinal process has been observed. Anteromedianly socket ridges united with thick notothyrial platform, passing anteriorly into thick median ridge which is an internal reflection of sulcus. Lanceolate adductor scars impressed on valve floor on either side of median ridge with apices directed posteromedianly.

DISCUSSION. When Öpik erected the genus *Kullervo* he divided the species into four groups on the basis of their external ornament (1934 : 162).
Group 1: is characterized by dominant radial ornament with fine concentric ridges, and a reticulate pattern developed only on the ears, e.g. *K. panderi* Öpik and *K. intacta* Öpik.


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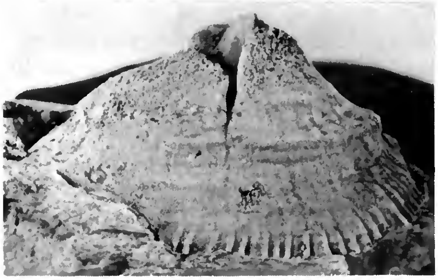
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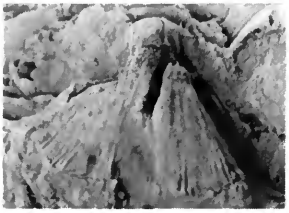
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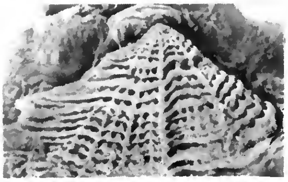
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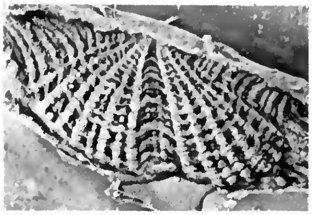
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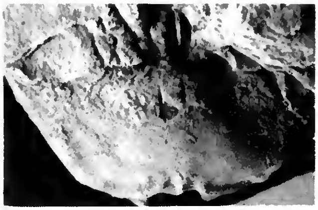
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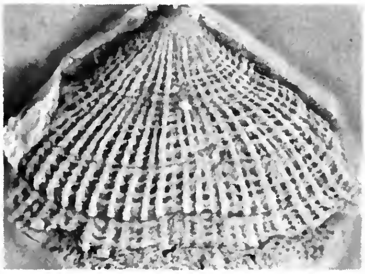
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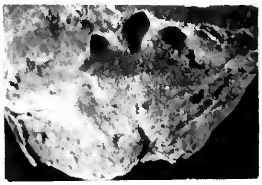
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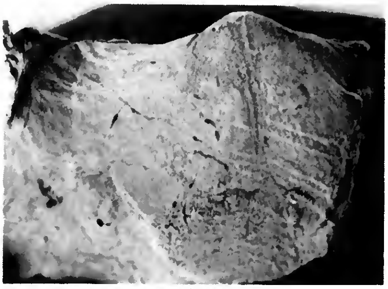
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Figs 230–231 *Vellamo* cf. *diversa* (Shaler). Dolhir Formation: Fig. 230, BB37403, Latex cast of the exterior of a brachial valve, ×4·0, loc. D14; Fig. 231, BB37400, Internal mould of a pedicle valve, ×2·0, loc. D15.

Group 2: with *K. lacunata* Öpik and *K. aluverensis* Öpik, has strong radial ribs in the middle sector but dominant concentric ornament on the ears.
Group 3: including *K. complectens* (Wiman), shows concentric ornamentation as strong as the radial over the whole valve surface.
Group 4: has concentric ornamentation dominant over the whole of the valve, and Öpik placed *K. complectens albida* (Reed) into this group.

The strong concentric ornament of the Glyn Ceiriog species immediately separates it from groups 1 and 2, and the arrangement of the radial ornament with only concentric ornamentation on the ears indicates a close affinity with *K. complectens albida* in group 4. When Reed erected his subspecies (1917 : 916) he stated that the ventral surface was covered with regular, strong, equidistant, thick, raised, rounded concentric lines and that the lateral margins of the sulcus were marked by one fine, strong straight rib, with traces of 2–3 very faint, smaller ribs on the lateral slopes of the valve. Therefore, it differs from *K. complectens* s.s. in having the radial ornamentation scarcely developed so that the reticulate ornament is not apparent; *K. complectens* shows strong reticulation. Of the Glyn Ceiriog specimens, 3 out of 4 are similar to Reed's subspecies while the fourth, a broken valve, shows stronger radial ornament.

Two forms which are similarly ornamented to the Welsh species are *K. pyramidata* Cooper & Kindle, 1936 from the Upper Ordovician of Quebec and *K. ornata* Cooper, 1956 from the Middle Ordovician of Virginia and Alabama. The former differs from the Glyn Ceiriog species in lacking a sulcus on the pedicle valve, and the latter has a concave brachial valve and lacks the alate hinge-line.

Thus the Welsh form has closest affinities with *K. complectens albida* in having the sulcus bounded by a rib stronger than the others and the concentric ornamentation being generally dominant.

Kullervo sp.
Fig. 239

Material and horizon. A single external mould of a pedicle valve, BB37410, from the upper part of the Dolhir Formation. Length 8·1 mm.

Description. Pyramidal pedicle valve with gently convex anterior profile. Ornament of strong concentric ridges equal in strength to radial ornament over whole of valve surface; radial costae of equal strength. Frequency of concentric ridges is 5 per 2 mm measured anteromedianly from 3 mm growth stage.

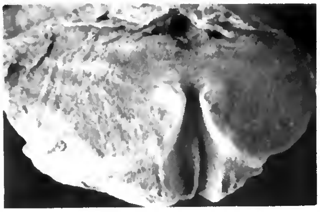
Brachial valve and interior unknown.

Discussion. This pedicle valve is distinct from *K. complectens albida* in its much stronger radial ornamentation, so that the reticulate pattern is more marked; also it lacks a well defined sulcus. The specimen does not have the posterolateral areas preserved, so further identification cannot be attempted.

Figs 232–238 *Kullervo complectens albida* (Reed). Dolhir Formation: Fig. 232, BB37409, Latex cast of a fragment of the exterior of a pedicle valve, ×4·2, loc. D4; Fig. 233, BB37405, Internal mould of a pedicle valve, ×4·1, loc. D6; Fig. 234, BB37405, Latex cast of the exterior of a pedicle valve, ×4·1, loc. D6; Fig. 235, BB37406, Latex cast of a fragment of the exterior of a pedicle valve, ×3·9, loc. D15; Figs. 236–7, BB37407, Internal mould and latex cast of a brachial valve, ×4·1, loc. D6; Fig. 238, BB37407, Latex cast of the exterior of a brachial valve, ×4·1, loc. D6.

Fig. 239 *Kullervo* sp., Dolhir Formation, BB37410, Latex cast of the exterior of pedicle valve, ×4·0, loc. D6.

Figs 240–245 *Triplesia* cf. *insularis* (Eichwald), Dolhir Formation: Figs 244–5, BB37412, Internal mould of a pedicle valve, ×2·1, ×3·0, loc. D4; Fig. 243, BB37419, Internal mould of a brachial valve, ×2·4, loc. D6; Fig. 241, BB37415, Internal mould of a brachial valve, ×2·8, loc. D15; Fig. 242, BB37417, Internal mould of a brachial valve, ×2·2, loc. D15; Fig. 240, BB37420, Latex cast of cardinalia, ×2·5, loc. D4.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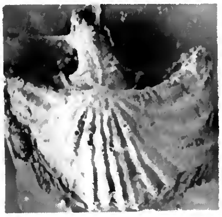
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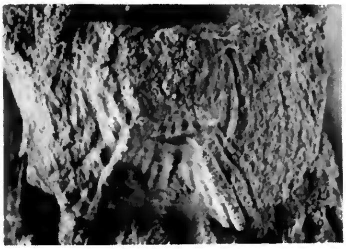
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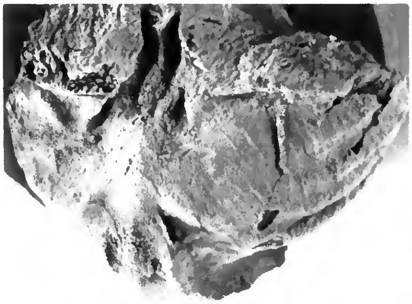
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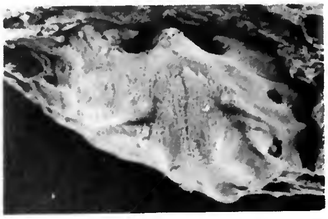
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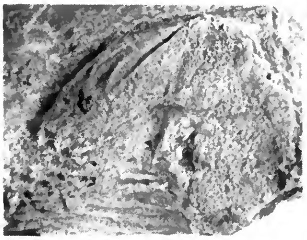
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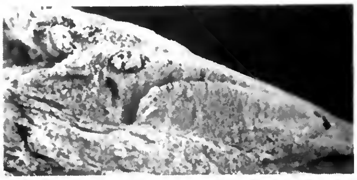
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Fig. 246 *Triplesia* cf. *insularis* (Eichwald). Dolhir Formation: BB37414, Internal mould of a brachial valve, ×2·6, loc. D11.

Fig. 248 *Cliftonia* sp. Plas Uchaf Formation: BB37422, Internal mould of a pedicle valve, ×2·7, loc. P1.

Suborder **TRIPLESIIDINA** Moore, 1952
Superfamily **TRIPLECIACEA** Schuchert, 1913
Family **TRIPLECIIDAE** Schuchert, 1913

TRIPLESIA Hall, 1859

Triplesia cf. ***insularis*** (Eichwald, 1842)
Figs 240–246

cf. 1842 *Terebratula insularis* Eichwald: 49, pl. 2, figs 6a–c.
1908 *Triplesia* cf. *insularis* Eichwald; Groom & Lake: 573, 578.
1922 *Triplecia insularis* Eichwald; Wills & Smith: 187, 191.

MATERIAL AND HORIZON. 70 brachial valves, 5 pedicle valves and 2 pairs of conjoined valves from throughout the Dolhir Formation and the Glyn Formation.

DESCRIPTION. Large dorsi-biconvex shells slightly wider than long with maximum width just posterior to mid-valve; cardinal angles rounded. Pedicle valve moderately convex in lateral profile; anterior profile with flat to slightly concave flanks on either side of rounded median sulcus originating about 3·5 mm from umbo; initially this is a shallow depression deepening anteriorly with development of rounded, dorsally projecting tongue. Interarea curved, apsacline, one-fifth as long as wide and about seven-tenths as wide as valve; delthyrium closed by flat pseudodeltidium with narrow median fold developed in all available specimens; apical foramen. Brachial valve strongly convex in both profiles, with low, gently convex median fold originating about 4 mm from umbo. Exterior devoid of ornament except for occasional concentric growth lines. Shell substance thick umbonally but becoming very thin near margins.

Ventral interior with slight development of pedicle passage in 2/6 specimens; teeth supported by thin, divergent dental lamellae. Large, cordate muscle field lightly impressed. Dorsal interior with strong, forked cardinal process whose width is about one-quarter of distance between ends of brachiophores; fork fused into single unit proximally, 'keeled' process of Wright (1971 : 354). Adductor scars and *vascula media* usually visible.

DIMENSIONS

	length	width
Internal mould of a pedicle valve, BB37412	17·5	—
Internal mould of a brachial valve, BB37414	—	16·6
Internal mould of a brachial valve, BB37317	14·6	19·2
Internal mould of a brachial valve, BB37419	c. 10	c. 14

DISCUSSION. The triplesiids have suffered more than any other brachiopods from tectonic distortion; it is probably the result of a combination of their fairly large size and the fact that their shells are quite thin except near the hinge-line. Wright (1964 : 246) points out that specific differentiation in *Triplesia* is based largely on shell shape and style of folding. In the case of the

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Figs 247, 249–255 *Oxoplecia* cf. *plicata* (Wiman): Dolhir Formation: Figs 249, 254, BB37426, Internal mould of a brachial valve and latex cast of the cardinalia, ×2·3, ×2·9, loc. D6; Fig. 252, BB37431, Internal mould of a pedicle valve, ×2·5, loc. D6; Fig. 255, BB37423, Internal mould of a brachial valve, ×4·4, loc. D1; Fig. 247, BB37432, Latex cast of the exterior of a brachial valve, ×2·8, loc. D4; Fig. 253, BB37430, Internal mould of a pedicle valve, ×3·5, loc. D6; Fig. 251, BB37425, Latex cast of the exterior of a brachial valve, ×2·2, loc. D4. Tyn-y-twmpath Member: Fig. 250, BB37429, Latex cast of the exterior of a pair of conjoined valves, ×2·3, loc. T1.

Figs 257–258 Triplesiid gen. et sp. indet. Dolhir Formation: BB37433, Internal mould of a pedicle valve, ×4·0, ×2·3, loc. D15.

Figs 256, 259–263 *Diambonia* cf. *gibbosa* (Winchell & Schuchert). Glyn Formation: Fig. 256, BB37435, Internal mould of a pedicle valve, ×5·4, loc. G1; Fig. 261, BB37438, Internal mould of a pedicle valve, ×5·4, loc. G1; Figs 259, 263, BB37436, Internal mould and latex cast of a brachial valve, ×6·5, loc. G1. Dolhir Formation: Fig. 262, BB37439, Internal mould of a pedicle valve, ×4·6, loc. D15; Fig. 260, BB37434, Latex cast of the exterior of a pedicle valve, ×4·5, loc. D16.


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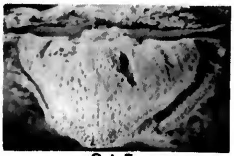
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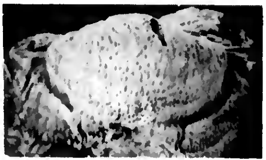
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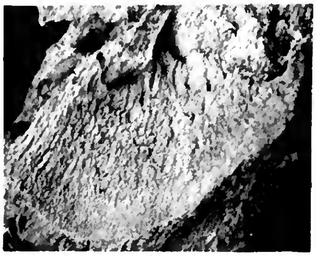
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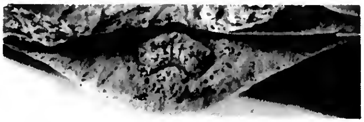
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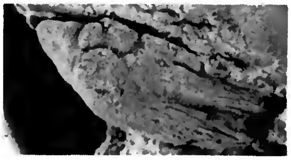
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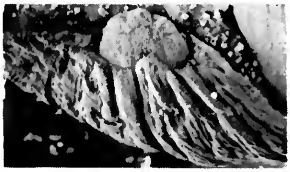
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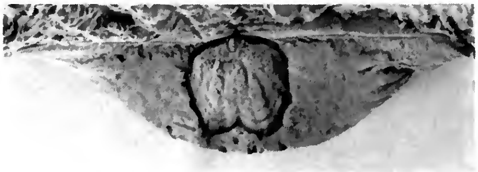
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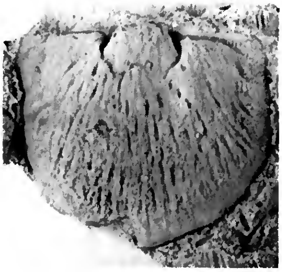
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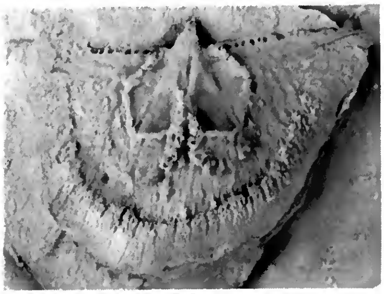
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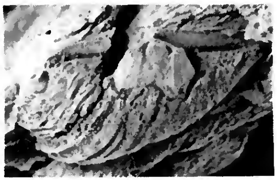
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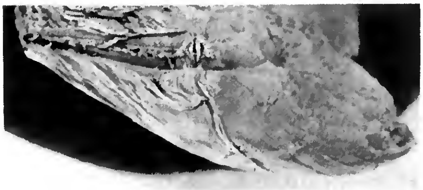
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Figs 264–271, 273 *Leangella* cf. *scissa* (Davidson). Dolhir Formation: Figs 264–267, BB37442, Internal mould and latex cast of a pedicle valve, ×5·0, ×4·9, ×5·1, ×5·0, loc. D5; Fig. 268, BB37447, Fragment of an internal mould of a brachial valve, ×5·0, loc. D15; Fig. 273, BB37444, External mould of a brachial valve, ×4·8, loc. D2; Fig. 270, BB37446, Latex cast of the exterior

Glyn Ceiriog specimens these have been altered by post-depositional distortion. The sulcus on the Welsh shells develops quite late, a sample of 5 valves showing a mean position of origin of 3·52 mm (var. 0·027) from the umbo. This is very similar to that for *T.* cf. *insularis* from the Portrane Limestone where 7 valves show a mean of 3·54 mm (var. 1·23) (Wright, 1964 : 246). Another form which also has a later developing sulcus is *T. uniplicata* (Cooper & Kindle, 1936) but this species has a narrower hinge-line, being only about one-half as wide as the valve, and has a much more delicate cardinal process.

The cardinalia of *Triplesia* are quite distinct from those of the associated *Oxoplecia* and the following data were obtained for a bivariate analysis of cardinal process width (x) : distance between the tips of the brachiophores (y), $n = 37$; $\bar{x}$(var. x) = 1·08 (0·089) mm; $\bar{y}$(var. y) = 4·60 (0·655) mm; $r = 0{\cdot}411$; a(var. a) = 2·72 (0·176). The width of the cardinal process was measured along a line joining the tips of the brachiophores. In a comparison of a's with *T.* cf. *insularis* from the Portrane Limestone, it was found that there was no significant difference in this character between the samples.

CLIFTONIA Foerste, 1909

Cliftonia sp.

Fig. 248

MATERIAL AND HORIZON. A single internal mould of a pedicle valve, BB37422, from near the top of the Plas Uchaf Formation on Cyrn-y-brain. Length 9·1 mm, width 12·9 mm.

DESCRIPTION. Pedicle valve about seven-tenths as long as wide and one-quarter as deep as long; maximum width about mid-valve; cardinal angles obtuse. Moderately convex in lateral profile, anterior profile convex with broad, flat-bottomed, median sulcus arising about 2 mm from umbo. Interarea curved, apsacline. External ornament, strongly impressed on valve interior, of broadly spaced concentric lamellae and radial costae and costellae which arise by branching. Dental plates short; other details of interior obscure.

DISCUSSION. This specimen is placed as *Cliftonia* on the basis of its ornament, even though this is only present as an impression on internal mould. Specimens of *Oxoplecia* from the same formation show the strongly impressed radial ornament on the interior but lack the concentric ornament which is too fine to be impressed on the internal mould. The only species of *Cliftonia* previously described from the Ordovician are *C. oxoplecioides* Wright, 1963 from the Chair of Kildare Limestone, and from the Kosov Formation, Bohemia (Marek & Havlíček, 1967), and *C. psittacina* (Wahlenberg, 1820) from the Ashgill of Sweden. The single specimen from Cyrn-y-brain has similarities with both of these species but until further material becomes available it cannot be assigned, with certainty, to either.

OXOPLECIA Wilson, 1913

Oxoplecia cf. ***plicata*** (Wiman, 1907)

Figs 247, 249–255

cf. 1907 *Triplecia plicata* Wiman: 12; pl. 2, figs 13–17b.
1908 *Triplesia* cf. *spiriferoides* M'Coy; Groom & Lake: 573.
1922 *Orthis* (*Platystrophia*) *spiriferoides* M'Coy; Wills & Smith: 191.

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of a pedicle valve, ×5·1, loc. D4. Dolhir Limestone Member: Fig. 269, BB37445, Internal mould of a pedicle valve, ×4·0, loc. L3. Tyn-y-twmpath Member: Fig. 271, BB37449, Internal mould of a pedicle valve, ×4·0, loc. T1.

Figs 272, 274–280 *Sampo* cf. *ruralis* (Reed). Dolhir Formation: Figs 277, 280, BB69160, Internal mould and latex cast of a brachial valve, ×2·5, loc. D2; Figs 274, 275, BB69162, Internal mould and latex cast of a pedicle valve, ×2·0, ×2·6, loc. D6; Fig. 272, Internal mould of a pedicle valve, ×3·5, loc. D6; Fig. 279, BB69161, External mould of a brachial valve, ×3·5, loc. D6; Fig. 278, BB69157, Internal mould of a pedicle valve, ×2·5, loc. D4. Glyn Formation: Fig. 276, BB69159, Internal mould of a pedicle valve, ×2·3, loc. G3.

MATERIAL AND HORIZON. Sixteen brachial and 8 pedicle valves from throughout the Dolhir Formation and from near the top of the Cyrn-y-brain Formation.

DESCRIPTION. Dorsi-biconvex shells of transversely subquadrate outline with maximum width about mid-valve; cardinal angles rounded, obtuse; pronounced dorsal fold and ventral sulcus. Pedicle valve about four-fifths as long as wide and almost one-quarter as deep as long; evenly convex in lateral profile but anterior profile with gently convex flanks separated by broad, flat-bottomed sulcus originating at just over 2 mm from umbo. Interarea curved, apsacline: delthyrium closed by flat pseudodeltidium, with narrow median fold developed in 1 out of 7 specimens; foramen apical. Brachial valve about two-thirds as long as wide and two-fifths as deep as long; strongly convex in lateral profile, maximum convexity near umbo; anterior profile with strongly convex flanks and flat-topped median fold, originating at about 2 mm from umbo. Concentric ornamentation of fine fila, about 7 per mm; radial ornamentation of stout rounded costae and costellae, the latter arising by bifurcation and intercalation. Fold and sulcus initially with 3 and 2 costae respectively; on brachial valve wavelength of ribs at 7·5 mm growth stage is about 1·4 mm, with total of 11–18 ribs developed at 5 mm growth stage. Development of hood not seen.

Ventral interior with pedicle tube developed; teeth strong, supported by receding dental lamellae. Details of muscle scars obscure. Dorsal interior with large, forked cardinal process deeply cleft proximally. Adductor scars and arcuate *vascula media* usually visible.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB37423	5·7	8·1
Internal mould of a brachial valve, BB37426	15·6	19·7
External mould of conjoined valves, BB37429	—	c. 17
Internal mould of a pedicle valve, BB37431	—	c. 22
External mould of a brachial valve, BB37432	6·7	11·5

DISCUSSION. Most of the specimens have been quite badly distorted so that measurements are of little use in assessing shell shape. The most useful criteria available for specific identification are the nature of the ornament and details of the cardinalia. (Wright 1964 : 248).

The development of 3 initial costae on the dorsal fold of 13 out of 14 Glyn Ceiriog specimens, the other having only 2, distinguishes them from all but a few species of *Oxoplecia*; viz. *O. subborealis* (Davidson, 1883) emend. Williams 1962; *O. platystrophoides* and *O. costata* Cooper 1930; *O. abnormis*, *O. gibbosa* and *O. parva* Cooper 1956; *O. perfecta* Cooper & Kindle 1936, and *O. plicata* Wiman 1907. Of these the last two most closely resemble the Welsh form, although good samples of these are as yet unavailable. In discussing the Portrane Limestone form, Wright (1964 : 248; 1971 : 354; 1972 : 7) regards the deeply grooved proximal end of the cardinal process as being of some importance and states that this is so far only known from *O. plicata*, and *Oxoplecia* sp. from Kildare although forms whose cardinalia have not yet been studied may show similarity. The Glyn Ceiriog specimens differ in small details from the Portrane species, e.g. they have a finer concentric ornament typically with 7 fila per mm compared to 5 per mm on the Irish shells, although this may be a result of preservation. The 'grooved' type of cardinal process associated with the general lack of a median fold on the pseudodeltidium suggests a close similarity with *O. plicata* whereas *Oxoplecia* sp. from Kildare has a fold on the pseudodeltidium.

The following statistical data were obtained:

Origin of dorsal fold (m), $n = 10$; $\overline{m}(\text{var. } m) = 2{\cdot}17\ (0{\cdot}16)$ mm

Origin of ventral sulcus (m), $n = 7$; $\overline{m}(\text{var. } m) = 2{\cdot}33\ (0{\cdot}089)$ mm

Concentric ornamentation of 5–8 fila per mm on 1, 6, 9, 2, specimens respectively.

Radial ornamentation in the ventral sulcus: (*a*) 8 out of 8 specimens show 2 initial costae; (*b*) at the 3 mm growth stage, 2, 3, 4, ribs occur on 8, 0, 0, valves respectively; at 5 mm on 5, 3, 0 valves; and at 10 mm on 5, 2, 1 valves.

Radial ornamentation on dorsal fold: (*a*) 2, 3 initial costae shown by 1, 13 valves respectively; (*b*) at the 3 mm growth stage 3, 4, 5, 6 ribs shown by 12, 1, 1, 0 valves; at 5 mm by 7, 5, 1, 0 valves; and at 10 mm by 3, 6, 1, 1 valves.

Total ribs on brachial valves at the 5 mm growth stage; 11–18 ribs on 1, 3, 2, 1, 1, 3, 1, 1, valves.

Triplesiid, gen. et sp. indet
Figs 257, 258

MATERIAL AND HORIZON. A single pedicle valve, BB37433, preserved as a damaged internal mould from high up in the Dolhir Formation. Length 13·1 mm.

DESCRIPTION. Pedicle valve asymmetrical, about nine-tenths as long as wide and about one-sixth as deep as long, maximum width anterior to hinge-line, cardinal angles obtuse; flatly convex in lateral profile, anterior profile becoming broadly and gently sulcata from about 2 mm anteromedianly from umbo. Interarea curved, apsacline, about one-sixth as long as valve. Ornament not seen.

Ventral interior with small teeth supported by thin, widely divergent dental plates. Muscle scars obscure. Pedicle tube seen in an apical position.

DISCUSSION. Such a poorly preserved specimen cannot be assigned with confidence to any species or genus.

Order **STROPHOMENIDA** Öpik, 1934
Suborder **STROPHOMENIDINA** Öpik, 1934
Superfamily **PLECTAMBONITACEA** Jones, 1928
Family **LEPTELLINIDAE** Ulrich & Cooper, 1936
Subfamily **LEPTESTIININAE** Havlíček, 1961

DIAMBONIA Cooper & Kindle, 1936

Diambonia cf. ***gibbosa*** (Winchell & Schuchert, 1895)
Figs 256, 259–263

cf. 1895 *Plectambonites gibbosa* Winchell & Schuchert: 416, pl. 32, figs 13–17.
1908 *Plectambonites* sp; Groom & Lake: 573, 577 (pars).
cf. 1936 *Diambonia gibbosa* (Winchell & Schuchert); Cooper & Kindle: 356.

MATERIAL AND HORIZON. Internal and external moulds of 11 pedicle valves and internal and external moulds of a single brachial valve; 5 specimens from the upper part of the Dolhir Formation and 7 from the Glyn Formation.

DESCRIPTION. Concavo-convex shells of transversely semi-circular outline with maximum width along hinge-line. Pedicle valve about two-thirds as long as wide and almost two-fifths as deep as long; lateral profile strongly convex but anterior profile flattening out at posterolateral edges. Interarea curved, apsacline; delthyrium wide, open. Brachial valve almost one-half as long as wide, both profiles concave; interarea flat, catacline; notothyrium filled by cardinal process lobes. External ornament segregated into sectors by accentuated costae and costellae; about 5 enlarged costae at umbo of pedicle valve.

Ventral interior with transverse, bilobed muscle field almost four-fifths as long as wide and about one-third as long as valve; small triangular adductor scars on either side of shallow median groove are separated from larger diductors by small, anteriorly convergent ridges. Divergent *vascula media* arise within diductor muscle field and extend from its anterolateral corners; some specimens show traces of other vascular canals with one pair in central position on either side of median septum and another pair in lateral position. Teeth supported by dental plates whose anterior continuance as low ridges defines muscle field. Median septum high, developed in front of muscle field and extending to about two-thirds of valve length. Some specimens show septum as continuance of that bisecting muscle field.

Dorsal interior with elevated, W-shaped muscle platform about one-half as long as wide and three-tenths as long as valve. Subperipheral rim parallel to margin anterolaterally but curving towards margin medianly. Poorly developed second rim seen on one side of single specimen. Widely divergent socket ridges apparently ankylosed to cardinal process but preservation rather poor.

DIMENSIONS

	length	width
External mould of a pedicle valve, BB37434	4·2	—
Internal mould of a pedicle valve, BB37435	4·2	—
Internal mould of a brachial valve, BB37436	3·8	7·8
Internal mould of a pedicle valve, BB37438	c. 4	—
Internal mould of a pedicle valve, BB37439	5·7	c. 9

DISCUSSION. The genus *Diambonia* was separated from the closely related *Leangella* Öpik by Cooper and Kindle (1936 : 356) on the presence of a marked ventral median septum in front of the muscle field on this form. On the evidence of a sample from Pomeroy, containing both septate and non-septate forms, Mitchell (1977 : 78) concludes that the generic status of *Diambonia* and *Leangella* may have to be reconsidered. Non-septate forms have also been found at Glyn Ceiriog but these occur in horizons above and below those containing the septate shells and consequently have been assigned to *Leangella*. There is variation in the strength of the septum among the Glyn Ceiriog *Diambonia*, but this is probably a result of preservation, and so *Leangella* and *Diambonia* are considered as separate here.

The genus is not common at Glyn Ceiriog, but the reasonably well preserved specimens recovered are distinct from *D.* cf. *discuneata* (Lamont, 1935), the only other Ashgill form for which statistical data are available (Mitchell, 1977 : 78). 10 Glyn Ceiriog pedicle valves have a mean *length of muscle field* : *length of valve* ratio of 29% (var. 12·56); 9 Pomeroy valves have 17·8% (var. 15·94) for the same statistic. A 't' test shows a significant difference between the two ($P < 0{\cdot}001$). A similar difference was observed in the relative length of the median septum which in 9 Glyn Ceiriog valves extended for 66·0% (var. 100·28) of valve length and 8 Pomeroy valves for 43·0% (var. 65·71) of valve length; a 't' test showed a significant difference ($0{\cdot}01 > P > 0{\cdot}002$). Of the two Ashgill species recorded by Cooper & Kindle (1936 : 356), *D. septata* (Cooper, 1930) and *D. gibbosa* (Winchell & Schuchert, 1895), the Glyn Ceiriog form is closer to the latter, which has a large ventral muscle field and a long median septum. However, until more data becomes available for these and other species the affinities of the Welsh form cannot be properly ascertained.

LEANGELLA Öpik, 1933

Leangella cf. ***scissa*** (Davidson, 1871)

Figs 264–271, 273

cf. 1871 *Leptaena scissa* Davidson: 325, pl. 47, figs 22–23 (non 25, ?21, ?24).
1908 *Leptella* (?) *Llandeiloensis*, Davidson; Groom & Lake: 577, 578 (pars).
1922 *Plectambonites scissa* (Salter); Wills & Smith: 187.
1928 *Leptelloidea scissa* (Davidson), pars; O. T. Jones: 481.

MATERIAL AND HORIZON. Internal and external moulds of 10 pedicle and 5 brachial valves mostly from the lower part of the Dolhir Formation.

DESCRIPTION. Strongly concavo-convex shells of transversely semi-circular outline with maximum width along hinge-line. Pedicle valve about three-fifths as long as wide and almost one-half as deep as long; lateral profile evenly convex but anterior profile flattening out posterolaterally. Interarea curved, apsacline, less than one-tenth as long as wide and about one-tenth as long as valve. Small, apical pseudodeltidium developed. Brachial valve deeply concave with catacline to hypercline interarea; chilidial plates well developed but not closing notothyrium. Ornamentation unequally parvicostellate with four or five widely spaced, accentuated costellae on pedicle valve and irregular rugae on brachial valve of some specimens.

Ventral interior with bilobate muscle field nearly three-quarters as long as wide and less than one-third as long as valve. Teeth small, supported by widely divergent dental lamellae passing anteriorly into low ridges bounding muscle field. Lanceolate adductor scars situated posteromedianly and almost enclosed by diductor scars. Sub-parallel to slightly divergent *vascula media* extend anteriolaterally from corners of diductor scars. Two specimens show faint ridges which may mark traces of another outer pair of vascular canals (?*vascula dentalia*) (Fig. 271). One specimen which has slight plication of anterior margin, shows sub-peripheral rim developed. This rim is absent from anteromedian portion of valve, over plication, and the flat area outside rim shows tracks of four vascular canals, two on either side of plication, *vascula media* in median position with (?) *vascula dentalia* in posterolateral position (Figs 264–267).

Dorsal interior with strong trilobed cardinal process differentiated into high median ridge flanked by lower lateral lobes, almost filling notothyrial cavity. Muscle field with elevated anterior margin which has median indentation from which broad median ridge extends posteriorly. Row of enlarged tubercles developed anterior to muscle field and parallel to its anterior edge. Floor of valve covered with elongate tubercles.

DIMENSIONS

	length	width
Internal mould of a pedicle valve, BB37442	3·0	6·3
External mould of a brachial valve, BB37444	4·8	c. 11
Internal mould of a pedicle valve, BB37445	6·2	11·3
External mould of a pedicle valve,BB37446	2·6	7·1

DISCUSSION. The genus *Leangella* may be confused with *Leptestiina* (Havlíček, 1952), the main difference between the two being the development of a sub-peripheral rim in the brachial valve of the former (Havlíček, 1967 : 29). The Glyn Ceiriog sample is made up largely of internal moulds of pedicle valves and at least one of these may prove to be *Leptestiina.* The only brachial valve interior found was broken and the margin of the shell was missing so it could belong to either genus, or even to *Diambonia*, although these specimens have been identified as *Leangella* because of the size and strength of the ventral muscle field. The genus is not common at Glyn Ceiriog but when *Diambonia* is found in the upper Dolhir Formation and Glyn Formation then *Leangella* is less common and after the disappearance of *Diambonia* at the end of the Ordovician, *Leangella* reappears in the Lower Llandovery Fron Frys Formation.

The only exclusively Ordovician species of *Leangella* so far recorded are *L. hamari* (Spjeldnaes, 1957) and *L. cylindrica* (Reed, 1917). The former differs from the Glyn Ceiriog shells in having a smaller ventral muscle field, while the latter differs in its much more alate outline. *L. scissa* is recorded from uppermost Ordovician and Llandovery beds and the Glyn Ceiriog specimens appear very similar to it, although the sample is too small for a reliable statistical comparison.

SAMPO Öpik, 1933

Sampo cf. ***ruralis*** (Reed, 1917)

Figs 272, 274–280

?1908 *Leptella* (?) *Llandeiloensis* (Davidson); Groom & Lake: 577 (pars).
cf. 1917 *Plectambonites ruralis*; Reed: 879, pl. xiv, figs 25–33.
cf. 1928 *Leptelloidea ruralis* Reed; O. T. Jones: 492.

MATERIAL AND HORIZON. Internal and external moulds of 15 pedicle and 4 brachial valves from the Dolhir Formation and Glyn Formation. Most specimens have been tectonically distorted so that few measurements are of use for statistical analysis.

DESCRIPTION. Strongly concavo-convex shells of transversely semi-circular outline with maximum width along hinge-line. Pedicle valve almost three-quarters as long as wide and three-tenths as deep as long; lateral profile evenly convex; anterior profile with convex median region and slightly concave flanks. Interarea curved, anacline, less than one-tenth as long as wide and less than one-tenth as long as valve; delthyrium open except for small apical pseudodeltidium. Brachial valve deeply concave and over one-half as long as wide; interarea flat, hypercline. Ornamentation unequally parvicostellate with about 10–12 widely spaced accentuated costellae at 5 mm growth stage separated by 8–12 very fine ribs.

Ventral interior with up to ten denticles developed along hinge-line on either side of delthyrium; teeth small; widely divergent dental plates seen as part of strong ridge bounding transverse bilobed muscle field, which is over four-fifths as long as wide and three-tenths as long as valve.

Elongate, oval, medianly situated adductor scars enclosed by lobate diductor scars. Vascular markings prominent over whole inner surface of valve. Dorsal interior with strong cardinal process differentiated into high median crest bounded by lower lateral ridges and almost filling notothyrial cavity. Blade-like socket ridges confluent with rim defining muscle field. These ridges meet along elevated anterior edge of muscle field to form median cusp, from which a median ridge runs posteriorly becoming lower until it merges with triangular thickened area immediately in front of cardinal process. This thickened area has two small median grooves which merge anteriorly, and from its antero-lateral angles run two *vascula myaria* which divide anterior and posterior adductor scars on either side of median ridge. Secondary, less pronounced platform developed in front of muscle field, edges defined by two rows of elongate, coarse pustules, originating from below median cusp and diverging from there in two arcs. These pustules probably supported the lophophore. Finer pustules ornament inner surface of valve outside platforms especially along crest of sub-peripheral thickening, which is dissected by radiating vascular canals (Fig. 9).

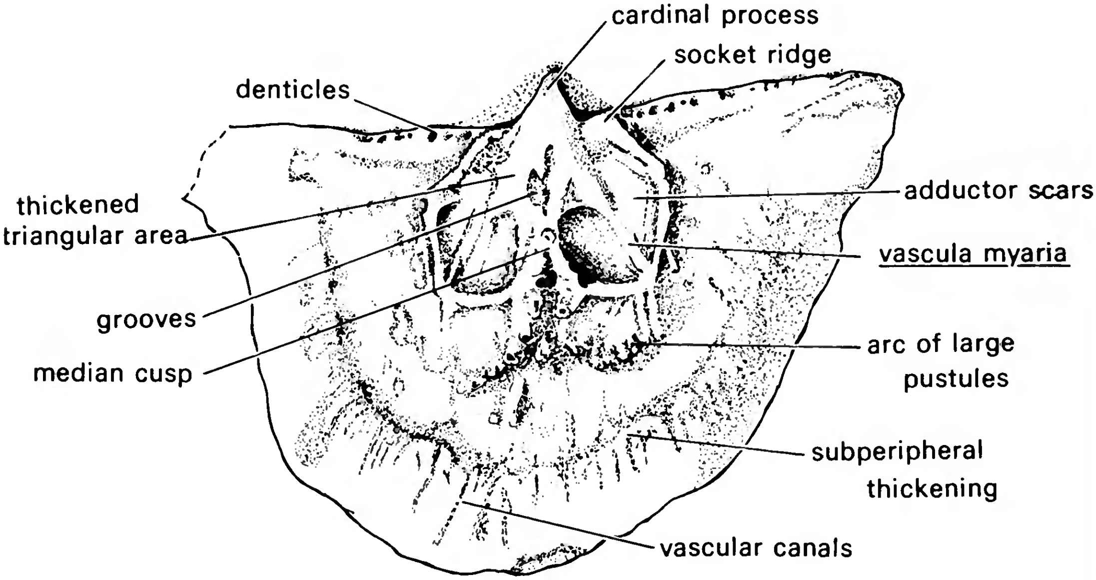


Fig. 9 Diagrammatic view of the dorsal interior of *Sampo* cf. *ruralis*.

DIMENSIONS

	length	width
Internal mould of a pedicle valve, BB69159	14·4	15·6
Internal mould of a brachial valve, BB69160	10·3	18·7
Internal mould of a pedicle valve, BB69162	—	27·5

DISCUSSION. *Sampo ruralis* (Reed, 1917) is a common species in the Ashgill rocks of the British Isles and the Glyn Ceiriog population is very like that from the Portrane Limestone (Wright, 1963 Ms) especially in the dimensions of the ventral muscle field, which in both populations is about four-fifths as long as wide and about one-third as long as valve. However, due to the deformation of the specimens, a statistical comparison of the two samples could only be very tentative.

A comparison of the external ornament with that on a small sample from Girvan shows a close similarity between the Glyn Ceiriog and Girvan species; the Scottish shells have 10–12 accentuated ribs at the 5 mm growth stage with 8–16 fine ribs between them. Thus the Welsh shells are considered to be very closely related to *S. ruralis* although better preserved material is required before statistical comparisons can be made.

Family **SOWERBYELLIDAE** Öpik, 1930

Subfamily **SOWERBYELLINAE** Öpik, 1930

SOWERBYELLA Jones, 1928

Sowerbyella cf. ***sladensis*** Jones, 1928

Figs 281–289, 292

1908 *Plectambonites sericea* (Sowerby); Groom & Lake: 573, 577.
1922 *Plectambonites sericea* (Sowerby); Wills & Smith: 191.
cf. 1928 *Sowerbyella sladensis* Jones: 421, pl. 21, figs 14–17.
1935 *Sowerbyella sladensis* Jones; Smith: 189, 198.

MATERIAL AND HORIZON. *Sowerbyella* is very common at Glyn Ceiriog with internal and external moulds of 54 brachial valves and 76 pedicle valves being recovered from throughout the Dolhir Formation and 26 brachial and 29 pedicle valves from the Glyn Formation. It is most common at the top of the Dolhir Formation and also quite common in beds of the same age on Mynydd Cricor (15 brachial and 5 pedicle valves) but proportionately less common in these beds in Cyrn-y-brain (6 brachial and 5 pedicle valves).

DESCRIPTION. Concavo-convex shells of transversely subquadrate outline with maximum width at hinge-line or just anterior to it; anterior commissure recti-marginate. Pedicle valve almost three-fifths as long as wide and just over one-quarter as deep as long; cardinal angles normally rectangular to slightly rounded but one small specimen has acute angles; lateral profile with maximum convexity just anterior to umbo; anterior profile moderately and evenly convex. Interarea gently curved, apsacline; delthyrium with small, convex pseudodeltidium.

Brachial valve gently concave in both profiles; anterior profile flattening towards cardinal angles. Interarea very short, flat, catacline; notothyrium partially closed by chilidial plates and almost filled by cardinal process lobe.

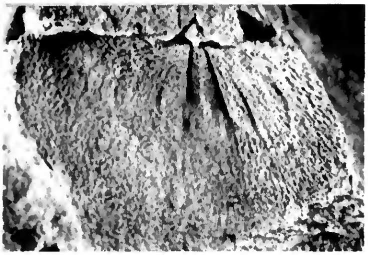
Ornament of fine costellae with density of 7–10 ribs per mm anteromedianly at 5 mm growth stage, segregated into narrow sectors by stronger ribs, with 4–7 ribs between them.

Ventral interior with bilobed diductor muscle scars about two-thirds as long as wide and over two-fifths as long as valve. Small posteromedianly situated adductor scars divided by short septum which extends anteriorly for less than one-fifth of valve length before bifurcating; deeply impressed *vascula media* with lemniscate pattern; teeth small, dental plates obsolescent in adult shells. Dorsal interior with socket ridges almost parallel to hinge-line and pair of narrowly divergent sub-median septa extending anteriorly for three-fifths of valve length. Slightly elevated adductor muscle scars about three-quarters as long as wide and almost two-thirds as long as valve. In some specimens thickened ridges bearing *vascula myaria* are seen to diagonally bisect the muscle scars. In larger specimens these ridges may be accentuated to become almost as strong as sub-median septa. Floors of both valves outside muscle fields covered with coarse pustules which may be ends of taleolae.

DIMENSIONS

	length	width
External mould of a brachial valve, BB69168	c. 10	c. 20
Internal mould of a pedicle valve, BB69170	8·5	13·7
Internal mould of a brachial valve, BB69171	3·5	4·8
Internal mould of a brachial valve, BB69172	4·8	7·9
Internal mould of a pedicle valve, BB69173	9·2	16·3
Internal mould of a brachial valve, BB69174	7·4	10·3
Internal mould of a brachial valve, BB69175	6·2	12·5

DISCUSSION. *Sowerbyella* from Glyn Ceiriog compares closely with *S. sladensis* Jones 1928 and *S. thraivensis* (Reed, 1917): these are distinguished from one another by the smaller size, acute cardinal angles and finer ornament of the latter according to Jones (1928 : 425). He records both forms from the Ceiriog area but only one small specimen has been recovered with acute cardinal angles, and growth lines on some large specimens show that they had acute angles when younger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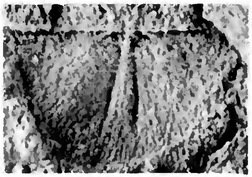
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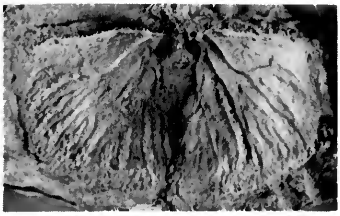
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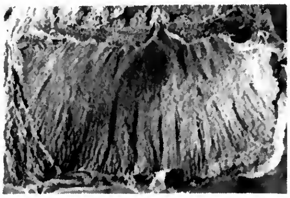
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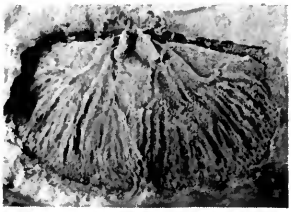
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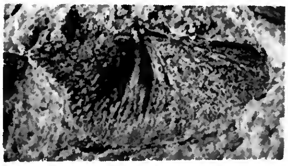
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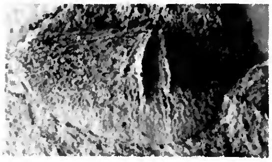
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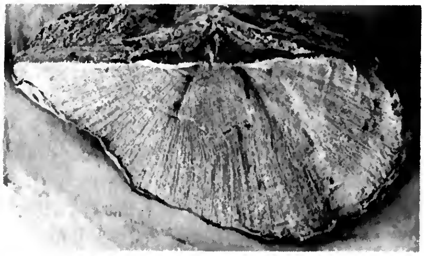
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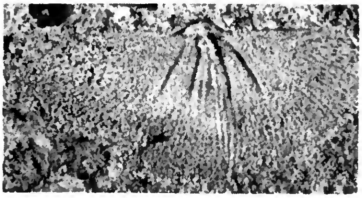
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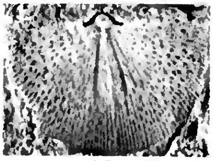
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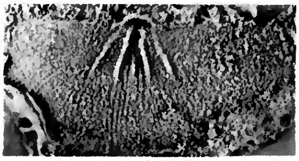
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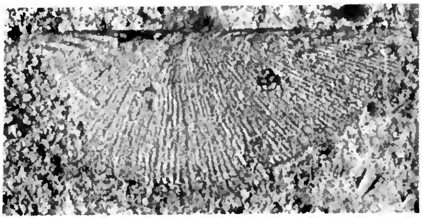
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Figs 281–289, 292 *Sowerbyella* cf. *sladensis* Jones. Cyrn-y-brain Formation: Figs 283, 286, BB69173, Internal mould and latex cast of a pedicle valve, ×2·6, ×2·8, loc. M2; Figs 284–5, BB69170, Internal mould and latex cast of a pedicle valve, ×2·6, ×2·6, loc. M2; Fig. 289, BB69168, Latex cast of the exterior of a brachial valve, ×2·8, loc. M2; Figs 287–8, BB69175, Internal mould and latex cast of a brachial valve, ×3·0, loc. C2. Glyn Formation: Fig. 281, BB69174, Internal mould but which become more rectangular during growth and more rounded as the shells grew larger. A rib density of 7–10 ribs per mm was observed anteromedianly at the 5 mm growth stage in 4, 4, 3, 4 Glyn Ceiriog shells respectively. This compares with the rib density of *S. sladensis* which Jones (1928 : 421) gives as 7 per mm whereas the figures for *S. thraivensis* from the Killey Bridge Formation, Pomeroy are 10–13 ribs per mm (Mitchell, 1977 : 81). From the evidence available the Glyn Ceiriog specimens are considered to be closely related to *S. sladensis*, although no figures are available from Jones' material for a statistical comparison.

EOPLECTODONTA Kozlowski, 1929

Eoplectodonta sp.

Figs 290, 291, 293, 295–297

?1908 *Plectambonites* sp.; Groom & Lake: 573, 577 (pars).
1922 *Plectambonites sericea*, var. *rhombica* (?); (M'Coy); Wills & Smith: 191.

Material and horizon. Internal and external moulds of 4 pedicle valves, e.g. BB69183, l = 10·5, w = 20·0; BB69184, l = 6·6, w = 12·2, and 6 brachial valves (e.g. BB69185, l = 6·2, w = 13·4) from the Glyn Formation, and 1 pedicle valve from the top of the Cyrn-y-brain Formation.

Description. Concavo-convex shells of transversely semi-circular outline, about one-half as long as wide; maximum width along hinge line. Pedicle valve convex in both profiles, about one-quarter as deep as long. Interarea short, gently curved, apsacline; small pseudodeltidium partially covering delthyrium. Brachial valve concave in both profiles; interarea very short, catacline. Ornament of fine parvicostellae with density of 10–13 per 2 mm anteromedianly 5 mm from ventral umbo, often segregated into sectors by thickened ribs with about 7 others between them; 6–8 posterolateral rugae occur within 3 mm of umbo, subtending an angle of between 12°–29° with posterior margin and extending anteromedianly through a sector of about 13°.

Ventral interior with up to 8 denticles developed in 2 mm on either side of umbo (only seen in 1 specimen). Bilobed muscle field about one-half as long as wide and three-tenths as long as valve; posteromedianly situated adductor scars separated by short septum which extends anteriorly for one-seventh of valve length. Thick *vascula media* extend from anterior edge of muscle field. Dorsal interior with cardinal process fused laterally with socket ridges. Median septum arises later than submedian pair, within 2 mm of umbo; straight submedian septa diverge anteriorly at about 26° and extend for over one-half of valve length. Adductor muscle scars not well defined but each is divided by thin septum which subtends an angle of about 45° with the other.

Discussion. Ashgill *Eoplectodonta* are poorly known when compared to Caradoc and Silurian forms. These few specimens from Glyn Ceiriog bear some resemblance in dimensions to *E. rhombica* (M'Coy, 1852) but appear to have a slightly coarser ornament, although the significance of this cannot be tested on such a small sample.

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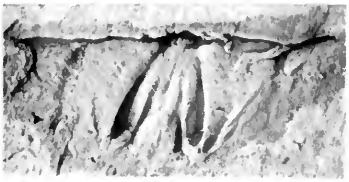
of a brachial valve, ×4·0, loc. G3. Dolhir Formation: Fig. 282, BB69172, Internal mould of a brachial valve, ×4·0, loc. D14; Fig. 292, BB69171, Internal mould of a brachial valve, ×5·4, loc. D14.

Figs 290–291, 293, 295–297 *Eoplectodonta* sp. Glyn Formation: Fig. 297, BB69185, External mould of a brachial valve, ×4·3, loc. G2; Figs 290, 293, BB69185, Internal mould and latex cast of a brachial valve, ×3·8, ×2·9, loc. G2; Fig. 296, BB69183, External mould of a pedicle valve, ×3·2, loc. G2; Fig. 291, BB69183, Internal mould of a pedicle valve, ×3·2, loc. G2. Cyrn-y-brain Formation: Fig. 295, BB69184, Internal mould of a pedicle valve, ×3·0, loc. C2.

Fig. 294 *Kozlowskites* sp. Dolhir Formation: BB69198, Internal mould of a brachial valve, ×6·0, loc. D6.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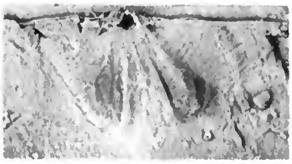
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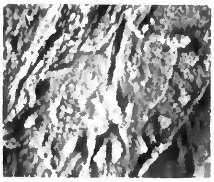
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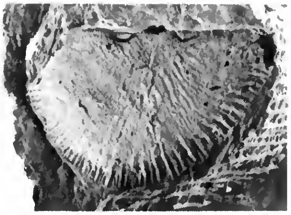
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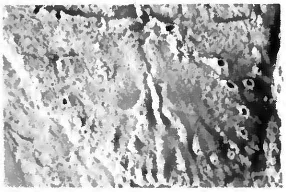
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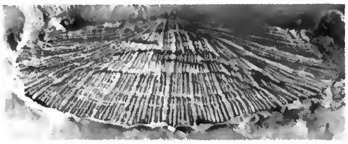
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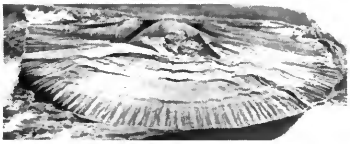
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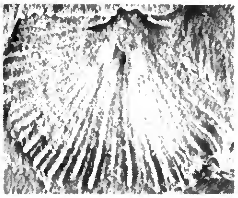
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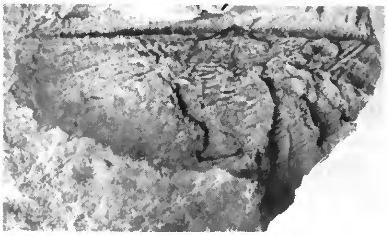
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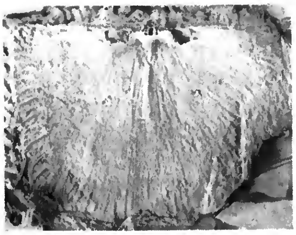
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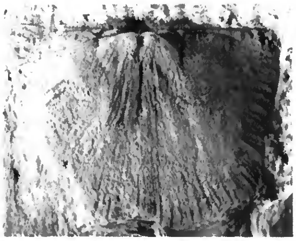
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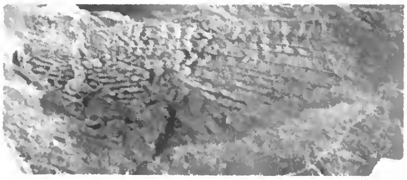
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Figs 298–299 ?*Kozlowskites* sp. Dolhir Formation: BB69197, Internal mould and latex cast of a brachial valve, ×4·4, loc. D5.

Figs 300–302, 305–306 *Chonetoidea* cf. *papillosa* (Reed). Dolhir Formation: Fig. 300, BB69199, Internal mould of a pedicle valve, ×6·0, loc. D4; Figs 301–2, BB69200, Internal mould and latex

KOZLOWSKITES Havlíček, 1952

?*Kozlowskites* sp.
Figs 294, 298, 299

MATERIAL AND HORIZON. Internal moulds of two brachial valves, BB69197–8, from the lower part of the Dolhir Formation 50 m above the Dolhir Limestone. BB69198 length 1·9, width 4·5.

DESCRIPTION. Pedicle valve unknown. Brachial valve concave in both profiles, transversely semicircular in outline; maximum width along hinge-line. Interarea very short, flat, hypercline; notothyrium filled by cardinal process lobes and chilidial plates. Ornament not seen.

Dorsal interior with cardinal process fused laterally to socket ridges; slender accessory sockets parallel to hinge-line developed about halfway between umbo and cardinal extremities. Smooth, suboval adductor scars raised on thickened platform, about three-fifths as long as wide and about two-thirds as long as valve; each scar divided by strong septum which together subtend an angle of about 45° posteriorly. Thin median septum extends for about one-half of valve length. One specimen (BB69198) shows small papillae developed between medium septum and each half of muscle field.

DISCUSSION. These two incomplete specimens are tentatively included in *Kozlowskites* on the basis of the development of accessory sockets, although no denticles are seen: this may be the result of poor preservation. They are also similar to *Anisopleurella.* No pedicle valves can be assigned with certainty to the genus but several small, strongly concavo-convex, indeterminate plectambonitaceans may prove to be associated with these brachial valves.

Subfamily **AEGEROMENINAE** Havlíček, 1961

CHONETOIDEA Jones, 1928

Chonetoidea cf. ***papillosa*** (Reed, 1905)
Figs 300–302, 305, 306

cf. 1905 *Plectambonites papillosa* Reed: 451, pl. 23, figs 13–15.
1922 *Plectambonites papillosa* Reed; Wills & Smith: 191.
cf. 1928 *Chonetoidea papillosa* (Reed); Jones: 498, pl. 25, figs 20–24.

MATERIAL AND HORIZON. Internal moulds of 3 pedicle and 2 brachial valves from the lower part of the Dolhir Formation, one specimen from the Tyn-y-twmpath Member, the others from 25 m above this horizon.

DESCRIPTION. Concavo-convex shells of semi-circular to subelliptical outline; maximum width along hinge-line; cardinal angles acute to rectangular. Pedicle valve over one-half as long as wide and almost three-tenths as deep as long; lateral profile with maximum convexity near umbo, anterior profile strongly convex medianly but less so laterally. Interarea short, flat, apsacline; delthyrium partially closed by small convex pseudodeltidium. Brachial valve over three-fifths

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cast of a brachial valve, ×10·0, loc. D4. Tyn-y-twmpath Member: Figs 305–6, BB69201, Internal mould and latex cast of a brachial valve, ×10·0, loc. T1.

Figs 303–304, 307–312 *Strophomena ceiriogensis* sp. nov. Dolhir Formation: Figs 303–4, BB69204, Internal mould and latex cast of a brachial valve, ×1·1, loc. D6; Fig. 307, Holotype, BB69202, Internal mould of a pedicle valve, ×1·4, loc. D6; Figs 311–12, BB69203, Internal mould and latex cast of a brachial valve, ×1·2, loc. D6; Fig. 309, BB69206, Internal mould of a pedicle valve, ×1·9, loc. D6; Fig. 310, BB69206, Latex cast of the exterior of a pedicle valve, ×1·8, loc. D6. Tyn-y-twmpath Member: Fig. 308, BB69207, Internal mould of a brachial valve, ×4·9, loc. T1.

Figs 313–314 *Gunnarella* sp. Dolhir Formation: Fig. 313, BB69209, Internal mould of a brachial valve, ×1·6, loc. D3; Fig. 314, BB69209, External mould of a brachial valve, ×2·2, loc. D3.

Fig. 315 ?*Luhaia* sp. Dolhir Formation: BB69210, Internal mould of a brachial valve, ×1·5, loc. D15.

as long as wide, shallowly concave in both profiles. Interarea very short, flat, hypercline. Ornament not seen.

Ventral interior with bilobed muscle field about two-thirds as long as wide and one-third as long as valve; posteromedianly situated adductor scars separated by short septum, one-fifth as long as valve, which bifurcates anteriorly to bound inner edges of diductors. Inner surface of valve outside muscle field covered by radial rows of pustules which occupy interspaces between impressed ribs. Dorsal interior with cardinalia consisting of narrow socket ridges lying almost parallel to hinge-line, fused medianly with cardinal process. Adductor muscle field about four-fifths as long as wide and about one-half as long as valve, defined by faint ridges. Anterior to muscle field a pair of arcs, of 8 septules each, extend from either side of one median and two submedian septa. Both specimens show the beginnings of a second arc anterior to the first.

DIMENSIONS

	length	width
Internal mould of a pedicle valve, BB69199	3·0	6·5
Internal mould of a brachial valve, BB69200	2·4	3·2
Internal mould of a brachial valve, BB69201	2·3	3·8

DISCUSSION. These specimens are placed in *Chonetoidea* because of their regularly arranged septules and developed in more than one arc. In known *Sericoidea*, the arrangement of septules in the brachial valve is not as well developed as in this species of *Chonetoidea.* Only *C. radiatula* (Barrande) and *C. papillosa* (Reed) are known to develop extra arcs of septules and the present specimens could equally be assigned to either species. Havlíček (1967 : 49) noted the close similarity between these two and Cocks (1970 : 194) in his discussion on *C. papillosa* states, 'Since they are contemporary, and do not appear to differ greatly from each other in material detail, it is possible that *C. papillosa*, *C. radiatula* and *C. tenerima* (Havlíček) might in future be synomymised'. However, Havlíček (1967 : 49) regarded the last to be fairly different because of its reduced number of septules, despite its occurrence in the same formation as *C. radiatula.*

Superfamily **STROPHOMENACEA** King, 1846
Family **STROPHOMENIDAE** King, 1846
Subfamily **STROPHOMENINAE** King, 1946
STROPHOMENA Rafinesque, 1825

Strophomena ceiriogensis sp. nov.
Figs 303, 304, 307–312

?1908 *Rafinesquina expansa* Sowerby; Groom & Lake: 573, 578.
1922 *Strophomena antiquata* Sowerby; Wills & Smith: 191 (pars).
1922 *Rafinesquina expansa* (?) Sowerby; Wills & Smith: 191 (pars).

DIAGNOSIS. Gently convexo-plane *Strophomena* with transverse semi-circular outline and well differentiated parvicostellate ornament, differing from *S. cancellata* in the longer brachial valve and shorter ventral muscle field.

MATERIAL AND HORIZON. Internal and external moulds of 15 pedicle and 20 brachial valves from throughout the Dolhir Formation.

DESCRIPTION. Convexoplanar shells of transversely semi-circular outline; maximum width along hinge-line or just anterior to it. Pedicle valve about seven-tenths as long as wide; lateral and anterior profiles flat except for slight convexity around umbo. Interarea high, flat, apsacline; delthyrium almost completely closed by convex pseudodeltidium. Supra-apical foramen. Brachial valve about four-fifths as long as wide and about one-tenth as deep as long; both profiles gently convex with some young forms displaying an initial median sulcus which fades by about 8 mm growth stage. Interarea short, flat, anacline; notothyrium and cardinal process lobes partially covered by convex chilidium. Unequally parvicostellate ornament yielding counts of 4–6 ribs per mm anteromedianly at 5 mm growth stage on 10, 12, 2 valves respectively. Radial ornament crossed by fine concentric lines with a density of about 7 per mm.

Ventral interior with large teeth supported by low, widely divergent dental plates. Subpentagonal muscle field poorly defined, about as long as wide and about three-tenths as long as valve; elongately oval adductor scar enclosed by diductor lobes. Some specimens with short, thick pedicle tube. Dorsal interior with conjunct cardinal process lobes each with median groove on posteroventral surface; deep sockets defined by strong socket ridges about three-tenths as wide as valve; curving laterally to lie parallel to hinge-line. Flabellate adductor scars, about three-fifths as long as wide and one-quarter as long as valve, divided longitudinally by faint median ridge. Faint traces of vascula media extending from anterior end of muscle field.

DIMENSIONS

	length	width
Internal mould of a pedicle valve, holotype, BB69202 . . .	16·0	25·6
Internal mould of a brachial valve, BB69203	26·5	34·4
Internal mould of a brachial valve, BB69204	22·6	31·5
Internal and external moulds of a pedicle valve, BB69206 . .	—	22·8

DISCUSSION. The Glyn Ceiriog *Strophomena* can be compared to *S. cancellata* (Portlock, 1843), which is regarded as a senior synonym of *S. bilix* (Lamont, 1935) by Mitchell (1977). Both these forms, from Pomeroy and Girvan, appear to be members of the *S. norvegica* Spjeldnaes (1957 : 144) species group which includes forms characterized by a transverse outline, gently convexo-concave profile and well differentiated parvicostellate ornament. The Welsh species differs from *S. cancellata* in having a relatively longer brachial valve and relatively shorter ventral muscle field. 15 Welsh brachial valves have a mean length : width ratio of 83·6 (var. 343·63)% compared to a mean of 61·4 (var. 49·53)% for 9 Pomeroy specimens, and a 't' test on these data shows a significant difference between the two forms ($P<0{\cdot}001$). Two Irish pedicle valves have length of muscle scar : valve length ratios of 46, 50% respectively; 9 Glyn Ceiriog specimens give ratios of 25, 26, 28, 28, 28, 33, 36, 37, 40% for the same statistic. Therefore, while the Welsh form is closely related to *S. cancellata* it is not conspecific with it and can be distinguished on the above characters.

The Glyn Ceiriog *Strophomena* can also be distinguished from other British species: *S. deficiens* Reed, 1917 is strongly convexo-concave, has stout cardinal process lobes and a longer ventral muscle field, as has *S. norvegica lata* Williams, 1962 and *S. grandis* (Sowerby, 1839). *S. shallockiensis* Davidson, 1883 differs in its larger ventral interarea and lack of pseudodeltidium. Contemporary American species, such as *S. fluctuosa* Billings, 1860 and *S. platocorrugata* Twenhofel, 1928 differ in the form of their shells, while Scandinavian species, such as *S. norvegica* Spjeldnaes, 1957 and *S. hirsuta* Spjeldnaes, 1957 can be distinguished by their shell shape and the form of their cardinalia.

GUNNARELLA Spjeldnaes, 1957

Gunnarella sp.

Figs 313, 314

?1908 *Rafinesquina corrugatella* Davidson; Groom & Lake: 573.
?1922 *Stropheodonta corrugatella* (Davidson); Elles: 172.

MATERIAL AND HORIZON. A single broken specimen of a brachial valve, BB69209, comprising both internal and external moulds, from a horizon 16 m above the Dolhir Limestone.

DESCRIPTION. Gently convex brachial valve, slightly concave umbonally, of approximately semicircular outline. Ornamentation of fine parvicostellae segregated into narrow sectors by about 16 thickened costellae which interrupt fairly strong concentric rugae. These have a density of about 3 per mm anteriomedianly at 5 mm growth stage and the sectors contain about six ribs each at this same stage.

Dorsal interior with small sockets defined by widely divergent socket ridges which curve posterolaterally to lie parallel with hinge-line. Cardinal process obscure. Notothyrial platform slightly thickened. Musculature not seen.


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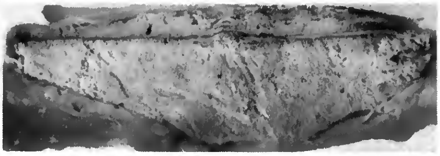
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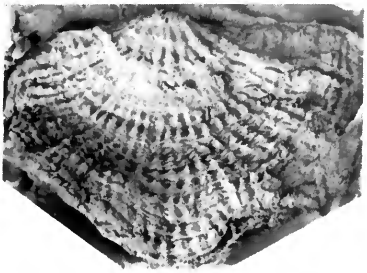
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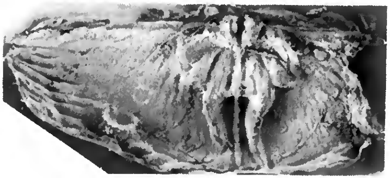
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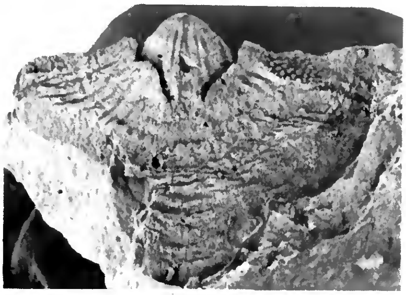
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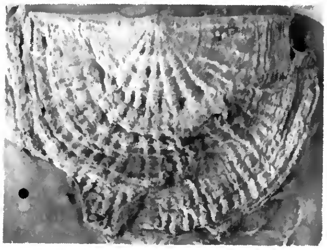
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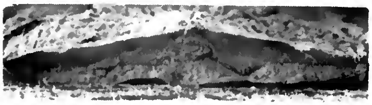
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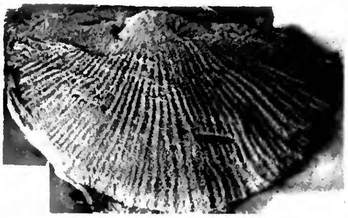
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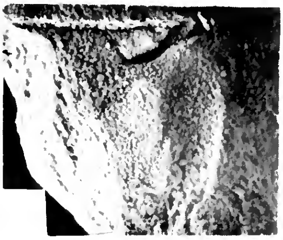
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Figs 316–317 ?*Luhaia* sp. Dolhir Formation: Fig. 316, BB69210, Internal mould of a brachial valve, ×1·5, loc. D15. Glyn Formation: Fig. 317, BB69211, Latex cast of the posterior end of a pair of conjoined valves, ×1·5, loc. G2.

Figs 318–326 *Katastrophomena dolhirensis* sp. nov. Dolhir Formation: Fig. 322, Holotype, BB69215, Internal mould of a pedicle valve, ×2·0, loc. D6; Fig. 319, Holotype, BB69215, Latex cast of the exterior of a pedicle valve, ×2·0, loc. D6; Figs 318, 320, BB69213, Internal mould and latex cast

DISCUSSION. The distinctive ornament of this specimen is enough to identify it as *Gunnarella* but more material is necessary before a more precise identification can be made.

LUHAIA Rõõmusoks, 1956

?*Luhaia* sp.

Figs 315–317

MATERIAL AND HORIZON. Internal and external moulds of 2 damaged brachial valves, one from the top of the Dolhir Formation, BB69210, the other from the Glyn Formation, BB69211 (width about 44 mm).

DESCRIPTION. Pedicle valve interarea quite long, flat, apsacline; delthyrium closed by pseudodeltidium. Brachial valve convex, broadly triangular in outline, with sharp, ventrally directed geniculation; maximum width along hinge-line. Lateral profile flat to gently convex until commissure is sharply deflected ventrally and develops broad median fold. Interarea short, flat, anacline; notothyrium covered by convex chilidium. Ornament, seen only on one small portion of shell near valve margin, consists of strong costellae crossed by faint concentric rugae (?).

Dorsal interior with long, narrow pair of anterior adductor scars separated by low, thin median septum and bounded laterally by low, gently curved ridges. Cardinalia and posterior adductor scars broken off both specimens.

DISCUSSION. These specimens are tentatively assigned to *Luhaia* on the basis of their strong ventral geniculation with folded trail. However, some North American species of *Strophomena*, particularly *S. fluctuosa* Billings, 1860 (Macomber, 1970 : 440), have been described as having features typical of *Luhaia*, the main difference being the well developed parvicostellate ornament of the American shells. *L. vardi* Rõõmusoks, 1956, the type species, develops a very faint parvicostellate ornament and it may be that the coarse preservation of the available Glyn Ceiriog exteriors does not show this, but the typical concentric rugae are not preserved either. It is possible that the longitudinal striations seen on the trail of one internal mould (BB69210) represent the impressions of *vascula terminalia* but apparently corresponding striations are observed on the fragmentary counterpart.

Subfamily **FURCITELLINAE** Williams, 1965

KATASTROPHOMENA Cocks, 1968

Katastrophomena dolhirensis sp. nov.

Figs 318–326

1908 *Strophomena antiquata* Sowerby; Groom & Lake: 573 (pars).
1922 *Strophomena antiquata* Sowerby; Wills & Smith: 191 (pars).

DIAGNOSIS. Resupinate to ventrally geniculate *Katastrophomena* with ornament of coarse irregular costellae and characterized by strongly developed lamellose growth lines.

MATERIAL AND HORIZON. Internal and external moulds of 32 pedicle and 25 brachial valves from the lower part of the Dolhir Formation, including the Dolhir Limestone Member.

DESCRIPTION. Variably resupinate shells of transversely subquadrate outline; maximum width on or immediately anterior to hinge-line; cardinal angles normally rectangular to roundedly

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of a brachial valve, ×2·3, ×2·1, loc. D6; Fig. 321, BB69214, Latex cast of the exterior of a brachial valve, ×1·5, loc. D6; Figs 324, 326, BB69214, Internal mould and latex cast of a brachial valve, ×2·5, ×3·0, loc. D6; Figs 323, 325, BB69212, Latex cast of the exterior of a pedicle valve, ×1·9, ×2·4, loc. D1.

Figs 327–328 *Mjoesina marri* sp. nov. Cyrn-y-brain Formation: Fig. 327, BB69220, Latex cast of the exterior of a pedicle valve, ×2·1, loc. C6; Fig. 328, BB69221, Broken internal mould of a brachial valve, ×4·5, loc. C6.

obtuse. Pedicle valve over three-quarters as long as wide; lateral profile ranging from flat to resupinate with maximum convexity at umbo, decreasing anteriorly until valve may become distinctly concave, almost geniculate; anterior profile gently convex becoming concave posterolaterally; faint, broad sulcus may develop on geniculate part of older shells and may form tongue-like projection. Interarea short, about one-seventh as long as valve, curved apsacline; wide delthyrium partially closed by convex pseudodeltidium. Brachial valve nearly nine-tenths as long as wide; lateral profile slightly concave umbonally, commonly geniculate in ventral direction; anterior profile convex with flattened median portion; small fold developed on trail of 4 out of 9 geniculate specimens. Interarea very short, flat, anacline; notothyrium covered by prominent convex chilidium with slight median groove. Ornament of coarse, rounded costellae which increase both by branching and intercalation from 10–11 initial costae; density of 1–2 ribs per mm 5 mm anteromedianly from ventral umbo. Well developed concentric ornament of closely spaced filae, 10–12 per mm at 5 mm growth stage, and prominent growth lines commonly extended into frilly lamellae, especially in later growth stages. Tendency for hollow spines to form where growth lines cross costellae.

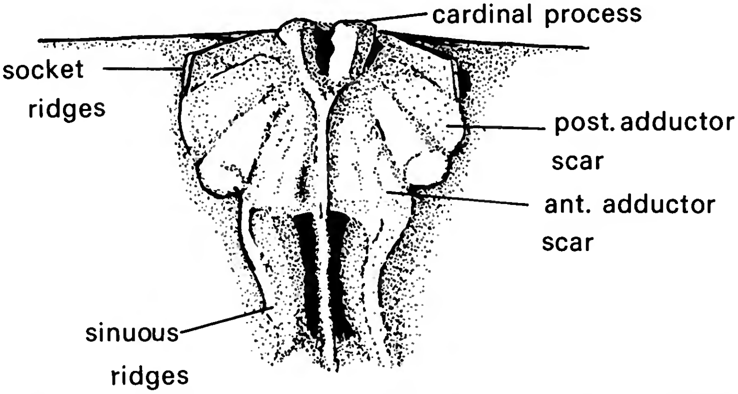

Fig. 10 Diagrammatic view of the dorsal interior of *Katastrophomena dolhirensis* sp. nov.

Ventral interior with strong teeth supported by low, widely divergent, receding dental plates which give rise to pair of inclined ridges at lateral edges of large sub-pentagonal muscle field. Muscle field about nine-tenths as long as wide and one-third as long as valve; well developed diductor lobes separated by low ridge on which is situated narrow adductor scar. Thick *vascula media* extend from anterior edge of muscle field. Dorsal interior with pair of strong, conjunct cardinal process lobes and widely divergent (c. 115°) socket ridges about two-fifths as wide as valve. Muscle field situated on platform of secondary shell, bisected by low median septum; posterior and anterior adductor scars separated by low diagonal ridge, possibly connected with *vascula myaria*, which terminates in stubby spine at anterolateral corner of platform. From anterior edge of platform pair of sinuous ridges extend anteriorly to over one-half of valve length. These bound long, narrow subrectangular area which is bisected by continuation of median septum (Fig. 10).

DIMENSIONS

	length	width
Internal and external moulds of a pedicle valve, holotype, BB69215 .	17·9	24·4
External mould of a pedicle valve, BB69212	15·0	22·0
Internal and external moulds of a brachial valve, BB69214 . .	20·0	—

DISCUSSION. This distinctive genus is fairly common in the lower part of the Dolhir Formation, above and below the Dolhir Limestone. However, it has not as yet been recorded from the upper part of the formation or from the Fron Frys Formation. One poorly preserved specimen from the Glyn Formation is tentatively assigned to the genus. It is a distinct species showing strong morphological resemblance to *Katastrophomena woodlandensis* (Reed, 1917), the type for the genus, and can be distinguished from the known Silurian species mainly by its more elaborate ornament. *K. woodlandensis* does not develop prominent lamellose growth lines and the ventral muscle field shows differences in size and shape with that of the Glyn Ceiriog form which, in these respects more closely resembles *K. woodlandensis geniculata* (Williams, 1951) and *K. scotica* (Bancroft, 1949). Apart from the lack of lamellose growth lines the brachial valve of the latter is not geniculate, neither is the dorsal muscle platform so well developed. *K. penkillensis* (Reed, 1917) is separated from all the other species by its well differentiated parvicostellate ornament.

Katastrophomena has not previously been recorded from the Ordovician, although records of '*Strophomena antiquata*' are widespread. Whether these shells are conspecific with *K. dolhirensis* sp. nov. remains to be seen.

Recently, Bassett (1974 : 106) described several subspecies of *K. antiquata* (Sowerby, 1839) from the Wenlock strata of south Wales and the Welsh Borderland. In his description of the muscle fields he gives a different interpretation of the distribution of the muscles to that given here which is more like the interpretation of Cooper (1956) in his descriptions of species of *Strophomena*. Bassett (ibid : 108) states that the anterior adductor scars are sited between the pair of sinuous ridges and separated by the median septum. This seems unlikely, although the anterior scars may extend along the sinuous ridges for a short way. However, more research on this and related genera is required before this problem can be resolved.

The following statistical data were obtained for the sample:

Pedicle Valve

Length of valve (l) : width of valve (w), n = 21; $\bar{l}$(var. l) = 14·4 (30·31) mm; $\bar{w}$(var. w) = 19·5 (51·42) mm; r = 0·522; a(var. a) = 1·30 (0·065).

Length of valve (l) : length of muscle field (m), n = 14; $\bar{l}$(var. l) = 14·4 (41·40) mm; $\bar{m}$(var. m) = 4·6 (3·86) mm; r = 0·915; a(var. a) = 0·31 (0·0013).

Length of muscle field (l) : width of muscle field (w), n = 18; $\bar{l}$(var. l) = 4·8 (3·43) mm; $\bar{w}$(var. w) = 5·5 (4·30) mm; r = 0·763; a(var. a) = 1·12 (0·033).

Brachial Valve

Width of valve (w) : width of socket ridges (s), n = 12; $\bar{w}$(var. w) = 17·8 (47·59) mm; $\bar{s}$(var. s) = 6·9 (4·95) mm; r = 0·937; a(var. a) = 0·32 (0·0013).

Length of valve (l) : length of muscle field (m), n = 11; $\bar{l}$(var. l) = 13·7 (17·59) mm; $\bar{m}$(var. m) = 7·2 (2·42) mm; r = 0·632; a(var. a) = 0·37 (0·0092).

Subfamily **RAFINESQUININAE** Schuchert, 1893

KJAERINA Bancroft, 1929

Kjaerina sp.

Figs 405–408

1908 *Rafinesquina deltoidea* Conrad; Groom & Lake: 573 (pars).

MATERIAL AND HORIZON. Internal and external moulds of 4 pedicle valves (e.g. BB69217, l = 11·5, w = 9·4; BB69218, w = 11·1, l = 70·4) and 2 brachial valves from the lower part of the Dolhir Formation 16 m above the Dolhir Limestone.

DESCRIPTION. Concavo-convex shells of elongately subquadrate outline; maximum width along hinge-line which may be slightly mucronate. Pedicle valve about nine-tenths as wide as long and one-tenth as deep as long; gently convex in both profiles. Interarea short, flat, orthocline. Brachial valve also about nine-tenths as wide as long; gently concave in both profiles. Interarea very short, flat, anacline. Ornamentation finely, unequally, parvicostellate with conspicuous thickened median costa.

Ventral interior with short, widely divergent dental plates less than one-tenth as long as valve. Poorly defined muscle field sometimes divided longitudinally by faint, short median ridge. Dorsal interior with pair of delicate, plate-like cardinal process lobes diverging anteriorly; socket ridges widely divergent, about one-sixth as wide as valve. Musculature not seen.

Discussion. Such a limited sample cannot be assigned to any species with certainty; indeed it was only after some difficulty that the generic assignment was determined. Bancroft (1945 : 246) listed a number of characters which, in association with one another, serve to distinguish between *Kjaerina* and *Rafinesquina*. They are: (1) the smaller size and more delicate cardinalia of *Kjaerina*; (2) the presence of a strong median rib on the pedicle valve of *Kjaerina*; (3) the ventral muscle field of *Rafinesquina* is large and flabellate; in *Kjaerina* the muscle field is restricted by the narrowly divergent plates; (4) the dorsal muscle field more deeply impressed in *Rafinesquina*; (5) *Kjaerina* interiors always show traces of the external ornament and the vascular markings are not seen.

Some of these points, especially 4 and 5, depend largely on preservation, but Bancroft does not mention the strong posterolateral rugae used by Williams (1965 : H388) to separate the genera. The Dolhir Formation specimens conform closely to Bancroft's diagnosis of *Kjaerina* and, despite the absence of posterolateral rugae, are placed in that genus.

Subfamily **GLYPTOMENINAE** Williams, 1965

MJOESINA Spjeldnaes, 1957

Mjoesina marri sp. nov.
Figs 327–330

Diagnosis. Transversely elliptical *Mjoesina* characterized by large ventral muscle field in which the adductors are not enclosed by diductors; and an ornament which is undifferentiated into sectors by enlarged costae or costellae.

Material and horizon. Internal and external moulds of 11 pedicle and 2 brachial valves from the top of the Dolhir and Cyrn-y-brain Formations.

Description. Strongly ventri-biconvex to plano-convex shells of transversely elliptical outline. Maximum width anterior to hinge-line, cardinal angles obtuse. Pedicle valve over three-quarters as long as wide and one-third as deep as long; lateral profile strongly convex with no distinct geniculation; anterior profile with maximum convexity medianly. Interarea flat, orthocline to slightly apsacline, about one-tenth as long as valve; wide delthyrium with small apical pseudodeltidium. Brachial valve represented by only two fragmentary specimens which appear to be flat umbonally. Interarea short, flat, catacline; notothyrium covered by small, convex chilidium. Ornamentation of fine costae and costellae, arising mostly by intercalation, with density of 4–5 ribs per 2 mm, 7·5 mm anteromedianly from ventral umbo. Ribs not differentiated into sectors by accentuated costae or costellae.

Ventral interior with large, strongly impressed, subpentagonal muscle field almost as wide as long and nearly two-fifths as long as valve. Narrow median adductor scars extend beyond broad diductor lobes; whole muscle field bisected longitudinally by narrow median ridge. Strong teeth supported by widely divergent dental plates which give rise to ridges defining muscle field. One specimen shows short, thick pedicle tube. Thick *vascula media* extend from anterior end of adductor scars.

Dorsal interior with small, discrete cardinal process lobes; socket ridges curve posterolaterally to lie parallel with hinge-line. Broad, rounded ridge extending anteriorly from notothyrial platform; muscle scars not well defined.

Dimensions

	length	width
Internal mould of a pedicle valve, holotype, BB69219 . . .	17·5	24·4
External mould of a pedicle valve, BB69220	13·3	21·6
Internal mould of a brachial valve, BB69221	—	—
Internal mould of a pedicle valve, BB69222	25·6	40·8

Discussion. *Mjoesina* is best known from the Caradoc of Girvan and Oslo; there is only one record from the Ashgill: from Pomeroy (Mitchell, 1977). The Welsh species differs in having a shallower pedicle valve, being one-third as deep as long compared to over one-half as deep as long for the Irish species, and the ventral muscle field of the Welsh form is relatively narrower.

However, the single Irish specimen does not allow these differences to be tested statistically.

The better known Caradoc species can be roughly separated into two groups on the basis of the brachial valve profile and relative size of the ventral muscle field (Mitchell, 1977 : 101). The fragmentary Welsh brachial valves cannot be referred to either group but the large ventral muscle field is more like that of the Oslo group which includes *M. mjoesensis* (Holtedahl, 1916) and *M. gregaria* Spjeldnaes, 1957. The principal difference between these and the Welsh specimens is the differentiation of the ornament into sectors bounded by enlarged costae or costellae, and a deeper pedicle valve in the case of *M. mjoesensis*. In the ventral muscle fields of these two species the adductor scars are enclosed by the diductor lobes.

The following statistical data were obtained for the sample:

Pedicle Valve

Valve length (l) : valve width (w), n = 8; $\bar{l}$(var. l) = 19·38 (22·156) mm; $\bar{w}$(var. w) = 26·49 (77·887) mm; r = 0·5603; a(var. a) = 1·875 (0·4019).

Valve length (l) : valve depth (d), n = 8; $\bar{l}$(var. l) = 19·38 (22·156) mm; $\bar{d}$(var. d) = 6·59 (11·51) mm; r = 0·5228; a(var. a) = 0·7207 (0·0629).

Valve length (l) : length of muscle field (m), n = 8; $\bar{l}$(var. l) = 19·46 (21·003) mm; $\bar{m}$(var. m) = 7·34 (8·574) mm; r = 0·7149; a(var. a) = 0·639 (0·0333).

Length of muscle field (m) : width of muscle field (f), n = 10; $\bar{m}$(var. m) = 6·84 (7·929) mm $\bar{f}$(var. f) = 6·16 (4·074) mm; r = 0·9162; a(var. a) = 0·717 (0·0103).

Family **CHRISTIANIIDAE** Williams, 1953

CHRISTIANIA Hall & Clarke, 1892

Christiania sp.

Figs 331–335

MATERIAL AND HORIZON. Internal and external moulds of 9 pedicle and 3 brachial valves from the lower and middle parts of the Dolhir Formation, above the Dolhir Limestone.

DESCRIPTION. Concavo-convex shells of elongately subquadrate outline with maximum width anterior to hinge-line. Pedicle valve about nine-tenths as wide as long and one-third as deep as long; lateral profile moderately convex; anterior profile strongly convex. Interarea flat, orthocline; delthyrium closed by convex pseudodeltidium perforated by small, circular apical foramen. Brachial valve about as long as wide, strongly concave in both profiles. Ornamentation of fine anastamosing concentric ridges with density of 5–8 per mm on 1, 1, 2, 1 valves at 5 mm growth stage.

Ventral interior with pedicle tube tapering posteriorly; teeth quite strong but dental plates obsolete; pair of subcircular diductor scars situated posteriorly on either side of short median ridge. Pair of thick, deeply impressed *vascula media* diverging slightly from diductor scars and seen to branch anteriorly. Internal surface of valve covered in elongate papillae (pseudopunctae ?). Dorsal interior represented by single poorly preserved specimen showing only inner and lateral septa and fragment of a socket ridge joined to lateral septum.

DIMENSIONS

	length	width
Internal mould of a pedicle valve, BB69224	9·5	11·3
External mould of a pedicle valve, BB69225	—	13·8
Internal mould of a pedicle valve, BB69226	17·0	12·5
External mould of a brachial valve, BB69228	5·0	10·9

DISCUSSION. The subquadrate shape and absence of radial ornament of this species of *Christiania* separate it from most other species except *Christiania* sp. (Wright, 1963 Ms) from Portrane, *C. portlocki*, Mitchell, 1977 from Pomeroy and *C. nilssoni* Sheehan, 1973 from Sweden. The crushing of the Welsh specimens rules out any statistical comparison of shell shape with these other species but the simpler development of septa in the brachial valve, poorly seen in the single dorsal interior available, suggests affinity with the Pomeroy form. However, all three of these


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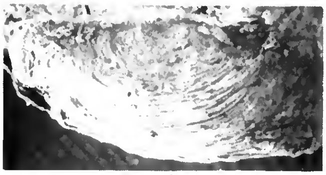
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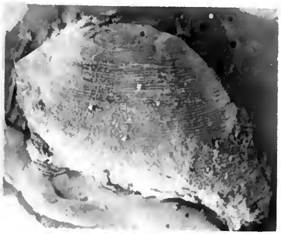
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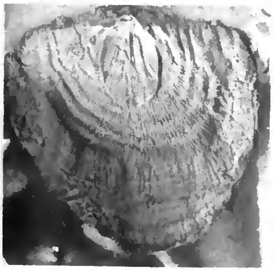
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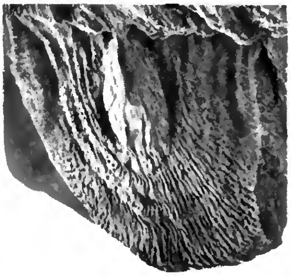
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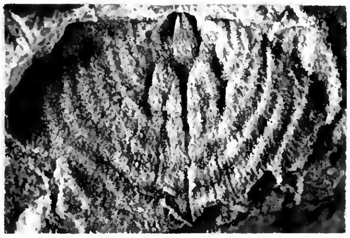
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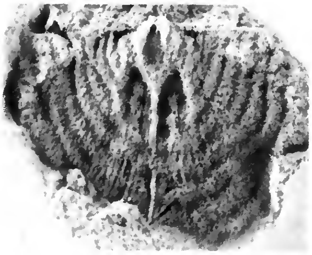
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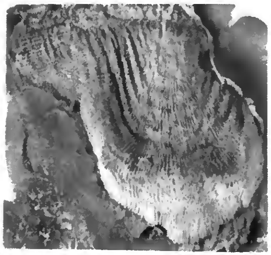
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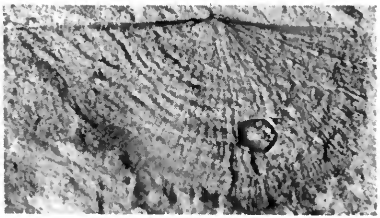
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Figs 329–330 *Mjoesina marri* sp. nov. Cyrn-y-brain Formation: Fig. 329, BB69222, Internal mould of a pedicle valve, ×1·2, loc. C6; Fig. 330, Holotype, BB69219, Internal mould of a pedicle valve, ×1·5, loc. C6.

Figs 331–335 *Christiania* sp. Dolhir Formation: Fig. 331, BB69227, Internal mould of a pedicle valve, ×2·4, loc. D6; Fig. 332, BB69228, External mould of a brachial valve, ×3·8, loc. D5;

species develop a sulcus in the pedicle valve, which is not in the Glyn Ceiriog shells. Another form similar to the Welsh one is *C. holtedahli* Spjeldnaes, 1957 but the transverse septum joining the inner and lateral septa is not seen in the Glyn Ceiriog specimen. Further well preserved dorsal interiors are required before the specific identity can be more satisfactorily assessed.

Family **LEPTAENIDAE** Hall & Clarke, 1894

LEPTAENA Dalman, 1828

Leptaena cf. ***rugosa*** Dalman, 1828

Figs 336–342

cf. 1828 *Leptaena rugosa* Dalman: 106, pl. 1, fig. 1.
1908 *Leptaena rhomboidalis*, Wilckens; Groom & Lake: 572, 577.
1922 *Leptaena rhomboidalis*, Wilckens; Wills & Smith: 187, 191.

MATERIAL AND HORIZON. *Leptaena* is one of the most commonly occurring genera in Glyn Ceiriog district, being found throughout the Dolhir Formation, Glyn Formation and Fron Frys Formation. It is also a common form in the Cyrn-y-brain Formation. The sample consists of 56 pedicle and 30 brachial valves and a number of fragments, mostly of exteriors.

DESCRIPTION. Concavo-convex, transversely subquadrate, dorsally geniculate *Leptaena* with maximum width along hinge-line; strongly raised marginal ruga on pedicle valve and corresponding deep groove on brachial valve delimiting discs. Ventral disc about two-thirds as long as wide, faintly convex umbonally; trail subtends angle of about 125° with disc, although there is some variation in this. Pedicle valve about three-quarters as long as wide with alate hinge-line. Interarea short, flat, apsacline; delthyrium with small apical pseudodeltidium. Trail typically without undulations. Brachial valve slightly concave, two-thirds as long as wide. Interarea very short, flat, anacline; notothyrium closed by strongly arched chilidium bearing median groove. Ornament of regularly developed concentric rugae, wavelength about 1 mm at 5 mm growth stage, with 5–11 present on disc, very faint near umbo; also fine costellate radial ornament yielding counts of 4–5 ribs per mm at 5 mm growth stage.

Ventral interior with large subquadrate muscle field just over four-fifths as wide as long and just over two-fifths as long as valve. Narrow adductor scars situated posteromedianly, separated by short, low septum and enclosed almost entirely by semiflabellate diductors. Teeth small, supported by widely divergent dental plates from in front of which sinuous ridges surround muscle field. In a few specimens papillae (?pseudopunctae) are seen to be roughly arranged into concentric rows approximately corresponding to rugae on external surface. Rugae clearly visible on valve interiors.

Dorsal interior with prominent cardinal process lobes diverging at about 50° sometimes separated by thin septum underlying median groove on chilidium. Socket ridges weakly developed and often obscured by secondary shell material; sockets small. Two pairs of laterally disposed, oval-shaped adductor scars defined by three ridges originating from notothyrial platform; median ridge narrows anteriorly and extends to front margin of disc as low, thin septum. Faint traces of trans muscle septa seen, in one specimen, to separate anterior and posterior parts of scars. Muscle field almost as wide as long and over one-third as long as valve.

Fig. 333, BB69224, Internal mould of a pedicle valve, ×3·0, loc. D6; Fig. 334, BB69225, Latex cast of the exterior of a pedicle valve, ×2·5, loc. D5; Fig. 335, BB69226, Internal mould of a pedicle valve, ×2·2, loc. D6.

Figs 336–342 *Leptaena* cf. *rugosa* Dalman. Dolhir Formation: Fig. 336, BB69237, Internal mould of a pedicle valve, ×1·7, loc. D15; Figs 337, 338, BB69235, Internal mould and latex cast of a pedicle valve, ×1·6, loc. D15; Fig. 339, BB69230, Internal mould of a pedicle valve, ×2·3, loc. D6. Cyrn-y-brain Formation: Figs 340, 341, BB69234, Internal mould and latex cast of a brachial valve, ×2·3, loc. C2; Fig. 342, BB69238, Latex cast of the exterior of a pedicle valve, ×1·0, loc. C2.

Fig. 343 Leptaenid gen et sp. indet. Dolhir Formation: BB69240, Internal mould of a pedicle valve, ×2·4, loc. D15.

DIMENSIONS

	length	width
Internal mould of a pedicle valve, BB69230	15·2	18·7
Internal mould of a pedicle valve, BB69235	24·4	21·9
Internal mould of a pedicle valve, BB69237	19·2	23·5
External mould of a pedicle valve, BB69238	19·3	c. 22

DISCUSSION. A large number of the specimens have been deformed so that some specimens have trails bearing undulations and one specimen has a deeply indented anterior margin. There is also considerable variation within the sample, but to what extent this is a reflection of deformation is uncertain and so any statistical comparison may be tentative. However, the major features are well enough preserved to allow comparisons to be made with other stocks. The large subquadrate ventral muscle scar and large range in numbers of rugae, 5 to 11 on 3, 9, 14, 9, 5, 6, 2 pedicle valves, suggest the nearest relatives are to be found amongst *L. rugosa* Dalman, *L. salopiensis* Williams and *L. valentia* Cocks. The two latter forms differ in that their trails are more sharply bent back, subtending angles of 100° and 90° to the disc respectively, compared with 125° in the Glyn Ceiriog form; according to Spjeldnaes (1957 : 173) the trail of *L. rugosa* subtends an angle of 120° or more with the disc. Further, the dorsal adductor scars of *L. valentia* taper forwards, whereas in the Glyn Ceiriog specimens they expand anteriorly.

Mitchell (1977 : 108) gave some statistics for the pedicle valves of *L.* cf. *rugosa* from Pomeroy, which do not indicate any significant difference between his form and the present specimens. In a comparison of the number of rugae on the pedicle valves, 7 and 8 are the most common numbers to be found on *L. rugosa* and *L. valentia*; for *L. salopiensis* 5 and 6 occur most frequently and in the Glyn Ceiriog sample 6, 7, and 8 are the most common numbers.

The thin posterior septum underlying the median groove on the chilidium was regarded as a distinguishing feature of *Leptaenopoma* Marek and Havlíček, 1967, but Bergström (1968 : 15) points out that this character is also seen in some specimens of *Leptaena rugosa*.

LIMBIMURINA Cooper, 1956

?***Limbimurina*** sp.

Figs 344, 345, 347

MATERIAL AND HORIZON. Internal and external moulds of a single broken valve, BB69239, from the lowest part of the Dolhir Beds, just below the Dolhir Limestone.

DESCRIPTION. Brachial valve flat with fine parvicostellate ornament interrupted by faint, impersistent, concentric rugae to give a reticulate pattern on umbonal regions. Rugae die out towards shell margin. Interarea quite long, flat, anacline; notothyrium and cardinal process lobes partially covered by strongly arched chilidium with slight median furrow.

Dorsal interior with pair of large, robust cardinal process lobes and weakly developed, widely divergent socket ridges. Musculature not seen.

DISCUSSION. The ornament of this single specimen shows a strong resemblance to that of *Limbimurina*, which is unequally parvicostellate with the stronger costellae breaking up weakly developed concentric rugae into zig-zag sets especially in umbonal regions. However, this zig-zag pattern dies out anteriorly and the parvicostellate ornament becomes dominant. The specimen does not show the elaborate frill with concentric fold typical of *Limbimurina*, but about two-thirds of valve-length from umbo is a zone of crushing which may represent such a fold. Until better material becomes available the identification as *Limbimurina* must remain tentative.

Leptaenid gen. et sp. indet

Fig. 343

MATERIAL AND HORIZON. A single internal mould of pedicle valve, BB69240, from the top of the Dolhir Formation. Length 11·0 mm, width 20·5 mm.

DESCRIPTION. Very gently convex, almost flat, pedicle valve of semi-circular outline over one-half as long as wide; maximum width along hinge-line; cardinal angles acute. Interarea very short, flat, apsacline with small pseudodeltidium. Ornament, as impressed on valve interior, of fine costellate ribbing and closely spaced, concentrically disposed, impersistent rugae, irregular posterolaterally, which may interrupt radial ornament.

Rib density of about 3 per mm at 5 mm growth stage. Ventral interior with short widely-divergent dental plates supporting fairly strong teeth. Muscle field not well defined.

DISCUSSION. The well developed concentric rugation of this specimen suggests affinities with the Leptaenidae, but it lacks the typical geniculation of that family and the fairly large, well defined ventral muscle field. The widely divergent dental plates and small, poorly defined muscle field on this internal mould are more like those found among the Rafinesquininae, a group which also develops concentric rugae.

Family **STROPHEODONTIDAE** Caster, 1939

Subfamily **STROPHEODONTINAE** Caster, 1939

EOSTROPHEODONTA Bancroft, 1949

Eostropheodonta hirnantensis (M'Coy, 1851)

Figs 346, 348–353

1851 *Orthis hirnantensis* M'Coy: 219, pl. 1H, fig. 11.
1922 *Orthis hirnantensis* M'Coy; Wills & Smith: 191.
1922 *Strophomena siluriana* Davidson; Wills & Smith: 191.
1965 *Eostropheodonta hirnantensis* (M'Coy); Temple: 410, pl. 17 figs 1–6, pl. 18, figs 1–7, pl. 19, figs 1–5.

MATERIAL AND HORIZON. Internal and external moulds of 12 pedicle and 2 brachial valves from the top of the Cyrn-y-brain Formation and Plas Uchaf Formation and 1 brachial valve from the Glyn Formation.

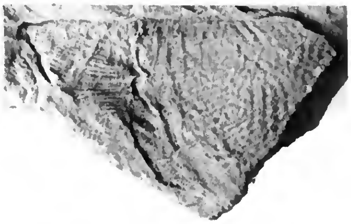
DESCRIPTION. Concavo-convex shells of transversely subquadrate outline; maximum width anterior to hinge-line. Pedicle valve nearly four-fifths as long as wide and about one-fifth as deep as long. Gently convex in both profiles; maximum convexity around umbo. Interarea short, flat, orthocline; delthyrium open. Brachial valve about three-quarters as long as wide; very gently concave. Interarea very short, flat, anacline; notothyrium closed by small convex chilidium. Unequally parvicostellate ornament yielding counts of 3–5 ribs per mm on 4, 1, 1 valves respectively, 5 mm anteromedianly from umbo; cancellated by fine concentric filae. Faint posterolateral rugae seen on some specimens.

Ventral interior with short dental plates diverging anteriorly at 60°–70° and extending for about one-tenth of valve length. Details of musculature not seen. Dorsal interior with plate-like cardinal process lobes diverging anteriorly at about 50°. Socket ridges widely divergent (c. 100°), about three-tenths as wide as valve, with about 4 denticles on posterior surface. Musculature obscure.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB69243	5·8	8·5
External mould of a pedicle valve, BB69244	5·1	8·2
Internal and external moulds of a pedicle valve, BB69245 . .	7·5	11·2

DISCUSSION. The Cyrn-y-brain specimens can be compared to *E. hirnantensis* (M'Coy 1851) and the closely related *E. siluriana* (Davidson, 1871). These two forms are very similar, the main difference between them being the coarser, more fascicostellate ribbing of the latter; a more detailed comparative study of the two is required. The fine parvicostellate ornament of the Cyrn-y-brain form would indicate a closer affinity with *E. hirnantensis* but there are some differences with previous descriptions of that species. However, a number of descriptions of *E. hirnantensis* e.g., Temple (1965 : 394), Bergström (1968 : 10) show that it must be a variable form; it has been described as plano-convex and concavo-convex, and the ornament as unequally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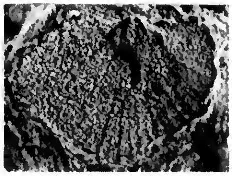
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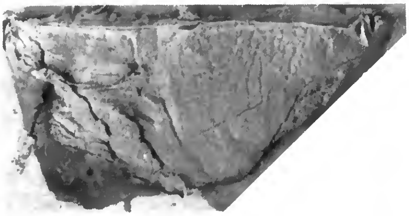
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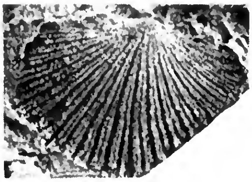
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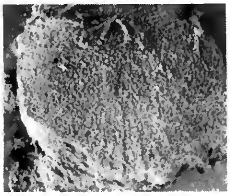
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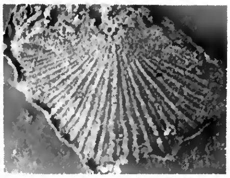
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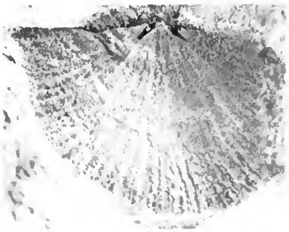
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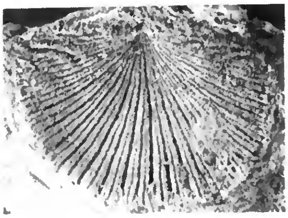
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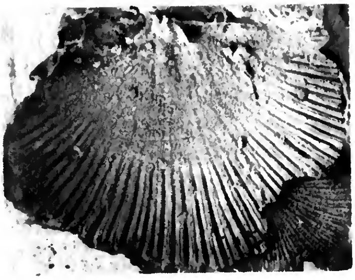
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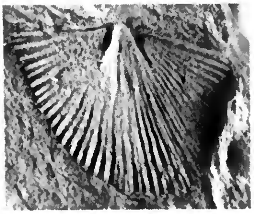
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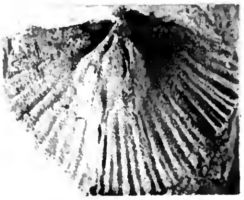
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Figs 344–345, 347 ?*Limbimurina* sp. Dolhir Limestone Member: Figs 345, 347, BB69239, Broken internal mould and latex cast of a brachial valve, ×1·4, ×1·3, loc. L3; Fig. 344, BB69239, Broken external mould of the same specimen, ×1·3, loc. L3.

Figs 346, 348–353 *Eostropheodonta hirnantensis* (M'Coy). Cyrn-y-brain Formation: Figs 346, 349, BB69243, Internal mould and latex cast of a brachial valve, ×3·4, loc. C3; Figs 348, 350, BB69244, parvicostellate and fascicostellate. The number of denticles recorded on the teeth and socket ridges varies and there appears to be considerable variation on the angles of divergence of dental plates, socket ridges and cardinal process lobes. The Cyrn-y-brain specimens fall within the ranges covered by these descriptions for each of the characteristics.

Analysis of a small topotype sample of *Eostropheodonta hirnantensis* from the Hirnant Limestone has shown that the Cyrn-y-brain specimens are very similar to it. The dental plates of the Hirnant species diverge at 60°–65°, the socket ridges at c. 110° and the cardinal process lobes at 50°–55°; the profile is concavo-convex and the ornament is fascicostellate with a density of 3–4 ribs per mm, 5 mm anteromedianly from the umbo.

Superfamily **DAVIDSONIACEA** King, 1850
Family **MEEKELLIDAE** Stehli, 1954
Subfamily **FARDENIINAE** Williams, 1965

FARDENIA Lamont, 1935

Fardenia scotica Lamont, 1935
Figs 354–359

1935 *Fardenia scotica* Lamont: 311, pl. 7, figs 1–7.

MATERIAL AND HORIZON. Internal and external moulds of 6 pedicle and 5 brachial valves from the middle and upper parts of the Dolhir Formation and from the Cyrn-y-brain Formation.

DESCRIPTION. Unequally biconvex, subquadrate shells with maximum width anterior to hinge-line. Pedicle valve over four-fifths as long as wide and nearly one-quarter as deep as long. Lateral profile gently convex; anterior profile strongly convex medianly with more gently convex flanks. Interarea fairly short, flat, apsacline; delthyrium closed by convex pseudodeltidium; one small specimen shows supra-apical foramen. Brachial valve almost three-quarters as long as wide and about one-seventh as deep as long; gently convex in both profiles. Interarea very short, flat, anacline; notothyrium and cardinal process lobes partially covered by small, convex chilidium. Ornamentation of strong costellae, arising both by branching and intercalation, numbering 3–4 per mm anteromedianly on 4 and 1 valves respectively, at 7·5 mm growth stage. Finer costellae developed between stronger ribs. Radial ornament crossed by fine concentric lines on some specimens.

Ventral interior with teeth supported by dental lamellae extending for one-quarter of valve length. Pentagonal muscle field usually weakly impressed, diductor lobes extend beyond median adductor scar, one small specimen showing short pedicle tube. Dorsal interior with pair of discrete cardinal process lobes; shallow sockets defined by short, divergent, straight socket ridges about one-fifth as wide as valve. Small, weakly impressed adductor scars lie on either side of very low, short, rounded ridge, just anterior to socket ridges.

DIMENSIONS

	length	width
Internal mould of a brachial valve, BB69247	17·6	23·5
External mould of a brachial valve, BB69248	11·1	17·5
Internal mould of a pedicle valve, BB69249	10·7	13·3
External mould of a pedicle valve, BB69250	9·0	10·2
Internal mould of a pedicle valve, BB69251	11·2	13·0

External mould and latex cast of a pedicle valve, ×4·1, ×3·3, loc. C3; Fig. 353, BB69245, Internal mould of a pedicle valve, ×1·7, loc. C3; Fig. 352, BB69245, External mould of the same specimen, ×2·1, loc. C3; Fig. 351, BB69246, Internal mould of a pedicle valve, ×2·6, loc. C3.

Figs 354–359 *Fardenia scotica* Lamont. Dolhir Formation: Figs 354, 355, BB69247, Internal mould and latex cast of a brachial valve, ×1·9, loc. D13; Fig. 358, BB69248, External mould of a brachial valve, ×2·3, loc. D13; Fig. 356, BB69250, Latex cast of the exterior of a pedicle valve, ×2·4, loc. D15. Cyrn-y-brain Formation: Fig. 357, BB69249, Internal mould of a pedicle valve, ×2·4, loc. C1; Fig. 359, BB69251, Internal mould of a pedicle valve, ×2·1, loc. C3.

Discussion. The Glyn Ceiriog and Cyrn-y-brain specimens of *Fardenia* are characterized by their unequal biconvexity, relatively short ventral interarea and straight socket ridges subtending an angle of approximately 90% at the umbo. *F. scotica* Lamont, 1935 from the Lower Drummuck Group of Girvan, is the form which most closely resembles the present specimens; it is biconvex, and has a similar ornament and straight socket ridges diverging at 90° to one another. However, there is not enough data available for this comparison to be tested statistically. Both forms can easily be separated from the resupinate *F. pertinax* (Reed, 1917) and *F. geoffreyi* (Bancroft, 1949), which also have a finer parvicostellate ornament. *F. scalena* Williams, 1962 is a biconvex form but has a high ventral interarea and strongly curved socket ridges. The present specimens can be regarded as being conspecific with *F. scotica*, which has also been recorded from the Cautley and Dent districts (Ingham, 1966 : 498).

Order **PENTAMERIDA** Schuchert & Cooper, 1931
Suborder **SYNTROPHIIDINA** Ulrich & Cooper, 1936
Superfamily **PORAMBONITACEA** Davidson, 1853
Family **PORAMBONITIDAE** Davidson, 1853

PORAMBONITES Pander, 1830

Porambonites sp.
Figs 360–363

Material and horizon. Badly crushed and sheared internal moulds of 5 valves, BB69254–57, and fragments of external moulds, all from the Tyn-y-twmpath Member of the Dolhir Formation.

Description. Ornament of fine costellae with a density of about 5 ribs per mm. Interspaces between ribs occupied by circular pores numbering about 4–6 per mm. Valve interiors showing long sub-parallel plates extending for about one-half of valve length. Details of musculature not seen. Shell substance very thin.

Discussion. The highly distinctive ornament readily enables the identification of even these very poorly preserved specimens as *Porambonites*, but in many cases it is not possible to identify brachial or pedicle valves. Although the material does not lend itself to specific identification, this Baltic genus is known from several localities in rocks of Ashgill age, e.g., Cautley (zone 3); Estonia; Quebec; and Portrane, again with only shell fragments.

Family **PARASTROPHINIDAE** Ulrich & Cooper, 1938

PARASTROPHINA Schuchert & Le Vene, 1929

?Parastrophina sp.
Figs 365, 366

1922 *Parastrophina divergens* Hall & Clarke; Wills & Smith: 191.

Material and horizon. One internal mould of a pedicle valve, BB69258 (length c. 9, width 12·5), and 1 external mould of a brachial valve, BB69259 (length 8·7, width 7·8), from the top of the Dolhir Formation.

Description. Dorsi-biconvex, roundedly subpentagonal shells; maximum width anterior to mid-valve. Pedicle valve about three-quarters as long as wide and one-fifth as deep as long; gently convex in lateral profile; anterior profile gently convex with broad shallow sulcus originating about mid-valve. Brachial valve nine-tenths as wide as long and approaching one-quarter as deep as long; convex in both profiles with low fold developing from about mid-valve. Ornamentation of broad costae, 4 on brachial valve and 5 on pedicle valve, developing with fold and sulcus; otherwise shell surface is smooth except for occasional growth lines.

Ventral interior showing spondylium supported by small, short septum. Details of muscle scars obscure. Dorsal interior unknown.

DISCUSSION. The present specimens are tentatively placed as *Parastrophina* although, without a well preserved dorsal interior displaying alate plates, the genus cannot be definitely separated from *Camerella*. There is also the problem of distinguishing between *Parastrophina* and *Parastrophinella*, which again cannot be done without a reasonably well preserved brachial valve interior (Wright, 1974 : 239).

Order **SPIRIFERIDA** Waagen, 1883
Suborder **ATRYPIDINA** Moore, 1952
Superfamily **ATRYPACEA** Gill, 1871
Family **ATRYPIDAE** Gill, 1871
Subfamily **ZYGOSPIRINAE** Waagen, 1883

CATAZYGA Hall & Clarke, 1893

Catazyga cf. ***headi*** (Billings, 1862)
Figs 370–377

cf. 1862 *Athyris headi* Billings: 147, fig 125.
cf. 1893 *Catazyga headi* (Billings); Hall & Clarke: 157, pl. 56, figs 7–11.

MATERIAL AND HORIZON. All the specimens were recovered from the lowest part of the Dolhir Formation, mostly from the Tyn-y-twmpath Member. Most of the specimens are badly distorted. The sample consists of 18 pedicle valves (including BB69263, length 11·0 mm, width 12·7 mm), 11 brachial valves, including BB69264 and BB69266, and 8 conjoined valves, including BB69265, BB69268–9, preserved as internal and external moulds.

DESCRIPTION. Subequally biconvex shells of subcircular outline. Anterior commissure faintly sulcate. Pedicle valve slightly deeper than brachial with evenly convex lateral profile becoming strongly so posteriorly, where incurved umbo conceals dorsal beak; anterior profile more strongly convex medianly than laterally. Subcircular outline varying from slightly elongate to slightly transverse; posterior margins almost straight, making obtuse angle at umbo; lateral and anterior margins evenly rounded. Interarea very short, curved, about one-half of maximum valve width, which is located near mid-valve. Faint fold of initial stages weakening anteriorly. Brachial valve evenly convex in both profiles; grooved medianly in anterior profile by faint sulcus which becomes progressively shallower towards anterior margin. Ornament consists of 50–60 fine, rounded costae; density of about 3 ribs per mm at 5 mm growth stage. Costellae are rarely developed by splitting of primary rib (see BB69268).

Ventral interior with stout teeth supported by short dental lamellae; deep triangular pedicle chamber, about as wide as long, situated posteriorly to triangular muscle field with diductors lateral to but not as long as adductors. Brachial valve with divided hinge plate; sockets small; low median septum broad posteriorly but narrowing forwards and extending for about one-half of valve length with poorly defined adductor scars on either side.

DISCUSSION. The most important features used in determining the specific identity of *Catazyga* are the density of ribbing and the style of fold and sulcus development.

The Glyn Ceiriog shells possess an initial sulcus in the brachial valve and complimentary ventral fold; these gradually fade anteriorly so that the anterior commissure is almost rectimarginate. The ornament is of fine costae with totals of 47, 48, 48, 50, 50, 52, 53, 54, 54, 55, 56, 58, 60 ribs in a sample of 13 valves. With rare exceptions, additional ribs do not develop with growth so that shell size is not important in consideration of this aspect; however, a density of 3, 4, 5, ribs per mm was observed at the 5 mm growth stage of 7, 3, 1 valves respectively.

The rib density of the Glyn Ceiriog species compares closely with that of *C. anglica* (Davidson, 1869), *C. arcana* Williams, 1962, *C. cartieri* Cooper & Kindle, 1936 and *C. headi* (Billings, 1862). The first of these has a ventral sulcus throughout its growth and *C. cartieri* has an initial sulcus in the brachial valve but reverts at about the 5 mm growth stage to a ventral sulcus and dorsal fold. The remaining two species, like that from Glyn Ceiriog, have a dorsal sulcus throughout


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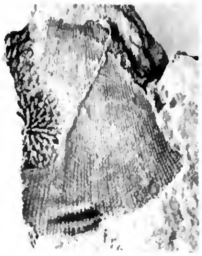
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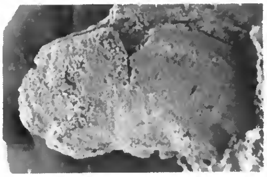
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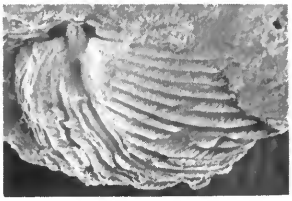
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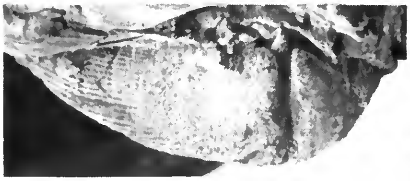
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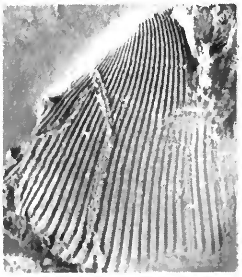
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Figs 360–363 *Porambonites* sp. Tyn-y-twmpath Member: Fig. 360, BB69254, Internal mould of a pedicle valve, ×4·2, loc. T1; Fig. 361, BB69255, Broken internal mould of a pedicle valve, ×2·6, loc. T1; Fig. 362, BB69256, Fragment of an external mould, ×2·6, loc. T1; Fig. 363, BB69257, Fragment of an external mould, ×2·4, loc. T1.

growth and of these *C. headi*, with its narrower sulcus, is more like the Glyn Ceiriog species. Descriptions and figures included in a recent review of *C. headi* (Copper, 1977 : 315) confirm this identification for the present specimens.

Catazyga cf. ***hicksi*** (Reed, 1905)
Figs 367–369

cf. 1905 *Zygospira Hicksi* Reed; 452; pl. 23, figs 17–19.
cf. 1977 *Catazyga hicksi* (Reed); Copper: 312, pl. 38, figs 20, 21.

DISCUSSION. Several small specimens of *Catazyga* (e.g. brachial valves BB69270, l = 6·9; BB69272, l = 4·9, w = c. 5) were recovered from a locality slightly higher in the succession than the others. Again they are subcircular in outline with a shallow sulcus in the brachial valve and a low fold in the pedicle valve, but where the ornament is seen it is coarser than for the other specimens, with two valves giving counts of 28 and 32 ribs respectively. The development of the sulcus and rib density compares closely with that of *C. hicksi* (Reed, 1905) from the Slade Beds of Haverfordwest and it is considered that these specimens are closely related to that species.

PROTOZYGA Hall & Clarke, 1893

Protozyga cf. ***perplexa*** Williams, 1962
Figs 378–385

cf. 1962 *Protozyga perplexa* Williams: 246, pl. 25, figs 54, 55, 61, 62.

MATERIAL AND HORIZON. Internal and external moulds of 8 pedicle and 3 brachial valves all from the same locality low in the Dolhir Formation, 50 m above the Dolhir Limestone. Brachial valves include BB69276 (length 7·6, width 9·8), BB69273–4, pedicle valves include BB69275 (length 6·9, width 8·0) and BB69277–8.

DESCRIPTION. Ventri-biconvex shells of subcircular to subpentagonal outline; maximum width anterior to hinge-line. Pedicle valve slightly longer than wide and about one-third as deep as long; lateral profile moderately convex, anterior profile strongly convex medianly. Brachial valve becoming relatively longer during growth with three valves showing length : width ratios of 60, 71, 81% respectively, one valve being about one-seventh as deep as long. Lateral profile gently convex; anterior profile with broad, shallow median sulcus rising near umbo and curving anteriorly towards pedicle valve. Exterior apparently without ornamentation.

Ventral interior with thin, slightly divergent dental plates extending anteriorly for about one-eighth of valve length. Diductor muscle scars weakly impressed on thickened platform of secondary shell, about nine-tenths as wide as long and less than one-half as long as valve. Dorsal interior with strong median septum extending for about three-quarters of valve length. Medianly

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Fig. 364 *Cyclospira* sp. Dolhir Formation: BB69290, Internal mould of a brachial valve, ×8, loc. D6.

Figs 365–366 ?*Parastrophina* sp. Dolhir Formation: Fig. 365, BB69258, Internal mould of a pedicle valve, ×2·6, loc. D15. Fig. 366, BB69259, Latex cast of the external mould of a brachial valve, ×3·3, loc. D15.

Figs 367–369 *Catazyga* cf. *hicksi* (Reed). Dolhir Formation: Fig. 367, BB69272, Internal mould of a brachial valve, ×5, loc. D6. Fig. 368, BB69271, Internal mould of a pedicle valve, ×4·4, loc. D6; Fig. 369, BB69270, Internal mould of a brachial valve, ×3·2, loc. D6.

Figs 370–376 *Catazyga* cf. *headi* (Billings). Tyn-y-twmpath Member: Figs 370, 373, BB69264, Latex cast and internal mould of a brachial valve, ×3·1, loc. T1; Fig. 371, BB69266, Internal mould of a brachial valve, ×2·4, loc. T1; Fig. 374, BB69269, Internal mould of conjoined valves, ×3·5, loc. T1; Fig. 375, BB69268, Latex cast of the exterior of conjoined valves, ×2·8, loc. T1. Dolhir Formation: Fig. 372, BB69263, Latex cast of the exterior of a pedicle valve, ×2·6, loc. D3; Fig. 376, BB69263, Internal mould of the same specimen, ×2·2, loc. D3.


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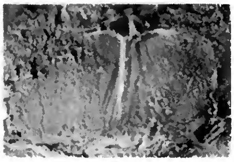
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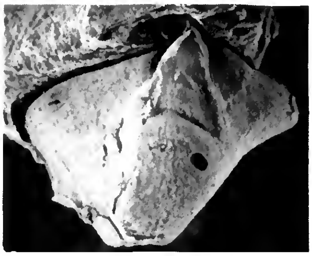
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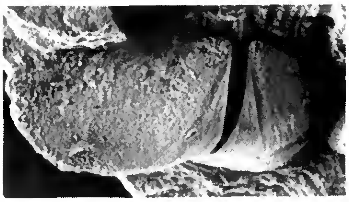
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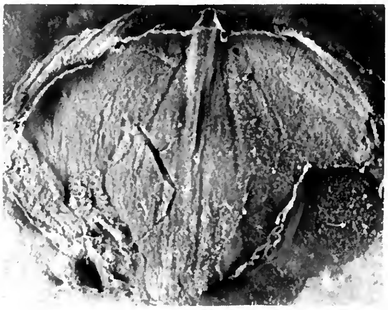
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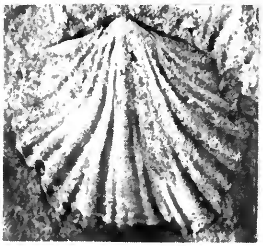
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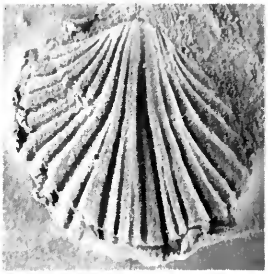
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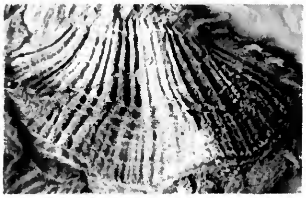
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Fig. 377 *Catazyga* cf. *headi* (Billings). BB 39265, Internal mould of conjoined valves, ×2·6, loc. T1.

Figs 378–385 *Protozyga* cf. *perplexa* Williams. Dolhir Formation: Figs 378, 379, BB69274, Internal mould and latex cast of a brachial valve, ×4·7, loc. D6; Fig. 380, BB69277, Internal mould of a pedicle valve, ×5, loc. D6; Fig. 381, BB69275, Internal mould of a pedicle valve, ×5·2, loc. D6;

cleft hinge-plate, about one-quarter as wide as valve, ankylosed to septum; crural bases situated medianly. Thin sockets placed laterally to hinge-plate. Traces of *vascula media* seen diverging, on either side of septum, from beneath hinge-plate. Position of muscle scars is unclear but one specimen (BB69274) indicates that they may have been sited on valve floor on either side of septum.

DISCUSSION. These specimens are placed in *Protozyga* on the basis of their well developed dental plates. A strong median septum, such as the 3 brachial valves possess, was once thought to be more typical of *Cyclospira* but has been described in *P. perplexa* Williams (1962 : 246) from Girvan and *P.* cf. *perplexa*, (Mitchell 1977 : 123) from the Killey Bridge Formation, Pomeroy. Another similarity with *Cyclospira* is seen in the platform of secondary shell supporting ventral diductor scars but this is also present in *P.* cf. *perplexa*. The Glyn Ceiriog form is closely related to *P. perplexa* and possesses a similarly unmodified dorsal sulcus which curves ventrally in later growth stages, to project towards pedicle valve. However, some differences are apparent; the dental plates of the Welsh species are relatively much shorter, being only about one-eighth as long as valve compared to one-fifth in *P.* cf. *perplexa* and about one-half in a ventral mould figured by Williams (1962 : pl. 25, fig. 61). The dorsal median septum of the Glyn Ceiriog specimens is relatively longer, three-quarters as long as valve compared to two-thirds, although this difference is not significant with the sample sizes involved. Another difference is that the hinge-plate of the Glyn Ceiriog specimens is apparently firmly ankylosed to the median septum but both Williams and Mitchell state that this is not the case for their specimens. It is uncertain what significance these differences may have but they could be considered sufficient to separate the Glyn Ceiriog form from *P. perplexa* although the two must be closely related. Perhaps *P. perplexa* is ancestral to the Welsh species.

Reed (1905 : 452) records an internal mould of a pedicle valve, which he identified as *Hyatella pentagonalis* Reed (?), and the figured specimen looks identical to the species described here.

Three brachial valves show *length of median septum* : *valve length* ratios of 65·4, 75·8, 88·2% respectively.

Five pedicle valves show *length of dental plates* : *valve length* ratios of 9·4, 10·7, 11·8, 13·2, 14·7% respectively.

Subfamily **ATRYPINAE** Gill, 1871

PLECTATRYPA Schuchert & Cooper, 1930

Plectatrypa cf. ***sulevi*** Jaanusson, 1954

Figs 386–387

cf. 1954 *Plectatrypa sulevi* Jaanusson: *in* Alikhova: 33, pl. 20, figs. 3–7.

MATERIAL AND HORIZON. Internal and external moulds of a single pedicle valve, BB69279, from the middle part of the Dolhir Formation. Length 12·5 mm, width 11·5 mm.

Figs 382, 385, BB69276, Internal mould and latex cast of a brachial valve, ×4·7, loc. D6; Fig. 383, BB69278, Internal mould of a pedicle valve, ×5·5, loc. D6; Fig. 384, BB69273, Internal mould of a brachial valve, ×4·7, loc. D6.

Figs 386–387 *Plectatrypa* cf. *sulevi* Jaanusson. Dolhir Formation: Fig. 386, BB69279, Internal mould of a pedicle valve, ×2, loc. D14; Fig. 387, BB69279, Latex cast of the exterior of the same specimen, ×2·1, loc. D14.

Figs 388–392 *Plectatrypa* cf. *gaspeensis* Cooper. Cyrn-y-brain Formation: Figs 388, 389, 390, BB69280, Dorsal, posterior and anterior views of an internal mould of conjoined valves, ×1·7, loc. C2; Fig. 392, BB69280, Latex cast of the exterior of the pedicle valve of the same specimen, ×1·7, loc. C2. Fron Frys Formation: Fig. 391, BB69283, Internal mould of a pedicle valve, ×1·6, loc. F1.

Description. Convex pedicle valve of subcircular outline; slightly longer than wide and almost one-quarter as deep as long; maximum width about mid-valve. Lateral profile moderately convex; anterior profile convex overall but with slightly convex flanks separated by narrow sulcus. Interarea short, curved, apsacline; delthyrium open. Ornament of coarse rounded costae and costellae; sulcus, containing single costa, bounded by pair of high ribs which branch at 2 mm and again at 5 mm growth stages. Total of 18 ribs at 5 mm growth stage. Only one strong growth lamella observed near margin of valve.

Ventral interior with teeth supported by short, narrow, widely divergent dental plates. Details of musculature not seen.

Brachial valve unknown.

Discussion. This specimen bears a strong resemblance externally to *P. sulevi* Jaanusson, 1954. Both forms have a narrow sulcus containing a single costa and have 6–7 primary ribs on each flank, with 4–5 costellae branching from these. Also, from the specimen figured by Jaanusson (1956 : pl. 1, fig. 7) it can be seen that the Estonian form is slightly longer than wide, just as the Welsh shell. No information on the interior of *P. sulevi* is available and with such small samples a full comparison cannot be made, but both forms are clearly morphologically very similar.

P. sulevi Jaanusson was transferred to the subgenus *Spirigerina* (*Eospirigerina*) by Boucot and Johnson (1967 : 87) but the open delthyrium and short curved interarea of the present specimen are more suggestive of *Plectatrypa*, although the single lamellose growth line may be more typical of *Eospirigerina* as defined by Boucot & Johnson (1967 : 90). However, until more material becomes available the species seems better left as originally designated by Jaanusson.

Plectatrypa cf. ***gaspeensis*** Cooper, 1930

Figs 388–394, 396, 397

1908 *Atrypa marginalis* Dalman; Groom & Lake: 578.
1922 *Atrypa marginalis* Dalman; Wills & Smith: 191.
cf. 1930 *Plectatrypa gaspeensis* Cooper: 279, pl. 2, figs 13–15.

Material and horizon. Internal and external moulds of 1 brachial and 1 pedicle valve from the Cyrn-y-brain Formation on Mynydd Cricor about 38 m below junction with Lower Llandovery slates; internal and external moulds of a pair of conjoined valves and an external mould of a pedicle valve from the Cyrn-y-brain Formation on Cyrn-y-brain, 15 m below the Plas Uchaf Formation; internal and external moulds of 8 brachial and 8 pedicle valves from the Fron Frys Formation.

Description. Dorsi-biconvex shells of transversely subquadrate outline; maximum width anterior to hinge-line. Pedicle valve over three-quarters as long as wide, about one-fifth as deep as long. Lateral profile moderately convex, anterior profile gently concave to gently convex on flanks, with well developed median sulcus bounded by strong ribs rising near umbo. In large pedicle valves sulcus develops into tongue-like extension. Umbo moderately curved; delthyrium open. Brachial valve also over three-quarters as long as wide and about one-quarter as deep as long. Lateral profile evenly convex; anterior profile convex on flanks with axial fold rising from faint initial sulcus at about 2 mm from umbo, and delimited laterally by fairly well defined bounding interspaces. Notothyrium open. Ornament of bold, rounded costae, and costellae which arise both by branching and by intercalation. Initial costa on dorsal fold bifurcates after about 2 mm and again at 10 mm to give 4 ribs; faint median rib intercalated at 5·5 mm. Total of about 22–24 ribs at 5 mm growth stage. Irregularly spaced, imbricate growth lamellae seen especially near margins of large shells.

Ventral interior with strong teeth supported by very short, thick dental plates. Muscle field distinguished only in large specimens; small, deeply impressed, elongately oval adductor scars flanked and enclosed anteriorly by diductors of triangular outline. Dorsal interior with divided hinge plate that defines sockets and gives rise to crural lobes. Floor of notothyrial chamber raised well above floor of valve. Site of diductor attachment convex, smooth; adductor scars obscure.

DIMENSIONS

	length	width
Internal and external moulds of conjoined valves, BB69280	17·0	26·6
External mould of a pedicle valve, BB69281	17·4	26·2
Internal mould of a pedicle valve, BB69282	17·4	28·8
Internal mould of a pedicle valve, BB69283	20·5	21·0
Internal and external moulds of a brachial valve, BB69284	11·7	12·2

DISCUSSION. The material described here appears to be very closely related to the Gasworks Mudstone species from Haverfordwest, *Spirigerina* (*Eospirigerina*) *gaspeensis* described by Boucot & Johnson, (1967 : 92) and restored to *Plectatrypa* by Temple (1970 : 60). Using the criteria laid down by Boucot & Johnson (1967 : 85) the Glyn Ceiriog specimens are placed in *Plectatrypa* because they possess lamellose growth lines and impressed ventral diductor scars. However, these features are only seen in the largest specimens and the smaller ones have features more like *Eospirigerina*, so the differences between the genera seem to be a matter of the age of individuals.

The Ordovician specimens from Cyrn-y-brain and Mynydd Cricor are the same as those from the Fron Frys Formation and these are practically identical to the form described by Temple from Meifod (1970 : 59) and are accordingly placed as *Plectatrypa* cf. *gaspeensis*.

Spiriferide, gen. et sp. indet

Fig. 402

MATERIAL AND HORIZON. 1 pedicle valve, BB69289, from a locality just below the Dolhir Limestone. Length 6·5 mm, width 4·4 mm.

DESCRIPTION. Pedicle valve about two-thirds as wide as long and one-quarter as deep as long. Moderately convex in both profiles. Ornament of fine growth lines. Interior with dental plates extending anteriorly for one-fifth of valve length. Deeply impressed, bilobed muscle scar almost one-half as wide as long, and nearly seven-tenths as long as valve.

DISCUSSION. The general appearance of this specimen is reminiscent of some species of *Protozyga*, but without more material it cannot be properly identified.

Superfamily **DAYIACEA** Waagen, 1883
Family **DAYIIDAE** Waagen, 1883
Subfamily **CYCLOSPIRINAE** Schuchert, 1913

CYCLOSPIRA Hall & Clarke, 1893

Cyclospira sp.

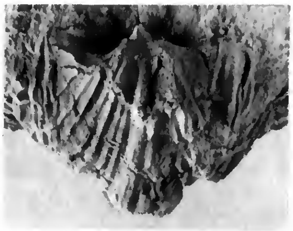
Fig. 364

MATERIAL ADD HORIZON. A single internal mould of a brachial valve, BB69290, from a locality 50 m above the Dolhir Limestone. Length 1·8 mm, width 2·6 mm.

DESCRIPTION. Almost flat, brachial valve, seven-tenths as long as wide, initially slightly convex. Ornament not seen. Interior with narrow, medianly cleft hinge-plate. Crural bases situated medianly; small sockets well developed. Strong median septum not ankylosed to hinge-plate and extending close to anterior margin of valve. Musculature obscure.

DISCUSSION. This slightly crushed form is characterized by its long median septum but the British Ashgill species of *Cyclospira* are too poorly known for comparisons to be made, and a single specimen is not enough to compare with the better-known North American species.

Suborder **ATHYRIDIDINA** Boucot, Johnson & Staton, 1964
Superfamily **ATHYRIDACEA** M'Coy, 1844
Family **MERISTELLIDAE** Waagen, 1883
Subfamily **MERISTELLINAE** Waagen, 1883



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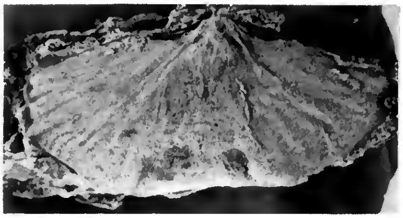

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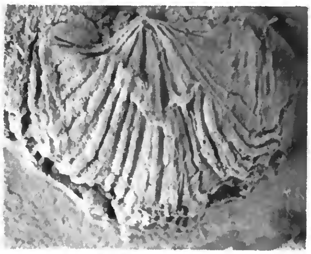

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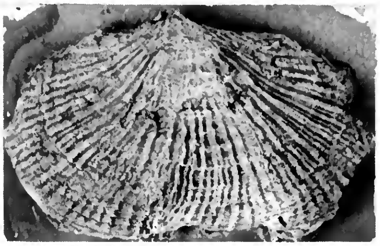

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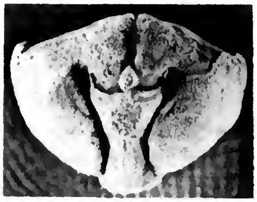

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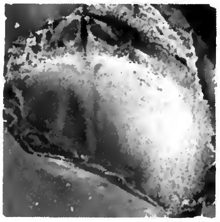

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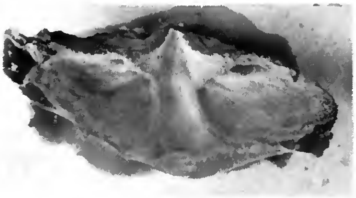

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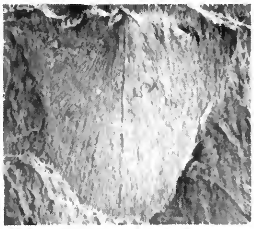

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Figs 393–394, 396–397 *Plectatrypa* cf. *gaspeensis* Cooper. Cyrn-y-brain Formation: Fig. 393, BB69284, Internal mould of a brachial valve, ×2·2, loc. M1; Fig. 396, BB69284, Latex cast of the exterior of the same specimen, ×2·4, loc. M1. Fron Frys Formation: Fig. 397, BB69281, Latex cast of the exterior of a pedicle valve, ×1·8, loc. F1; Fig. 394, BB69282, Internal mould of a pedicle valve, ×1·8, loc. F1.

CRYPTOTHYRELLA Cooper, 1942

Cryptothyrella crassa (Sowerby, 1839) ***incipiens*** (Williams, 1951)
Figs 395, 398–401, 403, 404

1908 *Meristina* (?) *crassa* Sowerby; Groom & Lake: 578 (pars).
1922 *Meristina crissa* Sowerby; Wills & Smith: 191.
1951 *Meristina crassa* Sowerby *incipiens* Williams: 112, pl. 6, figs 14–17.
1977 *Hindella crassa incipiens* (Williams); Sheehan: 34, pl. 2, figs 1–11, pl. 3, figs 22–24

MATERIAL AND HORIZON. A single pedicle valve internal mould from the upper part of the Dolhir Formation and 41 pedicle, 10 brachial and 5 pairs of conjoined valves from the top of the Cyrn-y-brain Formation.

DESCRIPTION. Strongly biconvex shells varying from elongately to slightly transversely suboval in outline; maximum width anterior to hinge-line. Pedicle valve almost two-fifths as deep as long; interarea only faintly developed; umbo slightly incurved. Brachial valve almost one-third as deep as long; umbo inconspicuous. Exterior smooth except for rare, subdued growth lines. Shell quite thick around umbones but much thinner away from body cavity. Ventral interior with teeth supported by strong, dental plates which converge towards floor before diverging anteriorly, to extend for almost three-tenths of valve length, and enclosing posterior end of muscle scars. Pedicle chamber fairly large, triangular, about three-quarters as long as wide and about one-sixth as long as valve; muscle scar obscure. Platform between pedicle chamber and anterior muscle scar fairly short, about one-tenth as long as valve. Muscle scar triangular, flabellate, about four-fifths as wide as long and about two-fifths as long as valve; diductors extend anteriorly from adductors. Valve floor outside dental plates may show chevron-like corrugations, representing mantle canals; gonocoel impressions seen outside these in some specimens.

Dorsal interior with rather wide hingeplate, over two-fifths as wide as valve, divided medianly by narrow cleft and supported by pair of short plates uniting with weakly developed septum to simulate septalium. Septum extends for about one-half of valve length. Widely divergent, long, slender sockets lateral to hingeplate. Elongately oval muscle scars, about one-half as wide as long, lightly impressed on either side of median septum. Again gonocoel impressions seen in postero-lateral position in some shells.

DIMENSIONS

	length	width
Internal mould of conjoined valves, BB69291	—	11·5
Internal mould of a pedicle valve, BB69292	10·4	11·0
Internal mould of a pedicle valve, BB69296	—	c. 20
Internal mould of a brachial valve, BB69297	10·5	13·0

DISCUSSION. Most of the specimens have been collected from the type locality for Williams' subspecies *Meristina crassa incipiens* (1951 : 112), which was included in *Cryptothyrella* by Boucot, Johnson & Staton (1964 : 817), along with the slightly younger *Meristina crassa* (Sowerby, 1839). Recently Sheehan (1977 : 36) transferred this species to *Hindella* after he had examined some specimens from Scandinavia. This was done because these specimens displayed

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Figs 395, 398–401, 403–404 *Cryptothyrella crassa incipiens* (Williams). Cyrn-y-brain Formation: Fig. 398, BB69291, Internal mould of conjoined valves, ×3·4, loc. C2; Fig. 395, BB69292, Internal mould of pedicle valve, ×2·5, loc. C2; Figs 399, 400, BB69293, Internal mould and latex cast of a brachial valve, ×4·6, ×4·7, loc. C2; Figs 401, 404, BB69296, Internal mould and latex cast of a pedicle valve, ×2·1, loc. C4; Fig. 403, BB69297, Internal mould of a brachial valve, ×2·4, loc. C1.

Fig. 402 Spiriferide, gen. et. sp. indet. Dolhir Limestone Member, BB69289, Internal mould of a pedicle valve, ×3·7, loc. L3.

Figs 405–408 *Kjaerina* sp. Dolhir Formation: Fig. 405, BB69217, Internal mould of a pedicle valve, ×2·6, loc. D3; Fig. 406, BB69218, External mould of a pedicle valve, ×2·7, loc. D3; Figs 407, 408, BB69217, Latex cast and external mould of a pedicle valve, ×2·5, ×2·6, loc. D3.

a prominent ventral umbo, well developed growth lines, dental plates which do not extend beyond the pedicle chamber, slightly divergent margins to the ventral muscle field and less robust cardinalia than is usual for *Cryptothyrella.* However, the specimens described herein, in accord with Williams' original description, show only weakly developed growth lines, a small, slightly incurved ventral umbo and dental plates which extend beyond the pedicle chamber. It is felt that preservation may affect the appearance of some of these features, and until more extensive research is done the species is best left within *Cryptothyrella.*

The following statistical data have been obtained for the sample:

Pedicle Valve

Length (l) : Width (w), $n = 30$; $\bar{l}$(var. l) = 11·5 (8·214) mm; $\bar{w}$(var. w) = 11·23 (11·266) mm; $r = 0{\cdot}717$; a(var. a) = 1·171 (0·0238).

Length of muscle scar (l) : width of muscle scar, $n = 24$; $\bar{l}$(var. l) = 4·53 (1·341) mm; $\bar{w}$(var. w) = 3·71 (1·003) mm; $r = 0{\cdot}7615$; a(var. a) = 0·865 (0·0143).

Length of valve (l) : length of muscle scar (m), $n = 22$; $\bar{l}$(var. l) = 11·17 (6·596) mm; $\bar{m}$(var. m) = 4·62 (1·349) mm; $r = 0{\cdot}7902$; a(var. a) = 0·452 (0·00384).

Length of pedicle chamber (l) : width of pedicle chamber (w), $n = 24$; $\bar{l}$(var. l) = 2·06 (0·218) mm; $\bar{w}$(var. w) = 2·79 (0·418) mm; $r = 0{\cdot}7934$; a(var. a) = 1·384 (0·0323).

Brachial Valve

Length (l) : depth (d), $n = 7$; $\bar{l}$(var. l) = 10·17 (5·306) mm; $\bar{d}$(var. d) = 3·17 (0·109) mm; $r = 0{\cdot}8183$; a(var. a) = 0·143 (0·00135).

Length of valve (l) : length of median septum (m), $n = 7$; $\bar{l}$(var. l) = 10·17 (5·306) mm; $\bar{m}$(var. m) = 5·06 (2·24) mm; $r = 0{\cdot}719$; a(var. a) = 0·65 (0·0408).

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Contents

Type specimens of some Upper Palaeozoic Athyridide brachiopods

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Synopsis

Type specimens are selected or recognized, and briefly described, of eleven Carboniferous and one Permian athyridide species, principally from the M'Coy, Phillips and Sowerby collections. These include the genotypes of *Actinoconchus—A. paradoxus* M'Coy, *Cleiothyridina—C. pectinifera* (J. de C. Sowerby) and *Composita—C. ambigua* (J. Sowerby). Species are assigned to genera and synonymies suggested where appropriate. A new subspecies *Actinoconchus expansus patulus* is described. Lectotypes are selected of *Actinoconchus paradoxus* M'Coy 1844, *A. expansus expansus* (Phillips 1836), *Atrypa*? *obtusa* M'Coy 1844 [?= *Actinoconchus oblongus* (J. de C. Sowerby 1840)], *Spirifer planosulcatus* Phillips 1836, *S. squamosa* Phillips 1836 [= *Actinoconchus lamellosus* (Léveillé 1835)], *Atrypa pectinifera* J. de C. Sowerby 1840, *Spirifer fimbriata* Phillips 1836, *Athyris squamigera* de Koninck 1887 [= *Cleiothyridina deroissyi* (Léveillé 1835)], *Spirifer ambiguus* J. Sowerby 1822 and *Athyris carringtoniana* Davidson 1862. A neotype is erected of *Spirifer lamellosus* Léveillé 1835.

Introduction

Some years ago, while working on the spire-bearing brachiopods from an Irish Viséan silicified fauna, it became apparent that type specimens had not been selected of several athyridide species in the collections of nineteenth-century authors. More recently correspondence with palaeontologists in Europe and Russia indicates the need for the selection of types in the genera *Actinoconchus*, *Cleiothyridina* and *Composita* without waiting for the publication of the complete Irish fauna. In addition I have already dealt with the case for the type species of *Cleiothyridina* (1972, 1976), and many of the specimens from which types should be chosen are in my care at the British Museum (Natural History).

The subfamily Athyridinae is represented by the following Carboniferous and Permian genera: *Athyris* M'Coy, *Actinoconchus* M'Coy, *Cleiothyridina* Buckman, *Composita* Brown, *Deltachania* Waterhouse, *Nordathyris* Grunt and *Planalvus* Carter. The relationship between M'Coy's two genera is complicated, and briefly discussed below, and the other genus I am concerned with is *Cleiothyridina*. In addition the type species of *Composita*, *Spirifer ambiguus* J. Sowerby, 1822, has its lectotype selected (Figs 26–28), and potential types of *Terebratula concentrica* von Buch 1834 are figured (Figs 1–3).

When distinguishing *Athyris* from *Actinoconchus* M'Coy (1844: 146, 149) stressed that the latter had greatly extended frills 'forming a flat, circular, striated disc', and, on the basis of his single species, he appears to have considered it a non-sulcate and flatter genus than *Athyris*. The type species of *Athyris*, by subsequent designation of King (1850), is *Terebratula concentrica* von Buch 1834, from the mid-Devonian of Gerolstein, Germany. In the Palaeontological Museum of the Humboldt University of Berlin there are six specimens, kindly lent by Dr Jaeger, from the L. von Buch collection, labelled by him as *T. concentrica*, or varieties of the species. Three were given variety names and three were simply called *T. concentrica* and said to be from Bensberg, near Köln. This locality conflicts with that given in the original publication, Gerolstein, which is generally considered to be correct. Von Buch (1834) did not figure his species, and since the Eifel region of Germany is rich in athyrid species it is important to establish a type specimen for *A. concentricus*. In my view this should be done using one of von Buch's original specimens, provided there is no good reason to doubt their validity, even if this results in a change in our concept of the species. However, the selection should be left to those German palaeontologists

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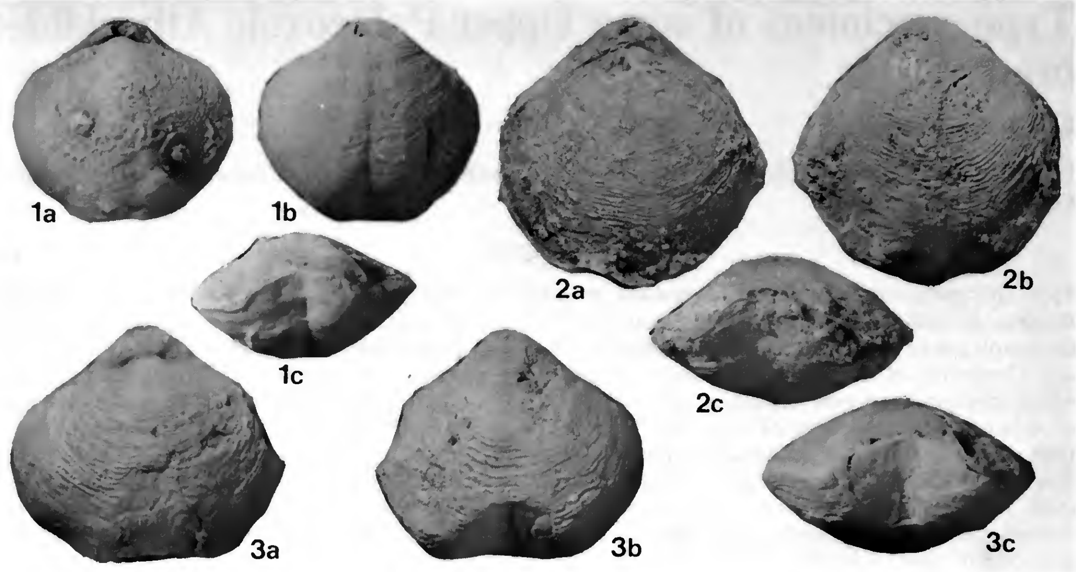

Figs 1–3 *Athyris concentricus* (von Buch). Possible syntypes from the mid-Devonian of the Eifel region, Germany. Von Buch coll., Humboldt University Museum, Berlin, nos 10–12, each viewed dorsally, ventrally and anteriorly. All ×1·5. Fig. 1a–c, no. 10. Fig. 2a–c, no. 11. Fig. 3a–c, no. 12.

most familiar with the athyrid faunas of the region and all possible von Buch material, and for this reason I do no more than figure (Figs 1–3) the three von Buch specimens known to me, which appear to represent his concept of the species, although differing somewhat from his original description.

In 1844 the only species M'Coy described under *Actinoconchus* was *A. paradoxus* M'Coy (1844 : 150; pl. 21, figs 6a–c), which is therefore the type species. Davidson (1859) placed *A. paradoxus* into synonymy with *Athyris planosulcata* (Phillips, 1836) and most authors have accepted this, with the result that the Treatise (Williams *et al.* 1965 : H662) states that Phillips' species is the type of *Actinoconchus*. I agree with Carter (1967) in believing the two species to be distinct and so retain the name *A. paradoxus* for the type species of *Actinoconchus*.

A complication in the differentiation of *Athyris* from *Actinoconchus* stems from M'Coy's own work (1844 : 149, footnote) when he added the information that a specimen he identified as *Athyris squamosa* (Phillips, 1836), which he correctly put in synonymy with *Spirifer lamellosus* Léveillé, 1835, had lamellose extensions forming frills, as in his species *Actinoconchus paradoxus*. He then, surprisingly, concluded that *A. paradoxus* '. . . may therefore be an *Athyris*'. M'Coy's assignment of *S. lamellosus* to *Athyris* has been followed and the species was figured in the Treatise (Williams *et al.* 1965 : fig. 537, 4b–d) as illustrating the genus. I believe, however, that *S. lamellosus* is more closely related to *A. paradoxus* than to *Athyris concentrica* and that it should be assigned to *Actinoconchus*. This means that *Athyris* remains a genus more typical of Devonian than Carboniferous rocks and contains species lacking the long lamellose shelly extensions typical of *Actinoconchus* and *Cleiothyridina* species.

The case has been presented (Brunton 1972) and accepted (ICZN 1976) for the validation of the generic name *Cleiothyridina* and for the acceptance of *Atrypa pectinifera* J. de C. Sowerby, 1840, as the type species. In the application it was pointed out that the name *S. deroissyi* Léveillé, 1835, had been misinterpreted by Davidson (1861) and confused with *Spirifer fimbriata* Phillips, 1836. Both these names belong to recognizable species assigned to *Cleiothyridina*, but *C. fimbriata* is the commoner species in Viséan rocks of western Europe and was figured by Davidson (1861 : pl. 18, figs 8, 10, 11) as '*Athyris Roysii*'. Léveillé's original spelling *De Roissyi* should now be accepted as *deroissyi*. The name was also used by de Koninck over many years to include several species, and by 1887 he had split his concept of the species into *Athyris Leveillei* and *Athyris roissyi*, which included not only Léveillé's true species but also *C. fimbriata*.

M'Coy's (1844) species were based on material in the Griffith Collection, housed in the National Museum of Ireland, Dublin; Phillips' (1836) species were mostly described from the Gilbertson Collection which, with collections of the Sowerbys, is housed in the British Museum (Natural History), London.

Few of the type species described here have ever been refigured since their original publications, and the figures herein are commonly the first photographic illustrations to be presented.

Systematic palaeontology

The notation in the synonymy lists follows Matthews (1973) and outline shape descriptions, where applicable, follow the Systematics Association Committee for Descriptive Biological Terminology (Exell & Lewis 1962).

Family **ATHYRIDIDAE** Davidson, 1881

Subfamily **ATHYRIDINAE** Davidson, 1881

Since the work of Boucot, Johnson & Staton (1964), for the brachiopod volume of the Treatise on Invertebrate Paleontology (Williams *et al.* 1965), the family name has usually been assigned to M'Coy, 1844. However, Alvarez, Brime & Brunton (1980) point out that M'Coy's (1844) use of the family name 'Athyridae' does not comply with the rules of the International Code of Zoological Nomenclature (1964) in Article 11, section (e), which states that a family-group name must, when first published, be based on the name of a valid contained genus. Although M'Coy established the new genus *Athyris* in 1844 he placed it in the 'Delthyridae', not the 'Athyridae', a family which remained without the genus name *Athyris* until united by Davidson (1881).

Genus *ATHYRIS* M'Coy, 1844

Type species. *Terebratula concentrica* von Buch, 1834 by subsequent designation of King, 1850.

Athyris concentricus (von Buch)

Type specimen. No type specimen has yet been selected. As already indicated, some possible syntypes from von Buch's collection, and named *T. concentrica* by von Buch, are in the Humboldt University Museum, Berlin (Figs 1–3). However, the situation of Devonian athyrids from the Eifel region of Germany is complex and until palaeontologists there designate a type for the species it is difficult to make a diagnosis of the species or genus.

I think the generic description needs to be emended, from that of Williams *et al.* (1965 : H662), to exclude the very wide and strongly lamellose forms like *A. lamellosus*, which I place in *Actinoconchus.*

Genus *ACTINOCONCHUS* M'Coy, 1844

Diagnosis. Athyridinae bearing long delicate flanges of shell from rugae or strong growth lines on both valves.

Type species. *Actinoconchus paradoxus* M'Coy (1844 : 150; pl. 21, figs 6a, b). The only species described by M'Coy in his new genus.

Actinoconchus paradoxus M'Coy

Figs 4–6

v. 1840 *Atrypa expansa* (Phillips); J. de C. Sowerby (*pars*) : 14; pl. 617, fig. 1 – lower right only.
v* 1844 *Actinoconchus paradoxus* M'Coy : 150; pl. 21, figs 6a, b (not 6c).
v. 1859 *Athyris planosulcata* (Phillips); Davidson (*pars*) : 80; pl. 16, figs 9, 10, 11.
1887 *Athyris planosulcata* (Phillips); *sensu* de Koninck (*pars*) : pl. 21, figs 17, 18, 19.


4


5

Figs 4–5 *Actinoconchus paradoxus* M'Coy. ×1·5. Fig. 4, **lectotype** (herein selected), from Millicent, Clane, Co. Kildare, Ireland. Griffith coll. in National Museum of Ireland, Dublin. Viewed dorsally, showing part of the radially striated flat shell flange. Fig. 5, from Kildare, Ireland. Davidson coll., BM(NH) B 5392. Viewed ventrally, showing the full extent of one flange and parts of others.

DIAGNOSIS. Subcircular outline, equibiconvex profile, lacking median sulcus or fold. Lamellose flanges flat with fine radiating striations.

TYPE SPECIMEN. In the National Museum of Ireland, Dublin there are five specimens labelled as *A. paradoxus* M'Coy in the Griffith Coll. Two of these are not *A. paradoxus*, and of the other three specimens none is clearly the subject of M'Coy's figs 6a–c. Two specimens, however, are of particular interest. One, from 'Knockagh, Dundalk', is a specimen on black limestone, also containing large fragments of the davidsoniacean brachiopod *Brochocarina* cf. *wexfordensis* (Smyth), one of which underlies the *A. paradoxus* specimen and was probably mistakenly believed to be the lamellose flange. This specimen may have been the origin of M'Coy's fig. 6c, since the illustrated flange extends too far posteriorly and is too strongly ribbed for true *A. paradoxus*, but resembles the combination of *A. paradoxus* with the davidsoniacean[1]. Another syntype, from 'Millicent, Clane', Co. Kildare, is well preserved and may have provided information for figure 6a. This specimen is here selected as **lectotype** and figured (Fig. 4). It is probably of early Viséan, Chadian age.

Actinoconchus expansus expansus (Phillips)
Fig. 10

v* 1836 *Spirifera expansa* Phillips : 220; pl. 10, fig. 18.
v. 1840 *Atrypa expansa* (Phillips) J. de C. Sowerby (*pars*) : 14; pl. 617, fig. 1 – middle two and lower left.
? 1859 *Athyris planosulcata* (Phillips); Davidson (*pars*) : pl. 16, fig. 4.
1859 *Athyris expansa* (Phillips); Davidson (*pars*) : pl. 16, figs 14, ? 16.

DIAGNOSIS. Transversely oval in outline, lacking median sulcus. Short delicate flanges from weakly developed growth lines.

TYPE SPECIMEN. *Spirifer expansa* Phillips (1836 : pl. 10, fig. 18). Gilbertson Coll., Bolland, Yorkshire; probably of late Chadian to early Arundian (early Viséan) age. Here selected **lectotype** – BM(NH) Pal. Dept. reg. no. B 314.

Actinoconchus expansus patulus subsp. nov.
Figs 7–9

1859 *Athyris expansa* (Phillips); Davidson (*pars*) : pl. 16, figs 17–18, ? 16.

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[1] Flanges as in M'Coy's fig. 6c would not have been possible in life as they would have prevented opening of the valves.

NAME. Latin *patulus*, meaning spread out or broad.

HOLOTYPE. BM(NH) Pal. Dept. reg. no. 74355. Etheridge Coll. From Viséan limestones of the Kendal region, Cumbria (Fig. 7). It is similar to the specimen illustrated by Davidson (1859 : pl. 16, fig. 17, 17a), also from Kendal.

DIAGNOSIS. Broad, flattened shells, wider than long. Faint external ornamentation of growth lines, rarely preserved, with short delicate lamellae. Exfoliated surfaces display a delicate radial pattern. Valves remain thin-shelled.

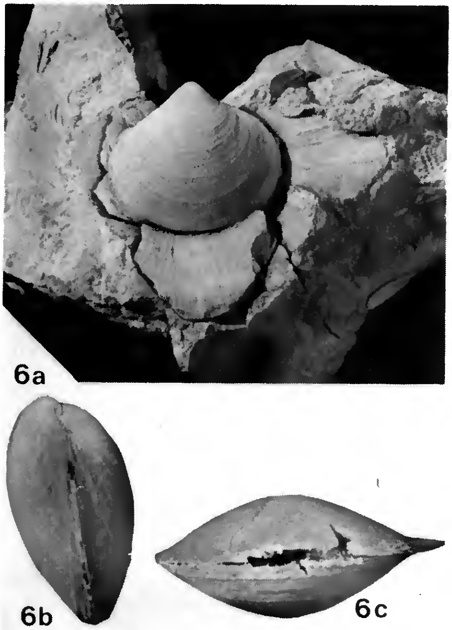
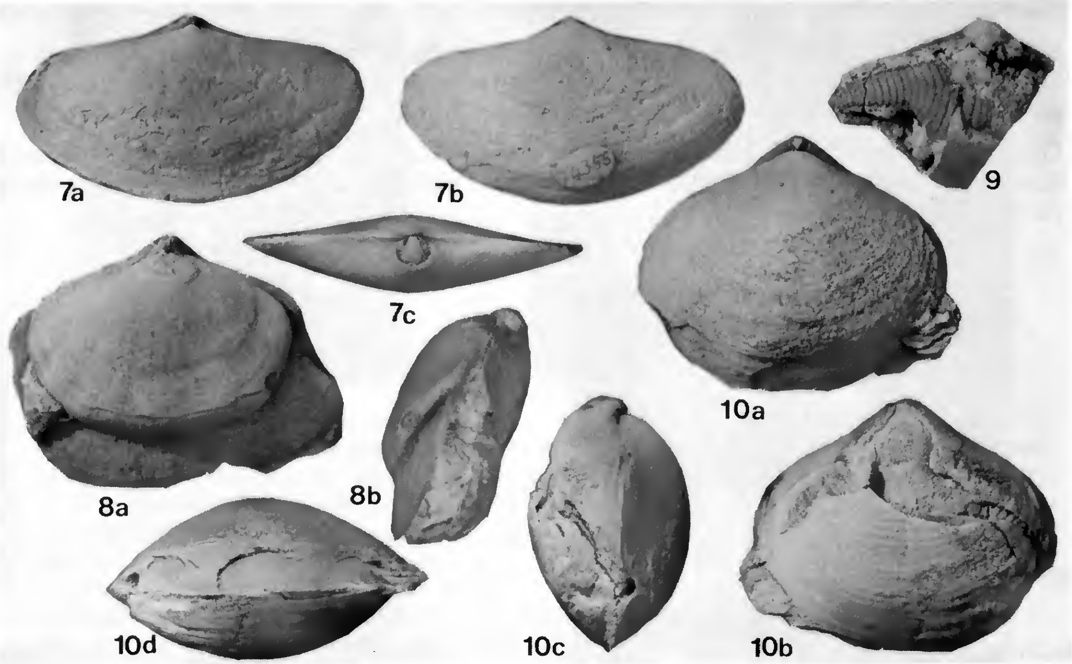


Fig. 6a–c *Actinoconchus paradoxus* M'Coy. From Wetton Hill, Staffordshire. Davidson coll., BM(NH) B 5396. Fig. 6a viewed ventrally in the rock, with its flanges, ×1. Figs 6b, c viewed laterally and anteriorly, free of the rock, ×1·5.

DISCUSSION. The name *Athyris expansa* has been used for many years for specimens having a wide variety of shapes. In particular there are low, wide and apparently rather smooth distinctive forms, such as illustrated by Davidson (1859 : pl. 16, figs 17, 18). The specimen for fig. 17 is in the collections of the Institute of Geological Sciences, Leeds, numbered GSL504. The original specimen for fig. 18 is in the Yorkshire Museum, York, YM817. These broad forms, having widths varying from just exceeding their length to almost twice their length, are characterized by having finer growth lamellae than *A. expansus expansus* and in displaying a fine radial ribbing when the outer shell layers are removed by abrasion (Fig. 8a). Unfortunately locality information accompanying the studied specimens (about 40) is insufficiently precise to tell what geographical or ecological factors controlled the distribution of these specimens. If distinctive distributions could be demonstrated I think these shells should be considered a new species, despite their broadly scattered dimensional plots, which almost include the plot for the lectotype of *A. expansus expansus*. At present, so as to allow easy reference to the specimens, I propose that they be treated as a sub species. Specimens thought to be conspecific with them are known (D. Mundy, personal communication) from the Asbian limestones of the Craven 'Reef' belt of north Yorkshire. Rocks of a similar late Viséan age also occur in the Kendal region of Cumbria.

Actinoconchus oblongus (J. de C. Sowerby)
Figs 11, 12

v* 1840 *Atrypa oblonga* J. de C. Sowerby : 16; pl. 617, fig. 3.



Figs 7–9 *Actinoconchus expansus patulus* subsp. nov. All ×1. Fig. 7, **holotype,** from near Kendal, Cumbria. Etheridge coll., BM(NH) 74355, viewed dorsally, ventrally and posteriorly. The shell material is broken from the ventral umbo. Fig. 8, from Settle, Yorkshire. Wheelton Hind coll., BM(NH) B 52835, viewed dorsally and laterally. Showing a step in growth, which affected both valves; this is not a marginal flange. Fig. 9, from Parkhouse Hill, Derbyshire. Wheelton Hind coll., BM(NH) B 52840. Ventral view showing part of the spiralia.

Fig. 10 *Actinoconchus expansus expansus* (Phillips), ×1. **Lectotype** (herein selected), from Bolland, Yorkshire. Gilbertson coll., BM(NH) B 314, viewed dorsally, ventrally, laterally and anteriorly.

v? 1844 *Atrypa*? *obtusa* M'Coy : 155; pl. 22, fig. 20[2].
1859 *Athyris planosulcata* var. *oblonga* (J. de C. Sowerby) Davidson : pl. 16, figs 13, 13a (copied from Sowerby 1840).

DIAGNOSIS. Elongate oval in outline with slight anterior sulcation in both valves forming marginal ligation. Thickness about three-quarters maximum width. Weakly lamellose exterior with? short delicate flanges.

TYPE SPECIMEN. *Atrypa oblonga* J. de C. Sowerby (1840 : pl. 617, fig. 3). BM(NH) Pal. Dept. reg. no. B 61035. Sowerby Coll., Queen's County (Co. Laois), Ireland. Here recognized as holotype, as being the only specimen available to Sowerby in 1840 (p. 16). Fig. 11.

Actinoconchus planosulcatus (Phillips)
Figs 13, 14

v* 1836 *Spirifera planosulcata* Phillips : 220; pl. 10, fig. 15.
v. 1840 *Atrypa planosulcata* (Phillips) J. de C. Sowerby : pl. 617, fig. 2, left side and bottom right.
1859 *Athyris planosulcata* (Phillips); Davidson : pl. 16, fig. 2 (redrawn from Phillips, 1836).

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[2] In the National Museum of Ireland, Dublin (Griffith Collection) there are two specimens of *Atrypa obtusa* M'Coy. The larger specimen, from 'Skerries, Milverton', about 18 miles north of Dublin, is very similar to this figure and is here selected **lectotype** (Fig. 12). The smaller specimen is also marked as coming from 'Milverton', and is conspecific. These specimens lack the slight anterior sulcation and are relatively slightly wider than the type specimen of *A. oblonga.*

Diagnosis. Irregular pentagonal outline, slightly wider than long with thickness approximately half of width. Both valves with persistent shallow median sulci forming ligate anterior. Ornament of weakly developed shell lamellae and rarely preserved broad delicate flanges.

Type specimen. *Spirifer planosulcata* Phillips (1836 : 220; pl. 10, fig. 15). BM(NH) Pal. Dept. reg. no. B 317. Gilbertson Coll., Bolland, Yorkshire. Here selected **lectotype.** Conspecific specimens from the Craven 'Reef' belt, north Yorkshire, are of late Viséan, Asbian age.

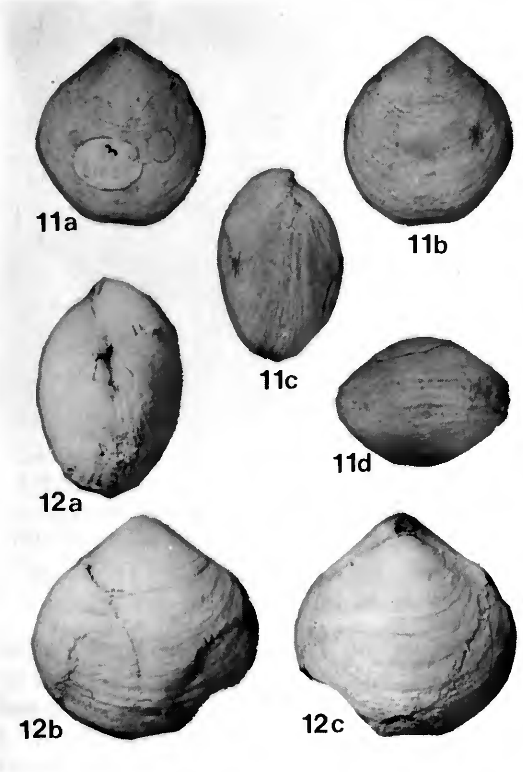


Fig. 11 *Actinoconchus oblongus* (J. de C. Sowerby), ×1. Holotype from Queen's County [Laois], Ireland. Sowerby coll., BM(NH) B 61035, viewed dorsally, ventrally, laterally and anteriorly. [= *Atrypa oblonga* J. de C. Sowerby 1840 : pl. 617, fig. 3.]

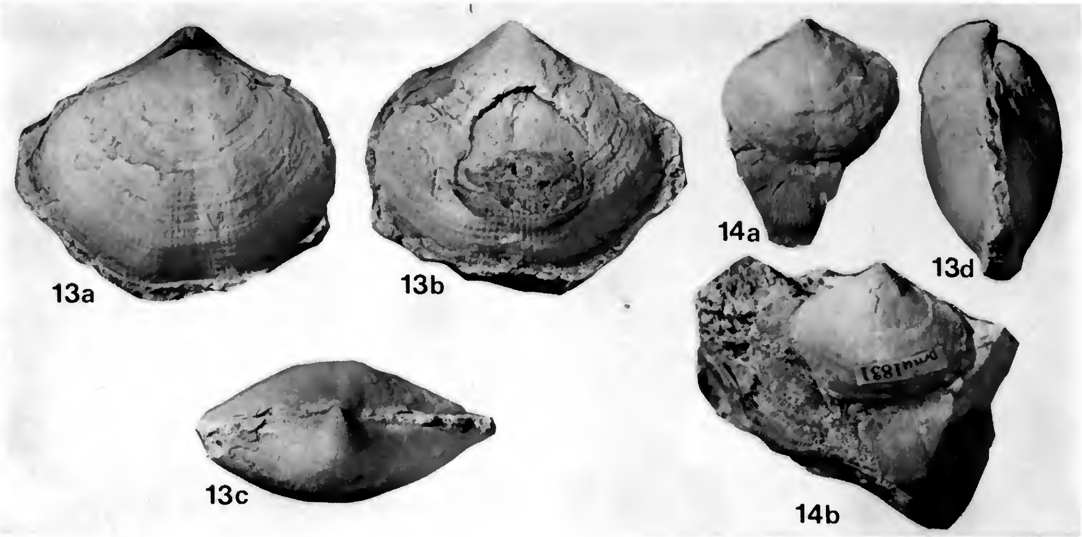
Fig. 12 *Actinoconchus obtusus* (M'Coy), ×1. **Lectotype** (herein selected), from Skerries, Milverton, Ireland. Griffith coll., National Museum of Ireland, Dublin; viewed laterally, ventrally and dorsally. [Here placed provisionally in synonymy with *A. oblongus*].

Actinoconchus lamellosus (Léveillé)
Figs 15–17

1835 *Spirifer lamellosus* Léveillé : 39; pl. 2, figs 21–23.
v* 1836 *Spirifer squamosa* Phillips : 220; pl. 10, fig. 21.
v. 1859 *Athyris lamellosa* (Léveillé); Davidson : pl. 16, figs 1, 1a, b.
v. 1863 *Athyris lamellosa* (Léveillé); Davidson : pl. 51, fig. 14.
1887 *Athyris lamellosa* (Léveillé); de Koninck; pl. 21, figs 1–3, ? 4, 5 (? 6–8) 11, 12.
1965 *Athyris lamellosa* (Léveillé); Boucot, Johnson & Staton *in* Williams *et al.* : fig. 535, 4a, b, c.

Diagnosis. Depressed obovate in outline. Persistent ventral sulcus, with or without shallow dorsal sulcus, and strong rounded uniplicate anterior commissure. Long, radially corrugated shell flanges extending from rugae displaying growth lines.

Type specimens. Léveillé's types appear to be lost (Gaetani 1968 : 711). M'Coy (1844 : 148) synonymized *S. squamosa* Phillips 1836 (**Lectotype** B 309, Fig. 15, in the Gilbertson Coll., BM(NH), herein selected) with *S. lamellosus* Léveillé, 1835, and this has been accepted by most subsequent authors. Léveillé described the species from the shales in the Tournai region, Belgium. A **neotype** (Fig. 16), closely corresponding to Léveillé's figs 21 and 23, and coming from the well-known silicified fossiliferous shales of that region, is here erected. It is from the Piret Coll., BM(NH) Pal. Dept. reg. no. B 20138, and most probably was collected from late Tournaisian (Tn3b) strata.



Figs 13–14 *Actinoconchus planosulcatus* (Phillips). Fig. 13, **lectotype** (herein selected), from Bolland, Yorkshire. Gilbertson coll., BM(NH) B 317, ×1·5 [= *S. planosulcata* Phillips 1836 : pl. 10, fig. 15]. Viewed dorsally, ventrally, posteriorly and laterally. Fig. 14, from Butter Haw Hill, Yorkshire. Mundy coll. 1831, BM(NH) BB 62974, ×0·9. Viewed dorsally, separate from the rock but with part of its flange, and ventrally, as in the rock.

Discussion. The five species assigned above to *Actinoconchus* include all the better known specific names used in nineteenth century western European literature. The type species of the genus, *A. paradoxus*, is distinctive in its subcircular outline and very flat, long shelly flanges, each having radial ornamentation. *A. expansus expansus* grew larger than typical examples of *A. paradoxus*, is broader than long, but had similar lamellose flanges; it could be that *A. expansus* is simply a large form of *A. paradoxus*, and if this proves to be so the name predates that of M'Coy. *A. oblongus* is an unusual species, the like of which, other than Sowerby's type, I have not seen. The length is greater than the width and at the opposed anterior margin the commissure is slightly ligate. In other respects the known features are similar to *A. paradoxus*, and since both came from southern Ireland it may be that *A. oblongus* is an unusually elongate form of *A. paradoxus*. *A. planosulcatus* is characterized by its pentagonal outline and ligate anterior. The name has been much confused and misused, largely because Davidson (1859) applied it to specimens as distinctive as *A. lamellosus* and *A. paradoxus*.

Actinoconchus species are known throughout the Lower Carboniferous of North America, Europe and the Middle East, but seem to be absent from north-eastern USSR and Australia. It does not extend into the Permian.

Genus *CLEIOTHYRIDINA* Buckman, 1906

Diagnosis. Athyridinae with lamellose growth bands bearing flattened spine-like frills.

Type species. *Atrypa pectinifera* J. de C. Sowerby (1840 : 14; pl. 616). Validated by the I.C.Z.N. (1976).

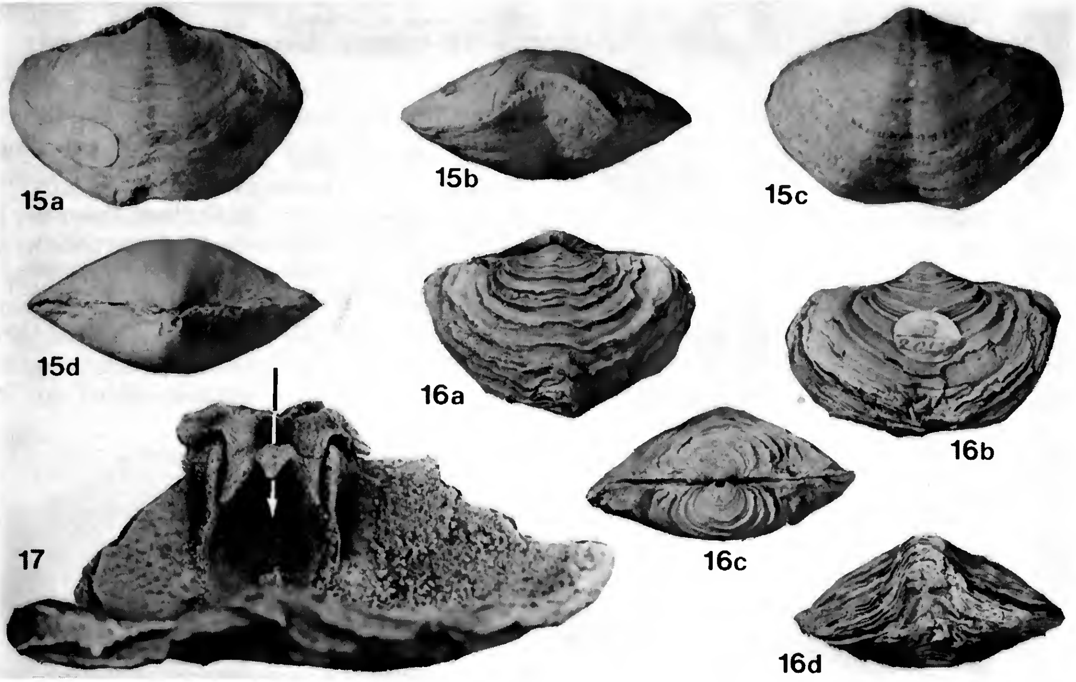


Fig. 15 *Actinoconchus squamosus* (Phillips), ×1·0. **Lectotype** (herein selected), from near Kendal, Cumbria. Gilbertson coll., BM(NH) B 309. Viewed dorsally, anteriorly, ventrally and posteriorly. [Here placed in synonymy with *A. lamellosus*].

Figs 16–17 *Actinoconchus lamellosus* (Léveillé). Fig. 16, **neotype** (herein erected), from the Tournai region, Belgium. Piret coll., BM(NH) B 20138, ×1. Viewed dorsally, ventrally, posteriorly and anteriorly. The well-preserved strongly lamellose ornamentation results from the specimen being silicified. Fig. 17, from the same collection as Fig. 16, BM(NH) BB 62961, ×3. The interior of the umbonal regions of a silicified specimen showing the articulation, dental plates, cardinal plate (perforated at arrow) and pedicle cavity.

Cleiothyridina pectinifera (J. de C. Sowerby)
Fig. 18

v* 1840 *Atrypa pectinifera* J. de C. Sowerby : 14; pl. 616.
1850 *Cleiothyris pectinifera* (J. de C. Sowerby) King : 138; pl. 10, figs 1–10.
1858 *Athyris pectinifera* (J. de C. Sowerby) Davidson : 21; pl. 1, figs 50–56; pl. 2, figs 1–5.

DIAGNOSIS. Small (up to about 15 mm wide), broadly ovate in outline and strongly biconvex in profile. Concentric shell lamellae with spinose frills.

TYPE SPECIMEN. *Atrypa pectinifera* J. de C. Sowerby (1840 : pl. 616, specimen illustrated at the bottom right and centre). BM(NH) Pal. Dept. reg. no. B 61055. Sowerby Coll., from Humbleton Hill, Co. Durham; of Upper Permian age. Here selected **lectotype.**

Cleiothyridina fimbriata (Phillips)
Figs 19–22

1836 *Spirifer fimbriata* Phillips : 220 (no figs).
1843 *Terebratula plano-sulcata* (Phillips); de Koninck : 301 (*pars*); pl. 21, figs 1e, f.
? 1844 *Athyris depressa* M'Coy : 147; pl. 18, fig. 7.
v. 1861 *Athyris Royssii* (Léveillé); Davidson : 84 (*pars*); pl. 18, figs 8–11 (fig. 11 from Phillips' specimen).

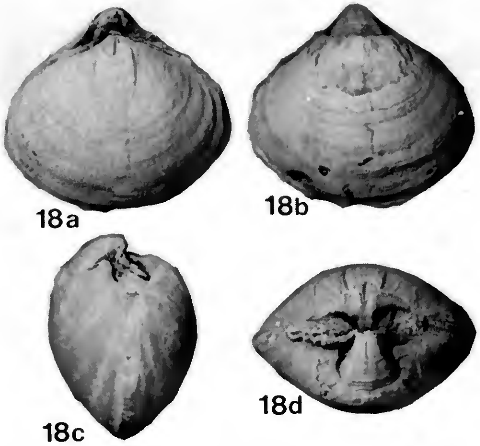
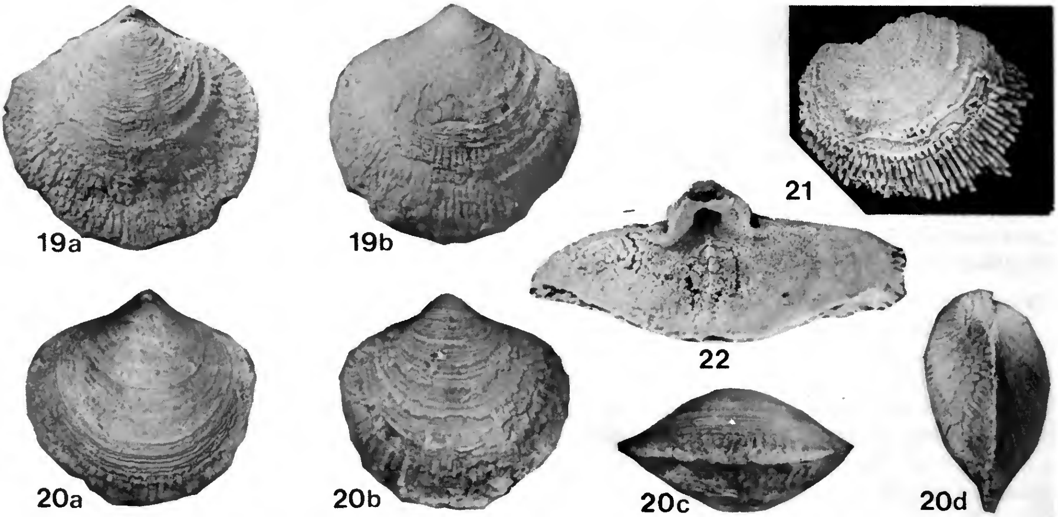


Fig. 18 *Cleiothyridina pectinifera* (J. de C. Sowerby), ×2. **Lectotype** (herein selected), from Humbleton Hill, Co. Durham. Sowerby coll., BM(NH) B 61055. [=*Atrypa pectinifera* J. de C. Sowerby 1840 : pl. 616, bottom centre and right.] Internal mould, viewed dorsally, ventrally, laterally and posteriorly.



Figs 19–22 *Cleiothyridina fimbriata* (Phillips). Fig. 19, **lectotype** (herein selected), from Florence Court, Co. Fermanagh, Ireland. Phillips coll., Oxford University Museum, E 1093, ×2. Viewed dorsally and ventrally. Fig. 20, from Lesmahago, Lanarkshire, Scotland. Davidson coll., BM(NH) BB 62973, ×1·5. Viewed dorsally, ventrally, anteriorly and laterally. Figs 21–22, silicified specimens from near Derrygonnelly, Co. Fermanagh, Ireland. Fig. 21, BM(NH) BB 62975, ×2·5; part of a dorsal valve, showing well-preserved ornamentation. Fig. 22, BM(NH) BB 62976, ×3; dorsal valve interior showing the inner socket ridges and perforated cardinal plate.

DIAGNOSIS. Subcircular to very broadly obovate in outline, with plain, rectimarginate anterior commissure. Thin concentric shell lamellae separate into long spinose frills.

TYPE SPECIMEN. *Spirifer fimbriata* Phillips (1836 : 220). Oxford University Museum, E 1093. Phillips Coll., from Florence Court, near Enniskillen, Co. Fermanagh, Ireland; probably of early D_1 Asbian age. Here selected **lectotype**; replica in BM(NH), Pal. Dept. reg. no. BB 58678.

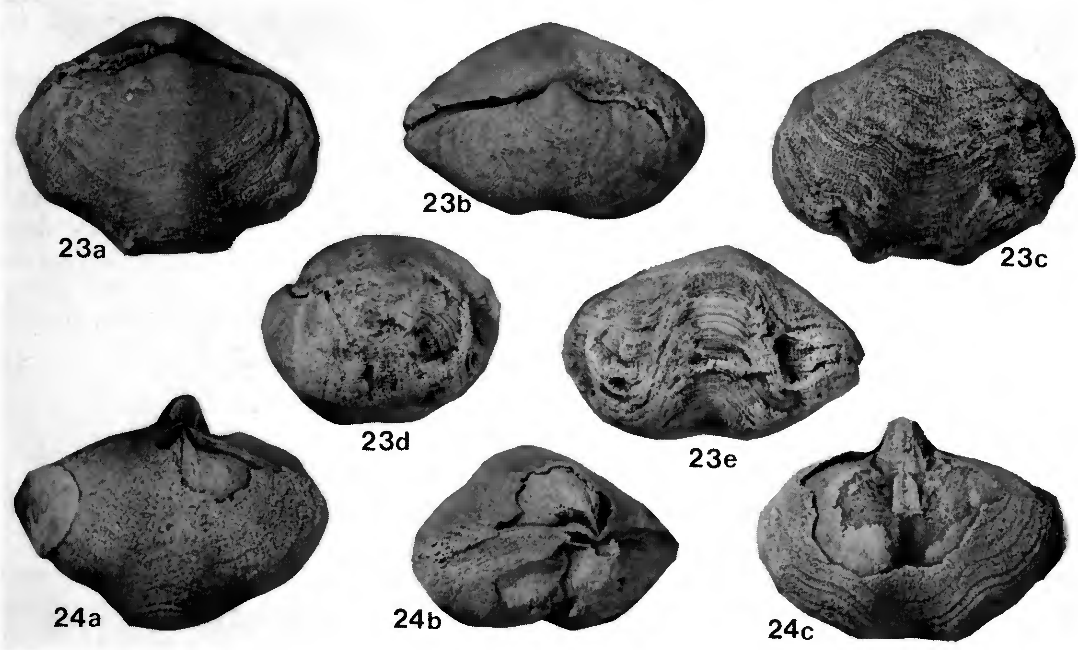
Cleiothyridina deroissyi (Léveillé)
Figs 23–24

1835 *Spirifer De Roissyi* Léveillé : 39; pl. 2, figs 18–20.
1843 *Terebratula Royssii* (Léveillé) de Koninck (*pars*) : 300; pl. 21, figs 1a?, 1b–d.

1887 *Athyris Roissyi* (Léveillé); de Koninck (*pars*) : 82; pl. 19, figs 28, 29.
1887 *Athyris squamigera* de Koninck : 82; pl. 20, figs 16–22.

DIAGNOSIS. Transversely elliptical in outline, strongly biconvex in profile, and with persistent dorsal fold and ventral sulcus forming strongly parasulcate anterior commissure. Pedicle aperture present. Closely spaced, radially aligned, concentric spinose frills. Cardinal process small for genus.

TYPE SPECIMEN. Léveillé's (1835) specimens appear to be lost. In the de Koninck collection, BM(NH), there are specimens with de Koninck's manuscript labels, called *A. squamigera* from the 'carb. sup. Tournay', Belgium. This is the area from which Léveillé described his species, and the specimen here selected as **lectotype** of *C. squamigera* de Koninck (Fig. 23; BM(NH) Pal. Dept. reg. no. BB 62968) is similar to Léveillé's illustrations of *S. De Roissyi*, and is typical of specimens which should now be called *C. deroissyi* (Léveillé) from the Tournai area, probably of late Tournaisian age.



Figs 23–24 *Cleiothyridina deroissyi* (Léveillé), × 1·5. Fig. 23, **lectotype** (herein selected) of *C. squamigera* (de Koninck), from the Tournai region of Belgium. De Koninck coll., BM(NH) BB 62968, viewed dorsally, posteriorly, ventrally, laterally and anteriorly. Fig. 24, from the same collection as Fig. 23, BM(NH) 65002, viewed dorsally, posterolaterally and ventrally showing the internal mould of the umbonal region.

Although this species name is common in the literature, from Davidson's (1861) misuse of the name for *C. fimbriata*, the species is uncommon in Europe, other than at the type area in Belgium. In Britain it forms only a minor constituent of some Viséan faunas. In the United States a closely similar species, *C. prouti* (Swallow), occurs near the Tournaisian/Viséan boundary.

Cleiothyridina glabristria (Phillips)

Fig. 25

v* 1836 *Spirifera glabristria* Phillips : 220; pl. 10, fig. 19.
1861 *Athyris Royssii* (Léveillé); Davidson (*pars*) : pl. 18, figs 1 (repeating Phillips 1836), 2, 4.
1887 *Athyris ingens* de Koninck : 83; pl. 20, figs 1–10.

Diagnosis. Large (*c.* 60 mm wide), depressed obovate in outline with strong uniplicate commissure developed from persistent ventral sulcus. Rugose anteriorly with? short spinose frills.

Type specimen. *Spirifer glabristria* Phillips (1836 : 220; pl. 10, fig. 19). BM(NH) Pal. Dept. reg. no. B 316. Gilbertson Coll., Bolland. Here recognized as holotype.

Discussion. The four *Cleiothyridina* species dealt with here are distinctive in shape. The Permian type species, *C. pectinifera*, is the smallest, reaching about 15 mm in width, the most circular in outline, and remains unfolded. *C. fimbriata* is larger, reaching 20 mm or more in width, and although rounded anteriorly has an unusually transverse posterior margin. The commissure remains rectimarginate. *C. deroissyi* is strongly transverse in outline and strongly uniplicate anteriorly. The spinose frills, so characteristic of the genus, are composed of needle-like 'spines' finer than the flattened ones of the other two species.

Other species names which should be included in *Cleiothyridina* are *C. depressa* (M'Coy, 1844) [?=*C. fimbriata* (Phillips, 1836)] (p. 227); *C. squamigera* (de Koninck, 1851) [=*C. deroissyi* (Léveillé, 1835)] (p. 228); *C. ingens* (de Koninck, 1887), which is probably the non-exfoliated form of *C. glabristria* (Phillips); and three other species names of de Koninck (1887), viz. *C. membranacea*, *C. ornata* and *C. waageni*, the true identities of which are questionable.

Species assigned to *Cleiothyridina* extend from Tournaisian through Carboniferous and Permian strata. Recently Grunt (*in* Sarytcheva 1977) has pointed out that about ten species occur in the Permian, especially late Permian, of the Russian platform. The assignment of the species herein to either *Actinoconchus* or *Cleiothyridina* is based principally on the external ornamentation of the shell. Unfortunately, the interiors of some species are unknown and are likely to remain so through a lack of suitable material for preparation. The use of different shell characteristics would lead to different classifications, but the nature of the shell lamellae is probably a more significant character than, for example, folding and sulcation, which alters during the ontogeny of the individual. The aim here is to provide data on the available species names, not the provision of a tight classification.

Genus *COMPOSITA* Brown, 1849

Type species. *Spirifer ambiguus* J. Sowerby (1822 : 105; pl. 376).

Composita ambigua (J. Sowerby)

Figs 26–28

Type specimen. **Lectotype,** here selected, the specimen, figured by J. Sowerby (1822 : pl. 376, top left) in the Sowerby Coll., BM(NH) Pal. Dept. reg. no. B 61041, from '. . . decomposed Mountain Limestone, near Bakewell . . .', Derbyshire. This, and the other two specimens in the Sowerby Coll., are silicified and partially broken revealing some of the interior (Figs 26, 28). The other two specimens are B 61042 (pl. 376, top right) and B 61043 (pl. 376, middle and bottom). The age of the strata yielding these specimens is probably uppermost Viséan, Brigantian, P_2.

Discussion. In general, European species of *Composita* are most prolific in late Devonian and Carboniferous rocks, especially if some Permian species are transferred to *Spirigerella* Waagen (1883). *Actinoconchus* species are confined to Carboniferous rocks found at low palaeolatitudes while *Cleiothyridina*, with its greatest European diversity in Lower Carboniferous rocks, extends through to the Permian of many areas, and especially the north-eastern U.S.S.R.

Other poorly-known species

Another athyridide species named in the nineteenth century is *Spirifer phalaena* Phillips (1841: 71; pl. 28, fig. 123), described from Hope, near Torquay in south Devon, England. The name was repeated, as *Martinia phalaena* (Phillips), by M'Coy (1844 : 140), but applied to a species distinct from Phillips', as is seen from Davidson's figure (1861 : pl. 18, figs 13, 13a, b) of the Griffith Collection specimen described by M'Coy. Davidson called this brachiopod *Athyris* *squamigera* de Koninck, but it should now be included in the species *Athyris hibernica* Douglas (1909 : 573; pl. 26, fig. 5). *Spirifera phalaena* Phillips is the type species of the Devonian genus *Anathyris* von Peets, 1901, and the type specimen is in the collections of The Institute of Geological Sciences, London, GSM 6866. The Devonian athyridide species related to *Anathyris* are being studied by F. Alvarez of Oviedo, Spain.

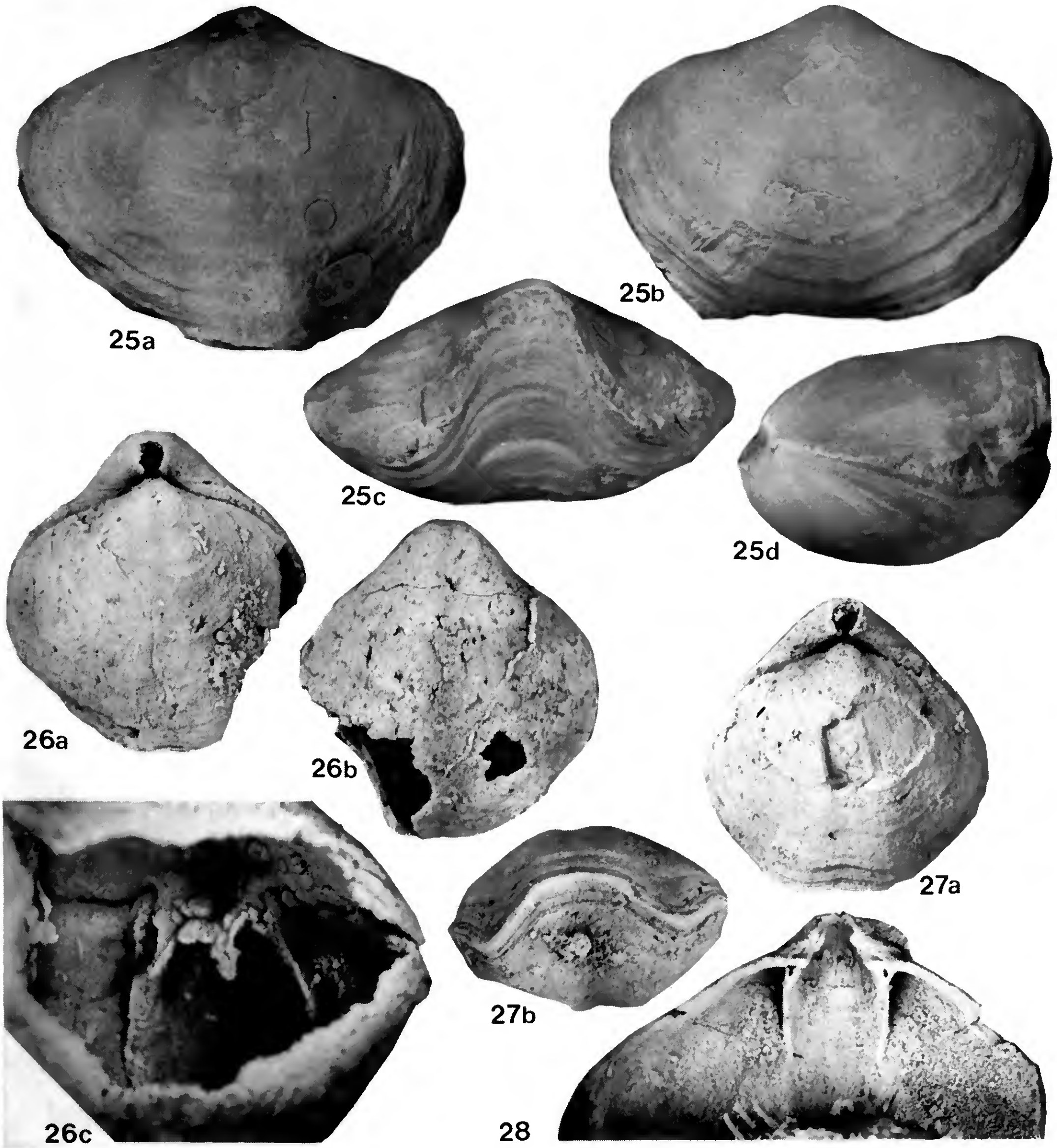


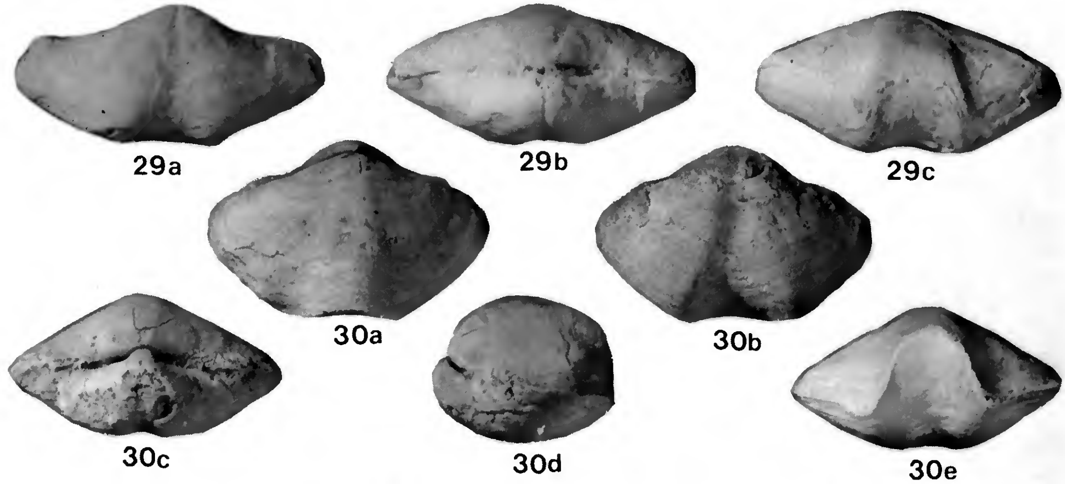
Fig. 25 *Cleiothyridina glabristria* (Phillips), ×1. Holotype from Bolland, Yorkshire. Gilbertson coll., BM(NH) B 316, viewed dorsally, ventrally, anteriorly and laterally.

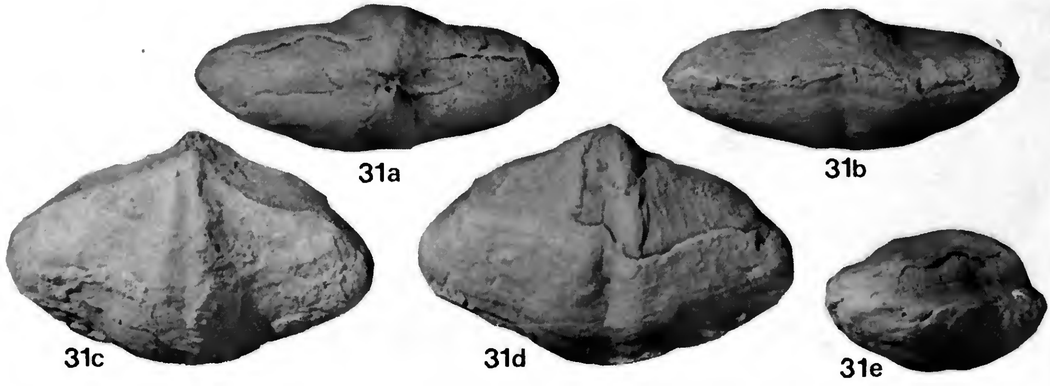
Figs 26–28 *Composita ambigua* (J. Sowerby). Syntypes from Bakewell, Derbyshire. Sowerby coll., BM(NH) B 61041–43. Fig. 26a, b, **lectotype** (herein selected), B 61041, viewed dorsally and ventrally, ×2·5. Fig. 26c the same specimen, umbonal region interior showing the articulation, dental plates, cardinal plate and crura, ×5. Fig. 27, B 61042, viewed dorsally and anteriorly, ×2·5. Fig. 28, B 61043a, ventral valve interior showing the posterior region, ×3.

The type specimen of *A. hibernica* Douglas is in the Oxford University Museum, E 148, with a replica in the BM(NH), Pal. Dept. reg. no. BB 61822 (Fig. 29). The assignment of the species to a more modern genus is uncertain, but it is probably closer to *Actinoconchus* than to *Athyris* or *Cleiothyridina*.

Yet another species name in the literature is *Athyris carringtoniana* Davidson, 1862, known from only three specimens from the Lower Carboniferous (probably mid-Viséan) of Wetton, Staffordshire (Davidson 1862 : pl. 52, figs 18–20). Davidson recorded that this species appeared to be a Carboniferous variety of *A. phalaena* (Phillips), but that it differed from the Devonian species in having a less straight posterior margin, less strongly or widely folded valves, but stronger ribs bordering the median sulci. The **lectotype** (here selected, Fig. 31) of *A. carringtoniana* Davidson is in the Davidson Coll., BM(NH) Pal. Dept. reg. no. B 7882, and was figured by Davidson (1862 : pl. 52, fig. 19). Interestingly, in the United States of America a closely similar and rare species is described as *Athyris papilioniformis* McChesney, from the Mississippian Chester series of Illinois.

The type specimen of *A. phalaena* (Phillips) is poorly preserved and provides no clear understanding of the species. If, however, the concept of the species is extended to include some of





Figs 29–30 '*Athyris*' *hibernica* Douglas, ×1. Fig. 29, holotype from Cratloe, Co. Clare, Ireland. Douglas coll., Oxford University Museum E 148, viewed ventrally, posteriorly and anteriorly. Fig. 30, from Killmallock, Co. Wexford, Ireland. J. Wright coll., BM(NH) B 40302, viewed dorsally, ventrally, posteriorly, laterally and anteriorly.

Fig. 31 '*Athyris*' *carringtoniana* Davidson, ×2. **Lectotype** (herein selected) from Wetton, Staffordshire. Davidson coll., BM(NH) B 7882, viewed posteriorly, anteriorly, dorsally, ventrally and laterally.

the abundant Devonian material from north Spain, it becomes clear that there is much variation in its external shape, and some of these forms resemble *A. carringtoniana* externally. Once the Spanish species have been fully described, and if more specimens of *A. carringtoniana* allow the morphology of the cardinalia and jugum to be discovered, it should be possible to decide whether or not Davidson's species should be included in *Anathyris*. If it does belong here it means that the range of the genus must be extended into the Dinantian; if it does not belong to *Anathyris* the external shape is more suggestive of assignment to *Cleiothyridina* than to other genera.

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Two new British Cretaceous Epitoniidae (Gastropoda): evidence for evolution of shell morphology

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Synopsis

Extensive preparation of the holotype of *Funis crebricostatus* Gardner 1876, from the Upper Campanian, reveals that it has a distinctive and elaborate ornament which justifies the erection of a new genus *Crossotrema*. A recently-discovered high-spired, solely spirally ornamented Albian epitoniid is named *Funis spirornatus*.

Ornament complexity and shell form within the Epitoniidae are discussed and used to suggest possible evolutionary trends within the family.

Introduction

The discovery of two new taxa, while examining material in preparation for a general revision of Cretaceous Epitoniidae, has prompted this short paper.

Apart from considerations of their stratigraphical and geographical distribution, the classification of fossil mollusca is solely dependent upon shell morphology and comparison with living forms. However, the classification of the Recent Epitoniacea is generally regarded as 'being in a complex nomenclatorial tangle' (Clench & Turner 1950 : 223). This confusion is partly the result of a paucity of good material, but has also arisen from the mistaken interpretation of the overlapping characters occurring within the family.

Dushane (1974 : 4) and Robertson (1971 : 62) believe that to classify epitoniids solely on the basis of shell characters is quite inadequate. They advocate a more biological approach utilizing non-morphological information on populations relating to their ecology, biochemistry and behaviour. However, in the restricted field of fossil epitoniids the use of shell ornament provides an acceptable classification.

Recent Epitoniidae are world-wide in distribution, rich in number of species and occur in a remarkable range of depths in all seas. Their fossil record suggests that the family has exhibited these characteristics since the Aptian. Throughout their history, the Epitoniidae appear to have formed a small proportion of the total marine molluscan fauna. However, during the Cretaceous this proportion appears to have comprised numerous individuals of a small number of species, whereas since the Eocene they are represented by a richer variety of species but with relatively fewer individuals. In general, Cretaceous species were much larger than later forms, particularly Recent ones. The majority of Cretaceous species have ornament composed of strong axial ribs and fine spiral cords above a marked basal keel. These features are characteristic of *Confusiscala* De Boury 1909, a genus to which many species have been assigned. Clench & Turner (1950 : 223) commented that the diversity shown by the Epitoniidae, both in the past and present, indicated that they were and are still 'an exceedingly vigorous family'.

The available descriptive literature on British Cretaceous Epitoniidae is virtually restricted to the original work of J. Starkie Gardner (1876). Particular species have been described by others in general works, e.g. J. de Carle Sowerby *in* Fitton (1836) and *in* Dixon (1850), and by Seeley (1861), but no other appraisal of the family has been attempted.

There has been little research on the fossil occurrence of this family outside Britain except for the notable reviews of De Boury (1890–1917) and Cossmann (1912); shorter contributions have been made by Wollemann (1908), Durham (1937) and Sohl (1964).

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It is the great rarity of fossil epitoniids that has convinced me of the need to describe these unique, but incomplete, British Cretaceous specimens, in the belief that other examples are unlikely to be discovered. I am not aware of any similar material in the collections of the Institute of Geological Sciences, the Sedgwick Museum, Cambridge, or the University Museum, Oxford.

Systematic Descriptions

British Museum (Natural History) register numbers are given of all the specimens figured. Specimens with numbers prefixed by G or GG are fossils in the Department of Palaeontology; other numbers refer to the Recent Mollusca collections of the Department of Zoology.

Class **GASTROPODA** Cuvier, 1797

Superfamily **EPITONIACEA** Berry, 1910

Family **EPITONIIDAE** Berry, 1910 [Lamarck, 1812 (? 1811), vernac.]

Genus ***CROSSOTREMA*** nov.

TYPE SPECIES. *Funis crebricostatus* Gardner 1876, designated here.

DIAGNOSIS. Moderately large, elongate turreted shell with strongly convex, firmly joined whorls. Elaborate axial and spiral sculpture, of equal significance, consisting of crenulate frilled opisthocyrt collabral lamellae and primary and secondary spiral cords. Lamellae alternate on adjacent whorls, obscuring the impressed suture. Whorls lacking varices; imperforate.

NAME. Greek, κροσσωτός, flounced, frilled + τρῆμα, a hole, aperture.

REMARKS. The complicated sculpture of *Crossotrema* (described below), suggests some relationship with the living genus *Cirsotrema* Mörch, 1852 (Fig. 3), but the lack of varices readily distinguishes *Crossotrema* from all other cirsotremids. Its apparent lack of either a marked basal disk, cord, or carination supplied another distinctive character. The alternation of its axial lamellae on adjacent whorls differs from the virtually continuous ornament exhibited by many Tertiary and Recent cirsotremid species, as a result of the coalescence of the axial ribs on neighbouring whorls.

Crossotrema is separated from *Cirsotremopsis* Thiele, 1928 by the latter's turreted outline, deep sutural channel and relatively weaker development of spiral sculpture. Yet, the comparable nature of their complex ornament (explained below) indicates a close affinity.

Investigations of other epitoniids, e.g. in the Australian Tertiary (Tate 1890), possessing ornament of axial lamellae revealed that such sculpture was dissimilar to that of *Crossotrema*. The North American Cretaceous species placed in *Striaticostatum* by Sohl (1964 : 317) have axial ribs composed of multiple lamellae; they can be further distinguished by the presence of a basal disk, an outer lip varix and only weak development of spiral sculpture.

Inevitably, *Crossotrema* has ornamental components in common with the epitoniids *Amaea* H. & A. Adams 1853 (see Fig. 14), *Amaea* (*Scalina*) Conrad 1865 [= *Ferminoscala* Dall 1908] and *Epitonium* (*Asperiscala*) Boury 1909, but the characteristic rectangular reticulate sculpture shown by the shells of all these Recent genera confirms their distinct identities.

Cossmann (1912 : 17), when he outlined the significance of the basal disk in the shell morphology of the Epitoniidae, began by stressing the great variability shown by this feature within the family. Although the basal disk, or its other manifestations such as basal cord and basal angulation, are used to distinguish taxa at several levels in Epitoniidae classification, this variability in strength and structure makes it an unreliable indicator of relationship (Clench & Turner 1951 : 250).

The key to the Epitoniidae provided by Burch (1956) utilized fine differences in the nature of the basal disk and ornamental varices to separate the various taxa mentioned above, but it is largely confined to considerations of Recent genera. If this key were followed, the absence of both varices and basal disk in *Crossotrema*, together with its equal development of both spiral and axial ornament, would separate it as a genus. The intricate and delicate ornament enables *Crossotrema* to be distinguished from all other Cretaceous epitoniids that have simpler and coarser axial ribs and are placed in either *Claviscala* Boury 1909 or *Clathroscala* Boury 1890*b*.

Cossmann (1912 : 53) recorded *Cirsotrema* (*Coroniscala*) *tournoueri* (Briart & Cornet 1877) [= *C. briarti* (Boury 1890*a*)], from the Montian of Belgium, as the earliest cirsotremid. However, the recognition that '*Funis*' *crebricostatus* Gardner is a cirsotremid extends the range of the group firmly back into the Cretaceous. The relative equality of both its axial and spiral sculpture elements would conform with the expected ornament of an ancestral form, although the elaborate frilled lamellae must be considered to represent a specialized character. This last feature, particularly the occasional occurrence of composite lamellae in the ornament of *C. crebricostata*, leads to the conjecture that it might be precursory to the cellular varices and multilayered lamellae occurring in the Cretaceous (Maastrichtian) *Striaticostatum*, Tertiary *Cirsotremopsis* and Recent *Cirsotrema*. Particular examples of Recent species with such features would be *C. togatum* Hertlein & Strong 1951, and the extreme development occurring in *C. dalli* Rehder 1945. The ornament in all these taxa consists of different combinations and degrees of emphasis of the same basic components as are present in the earlier genus *Crossotrema*. Extending this argument it is also possible to speculate that Recent *Amaea* (*Scalina*) may have a common ancestry with the genus. The occurrence of intermediate forms in the East African Neogene (see p. 240) and the Upper Cretaceous of north Africa (Abbass 1963, Wanner 1902), support such a view. Cossmann (1912 : 53) had considered that the genus *Cirsotrema* had achieved a cosmopolitan distribution by the Eocene. Rehder (1945 : 127) later postulated a geographical basis for grouping the numerous species assigned to this genus and also recognized stratigraphical restrictions. He indicated that true *Cirsotrema*, type species *C. varicosa* (Lamarck 1822), Fig. 3, was restricted to the Indo-Pacific region.

The only apparent anomaly in this argument is the lack of the distinctive cirsotremid features such as varices and basal disk in the single specimen assigned to *Crossotrema*. Yet, remembering the remarks of Cossmann (mentioned above) on the extreme variability of these features this is not so remarkable, nor is the fact that other Albian epitoniids had evolved a distinctive basal disk.

Crossotrema crebricostata (Gardner 1876)

Figs 5, 9

1876 *Funis crebricostatus* J. S. Gardner: 111; pl. 3, fig. 18.

MATERIAL. Holotype (and only specimen), BM(NH) Dept. of Palaeontology no. G 19065. J. S. Gardner coll.

LOCALITY AND HORIZON. Norwich, Norfolk; Chalk, Upper Campanian, Mucronata Zone.

DIMENSIONS.		
Actual height of incomplete specimen		= 27·6 mm
Estimated height of complete spire		= 59 mm
Diameter of whorl:	1st	= 14 mm
	2nd	= 17·3 mm
	3rd	= 21·9 mm (part cast, part shell)
External spire angle of preserved whorls		= 21°[1]

ORIGINAL DESCRIPTION. 'Shell elongated, angle 25°; whorls inflated and rounded; ribs numerous, probably twenty to twenty-five, very thin and salient; striae exceedingly strong and prominent, about one-third closer together than the ribs, which they cross, forming nodes at the intersections; suture indistinct. The height and prominence of the striae which is nearly as great as that of the ribs, give the shell a reticulated appearance, whilst the nodes at the frequent intersections give it a rugose aspect. There are very faint traces of ornamentation preserved on the cast' (Gardner 1876 : 111).

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[1] This is an approximation owing to the fragmentary nature of the specimen.

Description. The only specimen is lacking its early whorls and aperture. It consists of slightly more than two whorls of which only the shell of one side is preserved, the remainder being merely an internal mould with vestiges of the sculpture. The whorls are strongly inflated and joined, although separated by a deep, impressed suture that is obscured by the adapical curvature of the lamellae. There is some indication that the most abapical cord forms a slight basal ridge.

The shell ornament consists of elaborate and delicate axial lamellae (numbering 10, 11 and 12 on successive half-whorls) and spiral cords (Fig. 9). Shell growth from within the aperture culminates in thin frilled collabral lamellae. At the apertural margin, shell growth is reflected outwards and backwards to form a narrow flange, which appears to be normal to the whorl side and composes the lamella. Many become broken, producing a ragged and irregular appearance. These lamellae are opisthocyrt and their curvature is grossly accentuated at the adapical suture. The size of their crenulations is influenced by the spiral cords and is strongest towards the centre of the whorl, but weakens considerably adapically. The lamellae are seldom aligned, but generally alternate with those on adjacent whorls; occasionally coalescence occurs between those of successive whorls. Sometimes several lamellae emanate from virtually the same aperture, producing a composite reticulate network. Incomplete preservation of the shell prevents an accurate assessment of the frequency of this feature, but only a single instance is visible on each whorl and these are not aligned.

Spiral sculpture consists of strong double cords corresponding to the crest of each lamellar crenulation. The two cords, the abapical being slightly the weaker, are separated by a narrow groove. Nineteen composite cords are visible on the second preserved whorl, with the strongest eleven on the whorl side. The other eight weaken progressively towards the adapical suture. Interspaces are slightly broader than the two primary cords and secondary cords occur at their centre. All the spiral cords are crossed by fine collabral threads, which produce a slight beading on the primary cords and a lattice across the separating groove.

The base of the shell is not adequately preserved, but the lamellae extend part-way onto it and weaken. An umbilicus is not present.

Remarks. *Preparation.* Preliminary examination of the holotype suggested that more of the specimen might be embedded within the chalk matrix. The use of an S. S. White Airabrasive tool confirmed that part of the shell ornament was perfectly preserved[2]. In preparing the specimen, F. M. P. Howie of the Palaeontology Laboratory, BM(NH), used sodium bicarbonate (abrasive powder no. 4), and to minimize damage to the fragile frills of the shell kept the pressure of the carbon dioxide carrier gas between 10 and 20 psi. After cleaning, the exposed shell was hardened by using a three percent weight per volume solution of 'Butvar B98' in isopropanol.

Discussion. Although Gardner (1876) emphasized that only traces of ornament were preserved, the subsequent preparation of the holotype has revealed that this interpretation was inaccurate. The delicate, frilled sculpture immediately distinguishes *Crossotrema crebricostata* from the

[2] Hitherto rare examples of calcite preservation have only been known from the hard Irish Chalk of Co. Down.

Fig. 1 *Confusiscala dupiniana* (d'Orbigny 1842). Upper Greensand, Sidmouth, Devon. G 44. ×2. (Shell composed of inflated convex whorls).

Fig. 2 *Amaea decussata* (Lamarck 1801) [= *Cirsotrema kieneri* (Tapparone-Canefri, 1876)]. Recent Mauritius, Indian Ocean; C. T. Trechmann coll. 1979252. ×2. (Lacks varices, has rectangular ornament pattern). See also Fig. 7.

Fig. 3 *Cirsotrema varicosa* (Lamarck 1822), type species of *Cirsotrema*. Recent, collected under stones at low water, Bulusan, Province of Albay, Isle of Luzon, Philippines; Hugh Cuming collection 228/3. 1979253. ×2.

Fig. 4 ? *Crossotrema* sp. [= '*Epitonium*' *kieneri* (Canefri); Cox *in* Weir 1938 : 65]. Pliocene, cliff at Tanga, Tanganyika (Tanzania); coll. G. M. Stockley, 1929. G 49523. ×2. See also Fig. 8.

Fig. 5 *Crossotrema crebricostata* (Gardner 1876), holotype. Chalk, Upper Campanian, Mucronata Zone, Norwich, Norfolk; J. S. Gardner coll. G 19065, ×3. (Opposite side to that figured by Gardner 1876: pl. 3, fig. 18). See also Fig. 9.

Fig. 6 *Claviscala clementina* (Michelin 1833). Gault, Albian, Folkestone, Kent; history unrecorded. G 71938. ×1·25. (High-spired, elongate shell, narrow whorls). See also Fig. 10.

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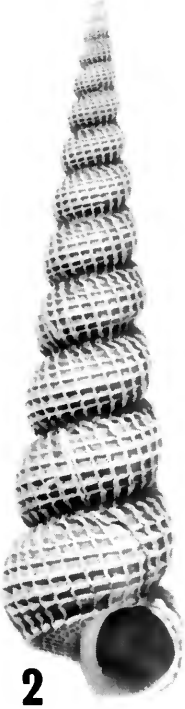

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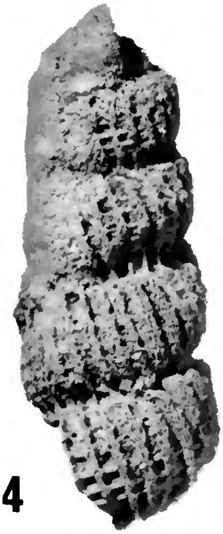

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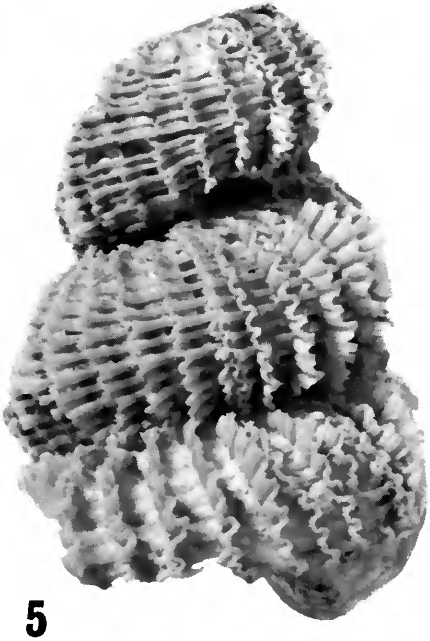

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essentially spirally-ornamented species included in *Funis* by Gardner (1876 : 111) and Cossmann (1912 : 73). Furthermore, *crebricostata* cannot be included in the genus *Funis* Seeley 1861, for its whorls are not elongate nor are they separate.

Affinities with and separation from the living genus *Cirsotrema* and other Recent and fossil forms have been discussed above. A very small and little-known Recent species, *Discoscala edgari* Boury (1912 : 90–3), from Macclesfield Bank, China Sea, has closely similar frilled axial lamellae and the same general round-whorled shell. It is difficult to discern any spiral ornament on Boury's poor figure (1912 : pl. 7, fig. 3), but its possession of a marked basal disk would separate the two species.

Two specimens from the Pliocene of Tanzania, BM(NH) nos G 49522–3, Figs 4, 8, have considerable sculptural resemblance to *Crossotrema* in that their ornament is composed of lamellar axial ribs and both primary and secondary spiral cords. Their slender, high-spired shell and development of a strong basal cord also makes them very reminiscent of the Recent '*Cirsotrema*' *kieneri* (Tapparone-Canefri 1876) from the East Indies, NW Australia and Indian Ocean. This similarity led L. R. Cox (*in* Weir 1938 : 65, 68) to refer these two African fossils to that species. The structural components of the ornament in *kieneri* suggest a common ancestry with *Crossotrema*, while its multiple lamellar ribs also indicate some affinity with the North American Cretaceous genus *Striaticostatum* Sohl.

The confusion in epitoniid nomenclature is well illustrated by this example. '*Cirsotrema*' *kieneri* appears to be virtually indistinguishable from another Indo-Pacific species *Amaea decussata* (Lamarck 1801, 1804), Figs 2, 7. This species, in turn, can only be distinguished from the Panamic–Galapagan species *A. deroyae* Dushane and the eastern Atlantic species *A. retifera* Dall by its slightly more convex whorls and the smaller size of the two American species. The latter are essentially separated by their geographic occurrence (Clench & Turner 1950 : 245, Dushane 1974 : 54). Elsewhere, Wagner & Abbott (1978 : 08-204) have recognized two further species of Indo-Pacific epitoniids as synonyms of *kieneri*, but placed the species in the subgenus *Amaea* (*Elegantiscala*).

Genus *FUNIS* Seeley, 1861

Type species. *Funis elongatus* Seeley 1861, by subsequent designation of Gardner 1876 : 10 —see Figs 12, 13.

Emended diagnosis. Slender, very elongate imperforate shell with joined whorls. Narrow, elongate rounded whorls form a loosely-coiled spiral and are separated by an impressed and partly grooved suture. Spiral cords form dominant sculptural element; axial ornament reduced and when present restricted to collabral threads. Basal ridge present and may be accentuated by spiral furrow. Ovate aperture with simple outer lip and inner lip not recurved.

Distribution. U.K.; *F. elongatus* Seeley: Upper Albian, Cambridgeshire; *F. spirornatus* sp. nov.: Albian, Bedfordshire.

Remarks. Seeley when describing this genus placed it in the Melaniadae (*sic*; = Thiaridae) on the basis of a comparison with *Melania* and *Melanopsis*, though noting the similarity of its axial ribs to those of the 'Scalidae'. Gardner (1876 : 110) was the first to recognize that *Funis* belonged to the Epitoniidae. Cossmann (1912 : 23, 72) included the genus in his subfamily Clathroscalinae on the basis of supposed apertural and ornamental features, while he included *Amaea* in his

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Fig. 7 *Amaea decussata* (Lamarck 1801). Same specimen as in Fig. 2, enlarged to show nature of axial ornament; note occasional close repetitive development of ribs. 1979252. ×5.

Fig. 8 ? *Crossotrema* sp. [='*Epitonium*' *kieneri* Cox 1938]. Same specimen as in Fig. 4, enlarged. Note composition of ornament and composite structure of axial ribs identical to Fig. 7. G 49523. ×3·6.

Fig. 9 *Crossotrema crebricostata* (Gardner 1876), holotype. Same specimen as in Fig. 5, enlarged to show detail of ornament; note occasional repetitive axial ornament, especially that at mid-whorl of central whorl. G 19065. ×5.

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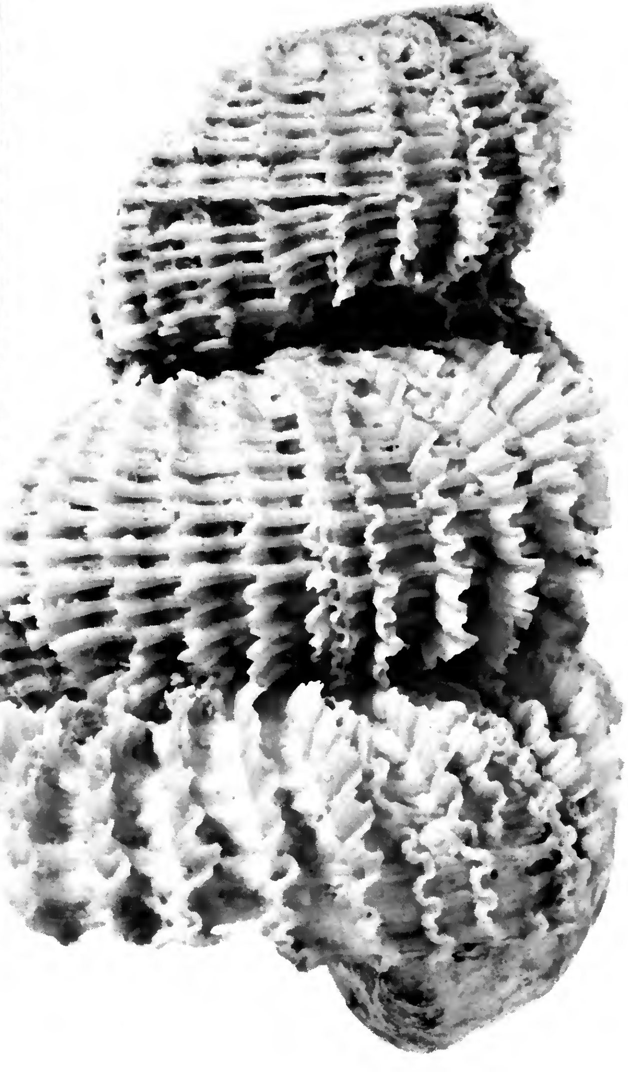

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Acrillinae. Later, Wenz (1939 : 803) incorporated *Funis* as one of sixteen subgenera listed under *Amaea* H. & A. Adams 1853, a position that reflects something of its true relationship even though many of the accompanying taxa have been re-assigned.

The inadequacy of the general characters originally used to define the genus was appreciated by both Gardner and Cossmann. The poorly preserved and incomplete material of the only species of which there were numerous examples, *F. elongatus*, contributed to that situation. The principal features in common with those of other Cretaceous Epitoniidae are its slender, elongate, imperforate shell, the rounded convex whorls, deeply impressed suture and ovate aperture.

The general shell morphology and the lack of strong axial ornament in *Funis* immediately relates it to *Amaea*. It can be distinguished from Recent *Amaea* s. str. by its more elongate whorls and smaller spiral angle. In comparison, the shell of *Funis* has a higher growth translation rate and lower expansion rate, while the generating curve is much closer to the axis of coiling. The resulting more loosely-coiled shell is further accentuated by a furrow occurring abapically at the suture, which may be described as 'grooved' rather than incised or impressed as in *Amaea*. Ornament in *Funis* is generally coarser than that of *Amaea*. Neither species of *Funis* appears to have a recurved inner lip as occurs in the type species *Amaea magnifica* G. B. Sowerby 1844 (Fig. 14). The apparent restriction of *Funis* to the Cretaceous, together with the morphological differences described above, would seem to warrant its consideration again as a full genus. However, several Cretaceous epitoniids described from Europe and north Africa indicate the contemporaneous existence of more-typical *Amaea*-like forms. A distinctive Recent Pacific–Galapagan species, *A. contexta* Dushane 1970, is shaped very similarly to the two *Funis* species and serves to emphasize the difficulties in classifying epitoniids on shell morphology.

From the species listed by both Gardner (1876 : 111) and Cossmann (1912 : 72), only the type species can still be accepted as a member of the genus. Gardner considered that *F. brevis* had to be regarded as a variety of *elongatus*; *F. crebricostatus* Gardner has now become the type species for the new genus *Crossotrema* (p. 237). The wider spiral angle and consequently broader and flatter whorls of *F. cancellatus* Gardner, from the Gault of Folkestone, suggests it would be better placed in *Amaea*.

Although cancellate ornament characterized those species originally placed in *Funis*, the distinctive ornamental trait of the genus would now appear to be the reduced significance of its axial component. Axial ornament is never dominant and in the new species described below it is limited to the collabral threads. The basal ridge or cord, although well-defined, is not as strong as that in *Amaea* and consequently *Funis* cannot be considered to have a true basal disk. Ornament below this ridge may differ from that on the whorl sides in the same manner or degree, as occurs in species of *Amaea*.

Funis spirornatus sp. nov.

Fig. 11

MATERIAL. Holotype (and only specimen), BM(NH) Dept. of Palaeontology no. GG 20892. Collected by R. J. Hogg.

LOCALITY AND HORIZON. Double Arches Pit (National Grid reference SP 939290), near Leighton Buzzard, Bedfordshire. Creamy-white limestone lenticle, Shenley Limestone, Cretaceous, Albian, Regularis Zone.

DIMENSIONS. Actual height of incomplete specimen = 50·5 mm
Estimated height of complete spire = 120 mm
Approximate height of last whorl = 25·7 mm
Diameter of last whorl = 19·3 mm
Height of aperture = 14·5 mm
External spire angle = 10°

DIAGNOSIS. Slender, very elongate shell characterized by ornament of dominant spiral cords and with axial component of ornament limited to collabral threads on its evenly biconvex whorls; whorls separated by an impressed suture which conceals a basal carina.

NAME. 'Ornamented with spirals'.

DESCRIPTION. This single, incomplete specimen shows four whorls of a moderately large, slender shell. The strongly convex whorls (widest at mid-whorl) are firmly joined, but separated by an impressed suture.

The whorl sides are ornamented by nine irregularly-spaced, spiral cords that vary in strength. The three mid-whorl cords are the strongest, while the first, third and seventh (from the adapical suture) are the weakest and are barely stronger than the intervening secondary cords. The secondary microscopic sculpture consists of irregularly positioned, very fine spiral threads lying between the primary cords. Fine opisthocyrt collabral growth lines cross the spirals and represent the only axial element; they are most apparent in the interspaces. The ninth primary spiral cord forms a basal angulation while the furrow between this and the eighth cord accentuates the suture.

The base of the whorl is ornamented by a further eight or nine spiral cords, of varying strength, which become progressively closer as they approach and virtually extend onto the inner lip. Neither the inner nor outer lip is preserved, but the aperture is distinctly ovate. An umbilicus is clearly not present.

REMARKS. Though attributed to the Epitoniidae, this species superficially exhibits features that are characteristic of the Turritellidae. The elongate, essentially spirally ornamented shell is reminiscent of the Turritellidae, which are more common that the Epitoniidae in the Upper Cretaceous. Yet the strongly inflated, convex whorls are quite distinct from the essentially flat-sided whorls of typical turritellids. The helical base of *Funis spirornatus* is clearly distinct from the relatively flat-bottomed whorls of '*Turritella*'; and its opisthocyrt growth lines are more evenly curved than those present in Cretaceous turritellids. The occurrence of this fossil in an assemblage in which epifaunal species predominante and in which epitoniids are relatively rare (only twenty specimens in a collection of more than five hundred molluscs), suggests that it is unlikely to belong to the infaunal Turritellidae that generally occur and are collected as fossils in large numbers.

The unusual predominance of spiral cords combined with the narrow spiral angle, resulting in tall whorls and a slender shell, distinguish this species from all other epitoniids. In other Cretaceous epitoniids, axial ornament is generally dominant, but two examples with cancellate sculpture require consideration. The loosely coiled whorls, high spire and whorl shape of *Funis elongatus* Seeley 1861 (Figs 12, 13) described from the Cambridge Greensand resemble the features of *F. spirornatus*. Although the majority of the specimens of *elongatus* are preserved as internal phosphatic mould fragments, its cancellate sculpture is readily apparent. A few show the ornament is composed of primary and secondary cords and slightly raised prosocline axial costae. The strength of these various elements can be extremely variable, resulting in the ornament ranging from a fine network to a much coarser trellis. Worn specimens indicate that the costae might be crenulate and better-preserved examples show that these costae become blade-like and alternate with those of adjacent whorls at the suture. The spiral cords, even those at the coarse end of the range, appear to be finer than those that occur in *spirornatus*. The adapical cord does not form a carina as is exaggeratedly shown in Seeley's original illustration (1861 : pl. 11, fig. 7). In contrast to *F. spirornatus* the whorl of *F. elongatus* is widest below the mid-whorl line.

Shell morphology and ornament in the Epitoniidae

The presence of these two species in the Cretaceous demonstrates that a much wider range of shell ornament occurred within the Epitoniidae at that time than had previously been suspected. The high-spired shell and elongate whorls of *Funis spirornatus* are reminiscent of the Zygopleuridae from which Cossmann (1912 : 19–20) postulated the Epitoniidae may have been derived. As indicated above (p. 240), *Crossotrema crebricostata* with its elaborate sculpture is a probable ancestor of the later and more specialized forms of Recent *Cirsotrema*. At present, there is no link between the Lower Albian epitoniids, e.g. *Confusiscala* with relatively simple ornament (Fig. 1) and the Upper Chalk ornate *Crossotrema*. Nor is there any evidence concerning the development of the characteristic basal disk present in the Gault epitoniids.

Many authors have emphasized our inability to interpret the functional significance of shell geometry. Among them, Raup (1966) stressed that consideration of surface sculpture is also required to complete such understanding. Vermeij (1971*b*) provided a model for the expression of shell sculpture in geometrical terms, used this to show why particular sculpture developed and indicated its ecological benefits. The function of elaborate shell ornament, particularly in those cases where a secondary shell surface is developed as in *Cirsotrema dalli* Rehder 1945 (for description see Clench & Turner 1950 : 226; pl. 98, figs 1, 3), might be attributed to the protection it affords from predation, or possibly encrustation. Alternatively the two-layered shell ornament could be a method of strengthening the shell without involving any undue increase in weight.

The significance of the typical epitoniid varix has only recently been understood and, presumably, the multicellular varix is simply a structural modification. The textbook definition of a varix is generally given as 'a periodic growth resting stage, marked by a thickening of the outer lip' (Keen 1971 : 916, Arnold 1965). Vermeij (1978), in his research on patterns of adaptation in gastropods, illustrated several examples in which varices benefitted the mollusc, indicating that the structure had developed a more particular function.

Vermeij mentions the work of Palmer (1977), who concluded that the varices in the muricid *Ceratostoma foliatum* had a stabilizing function and afforded some degree of protection against predatory fish. Elsewhere, Vermeij (1977, 1978 : 42–50) and Zipser & Vermeij (1978) give the results of their work on the crustacean predation of gastropods. This revealed that strong sculpture was effective against crushing and that apertural thickening at the outer lip provided resistance against the lip-peeling sand crabs of the Calappidae. The measurements of shell thickness provided revealed that a very small margin marked the difference between protection and predation. Ankel (1938) is quoted by Dushane (1974 : 5) as suggesting that the costae are a defence against boring naticids; she noted in support that few epitoniids showed damage from such predators.

The varix needs to be examined as a significant evolutionary character within the Epitoniidae; it would appear to provide another instance of pre-adaptation, in which a particular feature has changed, or extended its function. Cursory examination of Tertiary species suggests that typical epitoniid varices first occur in the Eocene, e.g. in *Cirsotrema gassinense* Sacco (1891 : pl. 2, figs 1–2), with more elaborate varices developing in Middle Miocene species, e.g. *Cirsotrema rusticum* (Defrance) and *C. miovaricosum* Sacco (1891 : pl. 2, figs 32, 35). An irregular widening of a rib occurs in some early Tertiary epitoniids, e.g. *Scalaria lamellosa* Brocchi [=*S. fimbriosa* S. V. Wood] and might represent a transitional stage.

As further support for the contention that only further biological research and observation of modern Epitoniidae will overcome the deficiencies of an existing classification based solely on shell shape, the observations of two Recent workers have contributed to our understanding of epitoniid shell morphology. Dushane (1974 : 7) classified living Panamic–Galapagan Epitoniidae with a height (i.e. length of shell) greater than 10 mm as being 'large'. A total of 36 of the 68 species she described fall within this category, but only nine species exceed 30 mm in height and not one attains 50 mm.

The initial impression gained from examining Cretaceous species is that early members of the family were exceptionally large and often exceeded 50 mm in height (see Table 1, p. 246).

Linsley (1977, 1978*a*, *b*) in his research on gastropod shell form, its evolution and influence on locomotion, concluded that modern Epitoniidae are, in his terminology, 'shell carriers', i.e. that they balance the shell at an angle above the body. This has enabled them to become relatively fast-moving gastropods (Linsley communication in seminar at BM(NH), 1978). On applying this to Cretaceous epitoniids, it seems very probable that those with long (i.e. 'high') shells, e.g. *Claviscala clementina* (Figs 6, 10) could only have been 'shell draggers' somewhat similar to modern *Terebra*. *Terebra*, however, is essentially infaunal, dragging its shell just below, or occasionally protruding through the surface of its habitat of clean sand (J. D. Taylor, personal communication). It seems unlikely that the Lower Albian epitoniids lived in the dark clay sediment in which they are found; presumably they occupied a more amenable neighbouring substrate. Yet, equally, it is difficult to conceive that such exceptionally high-spired shells were essentially epifaunal. It would appear that the small-sized animal occupying the limited space afforded by

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Fig. 10 *Claviscala clementina* (Michelin 1833). Gault, Albian, Folkestone, Kent; colld J. W. Butler. G 23792, ×1·7. See also Fig. 6.

Fig. 11 *Funis spirornatus* sp. nov., **holotype.** Creamy-white limestone lenticle, Shenley Limestone, Albian, Regularis Zone; Double Arches Pit, near Leighton Buzzard, Bedfordshire; colld R. J. Hogg. GG 20892. ×1·4.

Figs 12, 13 *Funis elongatus* Seeley 1861. Cambridge Greensand, Cenomanian, Cambridge; T. Jesson coll. Fig. 12, G 20745, ×2; Fig. 13, G 8757a, ×2·9.

Fig. 14 *Amaea magnifica* (G. B. Sowerby 1844), type species of *Amaea*. Recent, Awaji, Japan; C. T. Trechmann coll., *ex* Y. Hirase coll. 1964471. ×1·7

Table 1 Height (mm) of specimens of Cretaceous Epitoniidae in the Dept. of Palaeontology, BM(NH). *Estimated height

'*Scalaria*' *canaliculata* d'Orbigny [=*Confusiscala*]		
Aptian, Isle of Wight	28247	72
	G 9297	66
Claviscala clementina (Michelin)		
(i) Albian, Gault, Folkestone	G 71938	101
	several others exceed	70
(ii) ,, Regularis nodules, Arnold's Pit, Leighton Buzzard	GG 5984	101*
	others in excess of	70
(iii) ,, Double Arches Pit, Leighton Buzzard	GG 20938	42*
Confusiscala dupiniana (d'Orbigny)		
(i) Albian, Gault, Folkestone	G 71944	70*
(ii) ,, Upper Greensand, Blackdown	G 71071	49
(iii) ,, ,, ,, Sidmouth	G 44	53

such a narrow shell would certainly not be able to carry such a burden, but the lack of any indication of wear that could be associated with dragging, on the few complete fossils available, does not support this view.

Other studies provide confirmation that shell dragging locomotion is adopted by some epitoniids. In her analysis of locomotion in prosobranch gastropods, Miller (1974*a*, 1974*b*) recorded that *Opalia wroblewskii* progresses by means of indistinct arythmic locomotion, with only the most anterior part of the foot moving forward before dragging the remainder passively along. She included this locomotory method in her category of 'discontinuous locomotion' (type 1), in which the shell is pulled forward by means of contraction of the columellar muscles. This type of locomotion is found in gastropods with augur-shaped shells having a long, narrow spire and a relatively small aperture, which is identical to the shell of the Cretaceous *Claviscala clementina*.

Applying Miller's evidence that the locomotion type is directly related to the habitat, habits and substrate as a consequence of the speed required for the gastropod's activities, Perron (1978) conducted a laboratory study of the feeding behaviour of *Epitonium greenlandicum*. He established that this species also moved by discontinuous locomotion and was extremely slow. Its vulnerability to predation as a result of such slow movement and its inherent limited adhesion indicated it had to be essentially an infaunal gastropod. His observations confirmed this and demonstrated that its locomotion contributed to its facultative ectoparasitic predation of sea-anemones.

The diversity of shell form occurring within the fossil Epitoniidae suggests that a variation of locomotory types existed among them comparable with, or even greater than, that found in Recent species, and that the examples mentioned above are not therefore contradictory.

Linsley (1978*a* : 435), in referring to the parameters for expressing the properties of shell coiling provided by Raup (1961, 1966), pointed out that the major differences in shell form resulted from an alteration in the translation rate of the generating curve down the axis of coiling. Other important factors were attendant differences in the rate of expansion of the generating curve and in the distance of that curve from the axis. It is generally accepted that the greater the translation rate, the less the whorl expansion rate, the closer the whorls become to the axis of coiling and the less the degree of overlap of successive whorls. The high-spired shells of the earlier epitoniids are a product of these factors.

I suspect that one of the general trends in the evolution of the Epitoniidae has been to overcome the limitations presented by the elongate, tightly-coiled shell. In doing so, they have become more efficient and competitive molluscs and have been able to extend their habitat range considerably. Forms comparable with the earlier species still exist, but many later forms are shorter-spired and have more inflated whorls. Such shells have been produced by increasing the expansion rate of the generating curve and by increasing the distance of this curve from the axis. It is also possible that the development of the basal disk may well have initially assisted in overcoming the disadvantages of the lengthy shell. This would have been achieved by ensuring the overlap of the whorls (see function of overlap, Raup 1966 : 1189), and perhaps by altering the centre of gravity, a point which requires verification by measurement. The development of strong varices, sometimes overlapping, and axial ornament has almost certainly made the shell stronger and provided resistance to crushing predators.

Confirmation of this view is provided by Vermeij's (1971*a*) utilization of three of Raup's parameters in an analysis of conispirally-coiled gastropods. This demonstrated the effective exploitation of shell morphology for evolutionary development and ecological expansion within the Class. By using the angular orientation of the coiling relative to the plane of the generating curve, Vermeij produced a table of representative values for comparison of Recent gastropods. Among these, the figure obtained (Vermeij 1971*a* : 18) for the Recent *Epitonium fucatum* serves to demonstrate the improved position occupied by some modern epitoniids when compared with that of their high-spired relatives.

The two new Cretaceous forms described in this paper contribute to an understanding of the evolution of the Epitoniidae. A clearer picture can only be obtained by close examination of the total fossil record of the family.

Acknowledgements

I must first record my gratitude to R. J. Hogg and P. R. Payne for drawing my attention to their find of a rich fossiliferous lenticle in the Shenley Limestone, from which they obtained the unique specimen of *Funis*. My thanks are due to many colleagues at the British Museum (Natural History) for helpful discussion.

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Postscript

Further to my remark (p. 235) that since the Eocene Epitoniid species are generally represented by relatively few individuals, at late proof stage I learn (Amy Breyer, personal communication) that *Epitonium* (*Nitidiscala*) *tinctum* Carpenter 1865 occurs in considerable numbers at suitable habitats near Bodega Bay, California.

Regarding the unusual preservation of the holotype of *Crossotrema crebricostata* (p. 238), it may be relevant that in the Maastrichtian Chalk the calcite of some invertebrate fossils is found to be locally and incompletely replaced by chalcedonic quartz at many horizons (Håkansson, Bromley & Perch-Nielsen 1974: 226–7). Extremely rarely specimens have been found with delicate replacement of the shell by calcedony. These showed no traces of distortion, unlike normally preserved specimens, suggesting the silicification had occurred early in diagenesis.

Håkansson, E., Bromley, R. & Perch-Nielsen, K. 1974. Maastrichtian chalk of north-west Europe—a pelagic shelf sediment. *Spec. Publs int. Ass. Sedimentol.*, Oxford, **1**: 211–233.

Revision of the microproblematicum *Prethocoprolithus* Elliott, 1962

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Synopsis

The two species of the coprolite-genus *Prethocoprolithus* Elliott, *P. centripetalus* and *P. cucumeriformis*, are now reinterpreted as remains of invertebrate faecal ribbon and of invertebrate tube or burrow respectively. The second species is renamed *Thartharella cucumeriforme*.

Introduction

Prethocoprolithus was instituted by me for certain microproblematica in the Jurassic of the Middle East (Elliott 1962). Both the type species *P. centripetalus* Elliott, and a second species *P. cucumeriformis* Elliott, were considered to be coprolites.

Through the courtesy of Mr F. Bourgeois, who very kindly called on me in London to discuss these microfossils, I am able to give emended diagnoses and different interpretations of these objects. Mr Bourgeois, who has seen similar fossils in the Jurassic and Permian of the Middle East since my original descriptions, recognized that *P. centripetalus*, whilst coprolitic, was debris of faecal ribbons rather than separate faecal pellets, and that *P. cucumeriformis* was an organic tubular structure, not coprolitic.

Prethocoprolithus is thus available as a name for remains of this type of faecal ribbon, known to be common to several living bivalve genera where debris can be matched with the living mollusc, and the new figures given are taken from fossil material in the original type thin-section. '*P. cucumeriformis*', much less common in my experience, is renamed and reinterpreted, again from its original type thin-section.

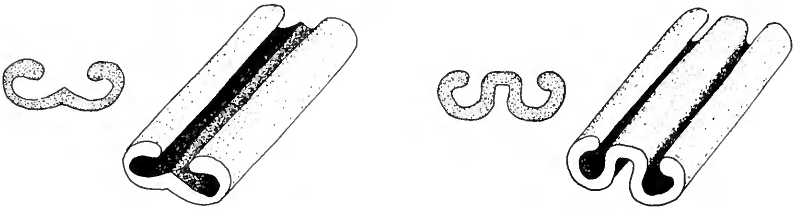


Fig. 1 Diagrammatic representations, section and projection, of faecal ribbons of present-day *Mytilus* (left: based on Moore 1939), and *Prethocoprolithus* (right).

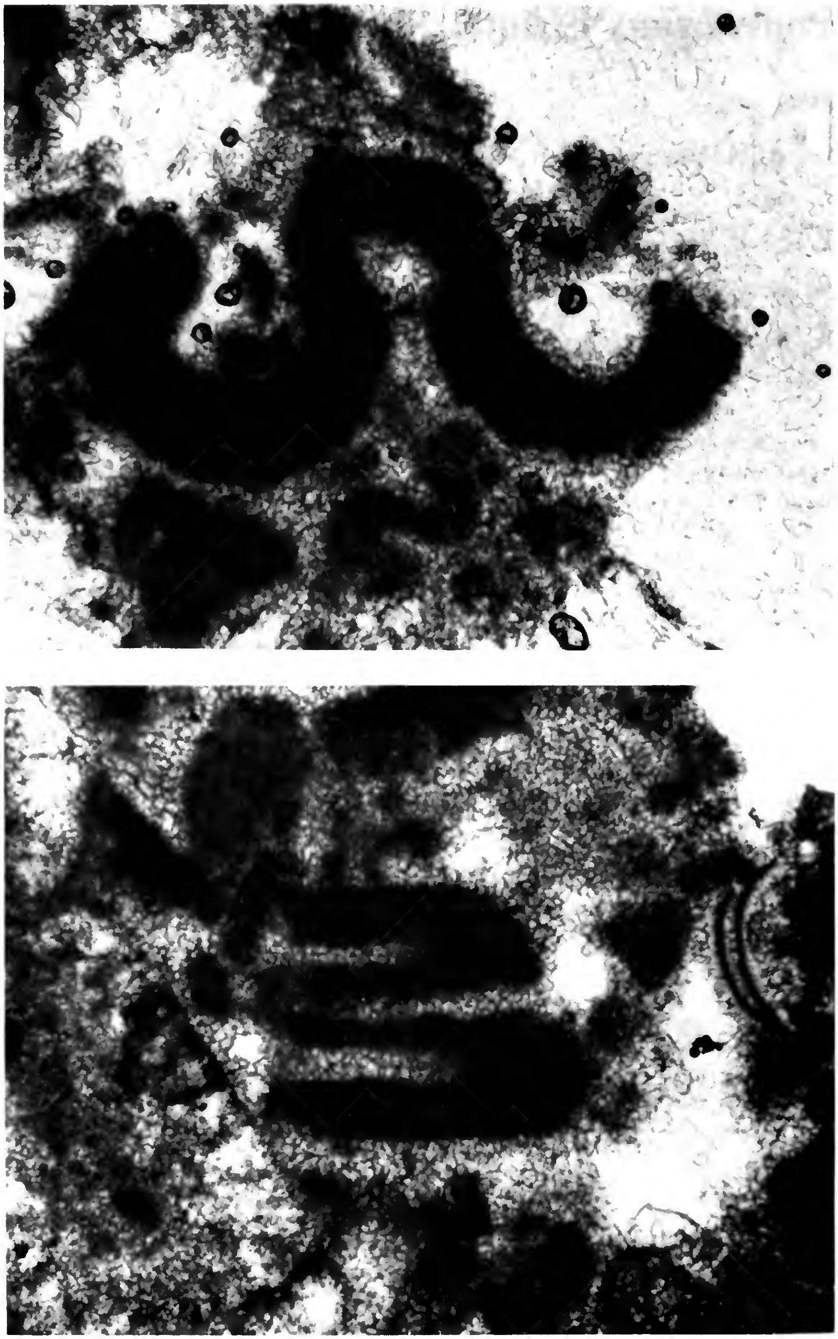
Systematic and discussion

Genus *PRETHOCOPROLITHUS* Elliott, 1962
Figs 1–3

Diagnosis (revised). Remains of ribbon-like faecal strips, the thin ribbon being strongly folded three times longitudinally, the rounded median fold being in the opposite direction to the two rounded lateral folds, to give a cross-section like a letter s with an additional turn. Originally described from the Mesozoic of the Middle East, but likely to be widespread from Upper Palaeozoic onwards.

Bull. Br. Mus. nat. Hist. (Geol.) **34** (4): 251–254

Issued 18 December 1980



Figs 2, 3 *Prethocoprolithus centripetalus* Elliott. 2, vertical cross-section, and 3, oblique cross-section, of faecal ribbon at right-angles to long axis. Thin section, ×100; BM(NH) Palaeont. Dept. reg. no. Z929. Upper Jurassic Najmah Formation, Mileh Tharthar Well no. 1, Dulaim Liwa, Iraq.

TYPE SPECIES. *P. centripetalus* Elliott 1962.

DESCRIPTION. Faecal ribbons of this general kind characterize some living bivalves (family Mytilidae, certain oysters, etc.) and have been figured many times (e.g. Edge 1934, Moore 1939, Manning & Kumpf 1959). In these living examples the treble folding is achieved partly by curvature but partly by thickening of the ribbon medially and to a lesser extent marginally (Fig. 1). *Prethocoprolithus* is exceptional in having rounded 'anticlinal and synclinal' folds along a ribbon of apparently near-uniform thickness. Much of the faecal material is broken, but the type slide shows a near-vertical true cross-section (Fig. 2), and also examples of an oblique-longitudinal section showing two paired sections each of the two walls of marginal folds, united at the ends where the plane of section cuts the connections (Fig. 3). In my original erroneous interpretation I regarded these as adventitious juxtaposition of separate tubular coprolites.

The original materials examined by me were from the Jurassic of Iraq, with one probable example from the Triassic of the same area. From the presumed origin of this type of faecal ribbon, they are likely to occur throughout the full geological range of the appropriate bivalves. A calcite-filled section of an indeterminate thin-shelled bivalve occurs in the type slide.

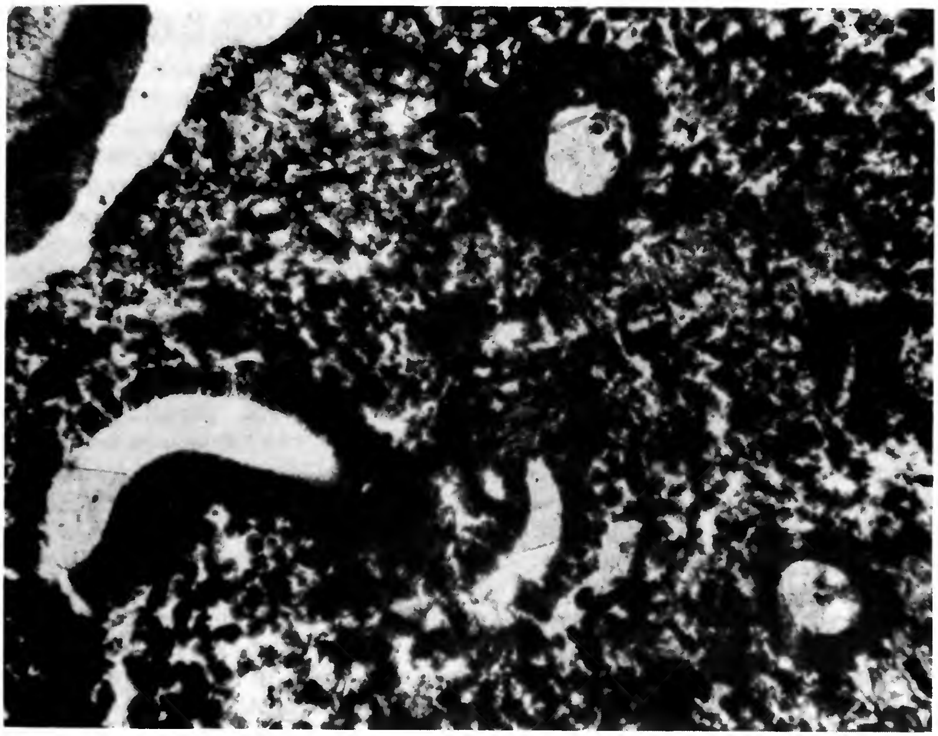


Fig. 4 *Thartharella cucumeriforme* (Elliott). Various sections of curved burrow with laminated walls. Thin-section, ×40, reg. no. Z928; Upper Jurassic Gotnia Formation, Mileh Tharthar Well no. 1, Dulaim Liwa, Iraq.

Genus *THARTHARELLA* nov.

Fig. 4

DIAGNOSIS. Small curved tubular structures, possibly burrows, showing a sharply delimited central tubular cavity, surrounded by a cylindrical zone of horizontally laminated material, with ragged outer edge. Generic name taken from the Iraqi type-locality.

TYPE SPECIES. *Prethocoprolithus cucumeriformis* Elliott 1962; Jurassic of Iraq.

Description. These structures are calcite-filled in the type material. Around this centrally-placed former cavity is a tubular zone of horizontal laminae, at right angles to the long axis. In vertical section this outer zone is strongly laminated; in cross-section a single lamella is flocculent or amorphous (Fig. 4).

The structure suggests a tube, or tubular burrow, possibly of an annelid or other marine worm, in which the animal occupied the centre and an outer zone of bristles or appendages modified the sediment by cementation with organic matter. Alternatively this could have been the effect of oral appendages 'moving-up' during growth.

I have seen a fossil like *Thartharella* from the Triassic of Iran, but have no precise records.

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Basilicus tyrannus (Murchison) and the glabellar structure of asaphid trilobites

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Synopsis

The type species of *Basilicus*, *Asaphus tyrannus* Murchison 1839, is refigured and discussed in relation to *B. peltastes* Salter. Lectotypes are selected. The glabellar structure of this and other Asaphinae suggests that the 'basal glabellar lobes' are of genal origin, beginning as bacculae which are progressively included within the cephalic axis in effaced species. This glabellar structure differs from that of other asaphids, and may be appropriate for the definition of monophyletic subfamilies.

Introduction

Basilicus tyrannus (Murchison 1839) is one of the most familiar British trilobites, represented in every student collection and any museum with Palaeozoic pretensions. It is a curious omission that it has not been given a recent scientific description or ever illustrated photographically, apart from a fragment by Whittard (1964) and some poor material by MacGregor (1963). Jaanusson (*in* Moore 1959: fig. 248, 3) gave a drawing of *B. tyrannus*, and a diagnosis of the genus based upon it. Since I have been studying asaphid trilobites, from Australia, Newfoundland, Spitsbergen and Wales, the problem of classifying this particularly intractable group has raised questions concerning the structure of the asaphid glabella. A redescription of *B. tyrannus* is combined here with some remarks on the construction of asaphid cephalic axes and the definition of the subfamilies in the group.

Glabellar structure of Asaphidae

Most asaphids are more or less effaced, and this involves the loss of visible cephalic segmentation and of definition of axial furrows. Since effacement is an advanced character capable of development in separate subgroups within the Asaphidae (i.e. is manifestly polyphyletic) we cannot base our classification of asaphids on effacement. It is accordingly important to find species or specimens in which the furrows are developed as clearly as possible; a similar problem exists in the Agnostida, among which smooth forms are repeatedly generated.

Jaanusson (*in* Moore 1959: 334–335) defined the subfamily Asaphinae as having an expanded frontal glabellar lobe, and 'lateral glabellar furrows commonly strong, obliquely directed', with a pair of 'lateral glabellar lobes' at the base of the glabella. This interpretation of asaphine morphology has been used in subsequent descriptions of *Asaphus*-like forms (e.g. Dean 1966) and is apparently generally accepted. Here we give a different interpretation. The so-called basal 'lateral glabellar lobes' are regarded as part of the fixed cheeks, inflated bacculae that became effectively incorporated in the axial region in some species. The 1P 'lateral glabellar furrows' are regarded simply as that part of the axial furrow lying between the frontal lobe and the bacculae, which are deepened into apodemes in the 1P position. This is at or near the point of maximum constriction of the glabella. Posteriorly the axial furrows are normally effaced in asaphines, but where they are not they diverge again from the constriction so that the general outline of the glabella is an hourglass-shape. Effacement usually increases with size during ontogeny so that large specimens often have the occipital furrow effaced, for example. In species with the whole posterior part effaced it is impossible to tell which parts of the axial region are of glabellar and which of extra-glabellar origin. In these cases assignment to the subfamily Asaphinae is made

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on the characteristic posterior constriction of the glabella behind the frontal lobe. There are several lines of evidence leading to this assessment of glabellar form:

1. Bacculae are commonly developed in asaphids other than asaphines. In these examples there is no doubt about the origin outside the glabella. See, for example, among the Niobinae *Niobella* aff. *imparilimbata* (Tjernvik 1956: pl. 5, fig. 11) and *Gog catillus* Fortey (1975 : pl. 3, fig. 1). However, even in these forms there is a tendency for the furrows separating bacculae from glabella to become effaced, that is, for incorporation of the bacculae into the axial structure; see *Niobella bohlini* Tjernvik (1956 : pl. 5, figs 4, 6).

2. Smaller specimens of *Asaphus* itself (Fig. 1) do not show conspicuous bacculae, but the course of the axial furrows shows up under alcohol. Note that the inner ends of the axial furrows show as a pair of dark patches, which represent thickening of the cuticle as a pair of calluses. These are the 1P apodemes. There is little indication of any cuticle thickening exterior to the axial furrows.

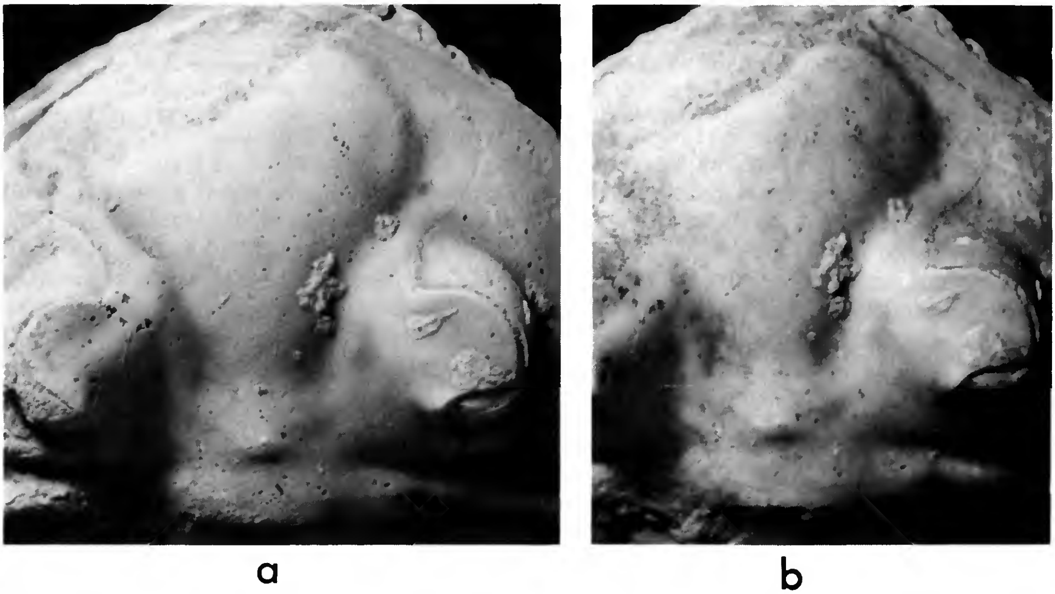

Fig. 1 *Asaphus* sp. of *expansus* type, mid-part of cephalon, ×5; a, whitened with ammonium chloride to show glabellar tubercle just in front of occipital furrow and general course of axial furrows; b, under alcohol to show thickened patches of exoskeleton representing muscle insertion areas at posterior end of defined axial furrows. Old coll., BM(NH) 42178; Pulkova, Leningrad, Russian platform; Ordovician, Llanvirn.

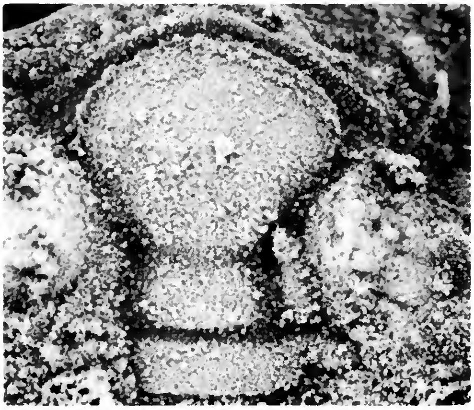

Fig. 2 Asaphid, gen. nov. Latex cast of cranidium preserved as external mould, ×6, showing 1P developed as transglabellar furrow, posterior course of axial furrow defined, and well-developed bacculae adjacent to basal lobe of glabella. Nora Formation, central Queensland, Bureau of Mineral Resources, Canberra, coll.

3. Some anomalous new asaphines from the early Ordovician of Australia have deep dorsal furrows (Fig. 2). In the form illustrated the 1P furrows have become conjoined across the glabella. The furrow defining the inside of the 'basal lobes' runs continuously to the occipital ring, and is not, therefore, effaced in the manner of most Asaphinae. In this case the only reasonable interpretation is that this furrow is axial. The furrow defining the *outside* of the baccula evidently meets the posterior border burrow (and is extra-axial).

4. Where the bacculae (and the adjacent axial furrows) are effaced in large individuals they are present in earlier growth stages. This is true of *Basilicus tyrannus* (Fig. 7, p. 260).

Subfamily classification in asaphids

If the interpretation of the glabella given in the previous section is correct there are implications for the classification of the family (Fig. 3). The fundamental cephalic character separating the Asaphinae from other subfamilies is the glabella with an expanded, often inflated frontal lobe, a posterior constriction at about the level of the palpebral lobes and a backward expansion to the occipital area. Bacculae may or may not be developed, although they usually are in the Arenig and later species, and are incorporated within the axial region to variable degrees. A glabellar tubercle placed in an immediately preoccipital position was used by Jaanusson (*in* Moore 1959) as one of the defining characters, and this obtains also with the new definition. The 1P apodemes are at or immediately anterior to the glabellar constriction. Under this concept of the subfamily certain genera of Tremadoc age, at first glance quite different in appearance from *Basilicus* and *Asaphus*, should be included within the same subfamily. In particular *Lachnostoma* Ross, 1951, has a glabella of asaphine type. I have observed on a meraspis cranidium of *Lachnostoma latucelsum*[1] Ross, 1951 small swellings alongside the base of the glabella which are apparently not present on larger cranidia. Also *Proasaphus* Balashova, 1966, from the Tremadoc of the Russian Platform, has an extraordinary hourglass-shaped glabella (Balashova 1966 : pl. 2, fig. 6) which cannot be easily explained without adopting the interpretation of glabellar structure given here. The same genus shows a tendency towards a transglabellar 1P, which has been mentioned on the new Australian form (Fig. 2). The origins of the group may lie in such early Tremadocian

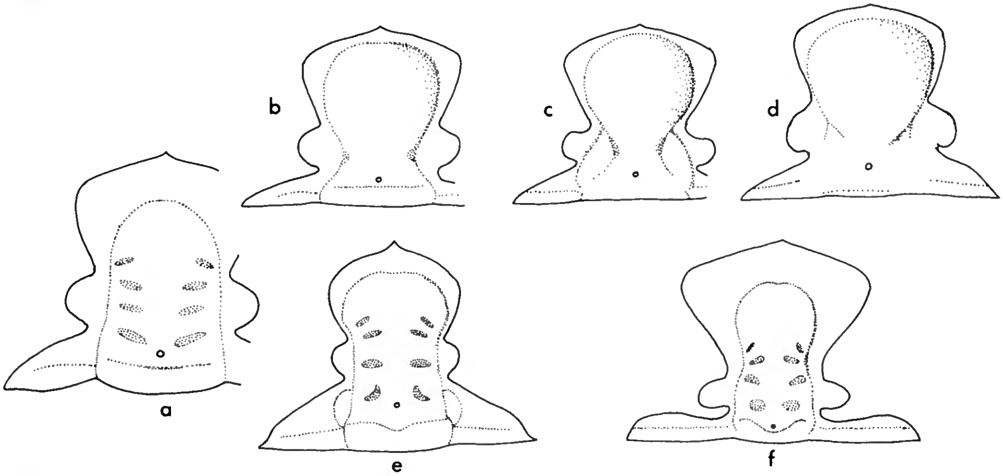

Fig. 3 Schematic diagram showing morphological history of asaphid glabella. 3a, primitive condition, retained apparently in isotelines—see, for example, *Golasaphus* in Shergold (1975 : pl. 56, fig. 7). 3b–d, asaphines tending towards effacement; b, defined, constricted glabella as in *Proasaphus* Balashova, 1966; c, with bacculae at base, cf. Fig. 2, opposite; d, secondarily effaced condition as in *Basilicus* and allied genera. 3e–f, niobine–ogygiocaridine condition; e, *Niobe*; f, *Ogygiocaris* such as *O. sarsi* in which glabellar tubercle and palpebral lobes have moved to a relatively posterior position.

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[1] For a comparable species, see Evitt 1961 : pl. 117, fig. 23.

forms as *Bellefontia* (particularly see *B. ibexensis* Hintze, 1953: pl. 4, fig. 2), which apparently have the beginnings of posterior glabellar constriction. Early asaphines, such as *Aulacoparia venta* (Hintze 1953), lack a fork in the hypostoma, which is therefore presumably a derived character.

In effaced forms it may be difficult to decide whether the affinities are asaphine or isoteline—but the back end of the frontal lobe of the former is usually defined. Glabellar structure in the latter group tends to be simple rectangular, but there may be some forward taper or expansion. Bacculae seem to be rare or unknown. Small isotelines (Whittington 1941) appear to have a true deep 1P glabellar furrow. In asaphids generally the width and shape of the cephalic and pygidial doublure is highly variable, and may be significant in the definition of genera, but scarcely at a higher taxonomic level. There has been a recent tendency to upgrade some of the old asaphid 'genera' into new subfamilies. Balashova has proposed three such, all based on species from the asaphid radiation on the Russian platform: Ptychopyginae (Balashova 1964), Pseudoasaphinae (Balashova 1969) and Pseudobasilicinae (Balashova 1971). The eponymous genera of the last two have a glabellar structure of asaphine type, and it seems to me extremely unlikely that the forms included within them have a separate status sufficient to warrant subfamilial distinction. *Ptychopyge* and allied genera proposed in Balashova (1964) have prominent nodes on the fixed cheeks just behind the eyes. Since the eyes in this group of species are all very far back, it seems reasonable to regard these nodes as constricted bacculae, and in essentials of glabellar form the Ptychopyginae are asaphine. Balashova may be correct in assuming separate and isolated radiations of the asaphids in the Baltic region, but this is a different matter from regarding each of these as meriting separate subfamilial recognition. The asaphids on each separate plate in the early to middle Ordovician appear to have been undergoing independent radiations (North America–Greenland, Baltic, southern Europe–South America, and Australia) but to dignify each of these with one or more subfamilies would be unwieldy and would also obscure the broader phylogenetic lines in the family.

In summary, there are three types of glabellar structure in Ordovician asaphids: asaphine, isoteline (which appears to be primitive) and niobine. The ogygiocaridine and thysanopygine glabellar structure appears to be fundamentally similar to that of the Niobinae. An unforked hypostoma is primitive, and development of a median notch was presumably independent in Ordovician subfamilies. In some genera assigned to the Ogygiocaridinae (*Ogygiocaris*, *Ogygiocarella*, *Merlinia*) a median protrusion was developed rather than a notch. If asaphid classification is to be based on glabellar structure three subfamilies of Ordovician asaphids can be justified: the Asaphinae, Isotelinae and Niobinae (but note that the name Ogygiocaridinae has nomenclatorial priority over Niobinae and Thysanopyginae), and in addition possibly the Tangyaiinae Lu, 1975. Another subfamily may be necessary to accommodate more or less plesiomorphic Cambrian forms. The subfamily Symphysurininae Kobayashi is not acceptable, because I have evidence that *Symphysurina* is not an asaphid.

Systematic description

Genus ***BASILICUS*** Salter, 1849[2]

TYPE SPECIES. *Asaphus tyrannus* Murchison 1839.

Basilicus tyrannus (Murchison 1839)

Figs 4–10

SYNONYMY. See Whittard (1964 : 229). The possibility that *B. peltastes* Salter, 1866, is a subjective synonym of *B. tyrannus* is considered below.

LECTOTYPE. Three specimens were figured by Murchison (1839). One of these (pl. 24) was considered as a variety of *tyrannus*, termed *ornata*, and is not available. Of the other two specimens

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[2] *Non* M. Oppel 1811 (*Die Ordnungen, Familien und Gattungen der Reptilien* ... [&c.]: 19. München), which is a misprint for *Basiliscus* Laurenti, 1768 (Reptilia); it is correctly spelled on p. 29 of Oppel's work, though there ascribed to Daudin. Because a misprint has no status in zoological nomenclature, no action is required to conserve *Basilicus* Salter, 1849.

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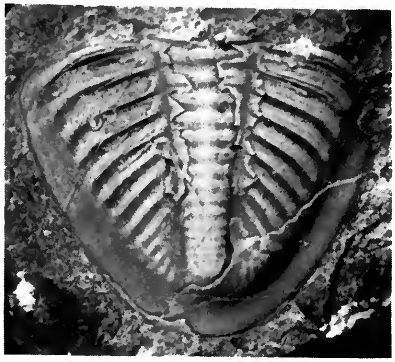

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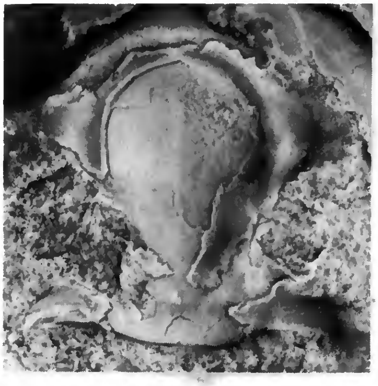
Figs 4–6 *Basilicus tyrannus* (Murchison), ×1. Fig. 4a, b, **lectotype** (herein selected), original of Murchison, 1839; pl. 24, fig. 1B, dorsal and lateral views. Institute of Geological Sciences, Geol. Soc. Coll. 6827. Llandeilo series of Llandilo, south Wales (presumably from Dynevor Park). Fig. 5, ventral view of large, exfoliated hypostoma. BM(NH) It.13227a, same block as originals of Figs 7, 9, 10 (p. 260). Fig. 6, pygidium, smaller than lectotype and with furrows well-developed. BM(NH) I.1312, locality data as lectotype.

the larger (original of Murchison 1839 : pl. 24, fig. 1b), a thorax and pygidium, is here selected as lectotype (IGS Geol. Soc. coll. 6827). Fig. 4.

Occurrence. Williams (1953) gives *B. tyrannus* a stratigraphic range in the Llandeilo district from the Upper Llanvirn to the Lower Llandeilo. The species is only common in this area, being only represented in Shropshire by a few fragments from the Meadowtown beds (Whittard 1964). MacGregor (1963) has illustrated possible *B. tyrannus* from the Berwyn Hills, north Wales. Like most large asaphids with thick cuticles it seems to be a shallow-water form, and presumably



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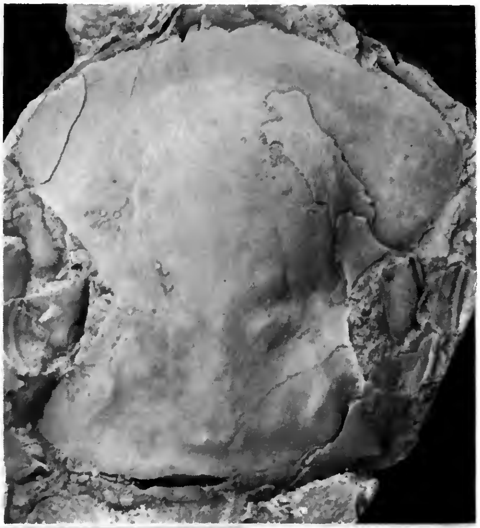

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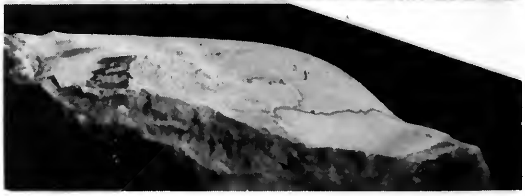

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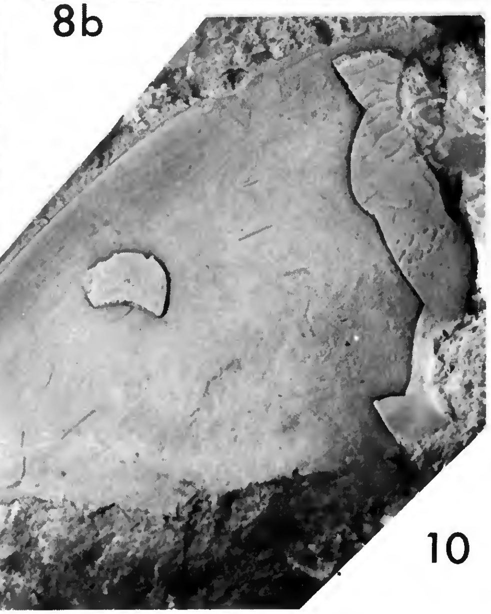

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Figs 7–10 *Basilicus tyrannus* (Murchison). Fig. 7, small cranidium, ×2; compare lectotype of *B. peltastes*, Fig. 11. BM(NH) It.13227b. Lower Llandeilo Series, Deer Park track in Dynevor Park, Llandilo, SN 609223. Coll. 1974. Fig. 8, large cranidium in relief, ×1; a, dorsal, and b, lateral view. BM(NH) It.9697. 130 m at 295° from Llan Mill, near Narberth, Dyfed, SN 1433 1394. Fig. 9, small free cheek, ×2; BM(NH) It.13227c, same block as large free cheek, Fig. 10. Fig. 10, large free cheek, ×1; typical of *B. tyrannus*, showing short genal spine compared with Fig. 9. Same bock as Figs 7 and 5. Lower Llandeilo Series, Dynevor Park, Llandilo, by Deer Park track, SN 609223.

its rarity outside south Wales is attributable to a difference in facies. Llandeilo 'flags' with *B. tyrannus* extend westwards to St Clears and Narberth.

COMPARATIVE REMARKS. Salter (1866 : 149–152) gave a good account of this species, and here the purpose is to consider the variation within the species, and the distinctness or otherwise of a second species, *B. peltastes* Salter 1866. As Salter noted, Murchison's variety *ornata* was based on a large specimen, BM(NH) 59785, on which the distinctive surface sculpture of broken and scalloped terrace lines is particularly prominent. The same sculpture is present on smaller specimens, although subdued on pygidia, for example, less than 5 cm long.

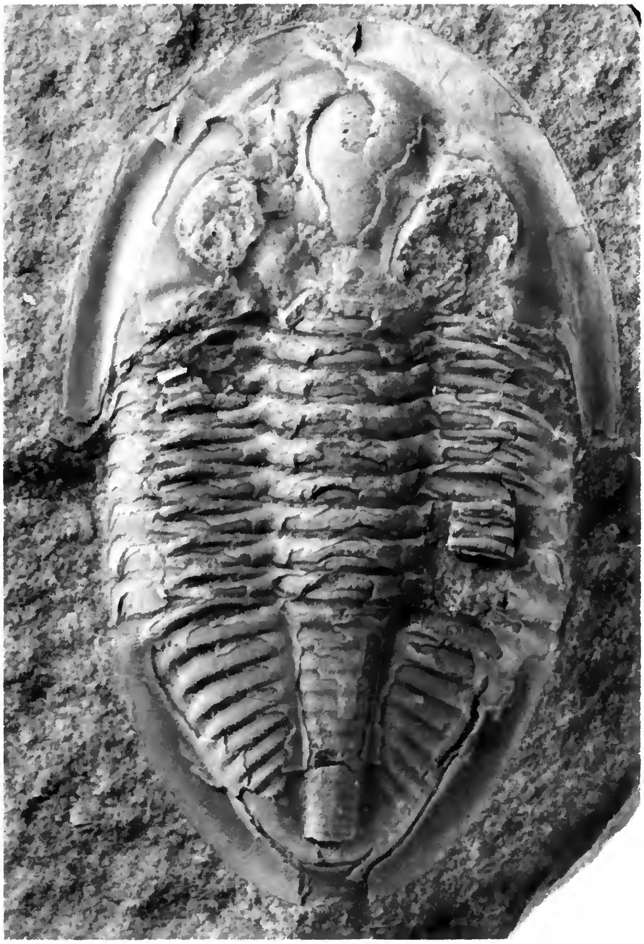

Fig. 11 **Lectotype** of *Basilicus peltastes* Salter, selected here, × 1½. Original of Salter 1866 : pl. 22, fig. 1. Note baccula on left. GSM 12793. Llandeilo Series within Dynevor Park, Llandilo.

The large cranidium in relief (Fig. 8) is from Llan Mill, one of Salter's localities for *B. tyrannus*. At this size the bacculae are not distinguishable. Note that what we have termed above the 'frontal lobe' on the glabella in fact shows traces of one pair of depressions, presumably the site of appendage attachment, and so strictly speaking the term frontal lobe should apply to the area in front of these. A small cranidium in relief (Fig. 7) shows a narrower and well-defined border, and the bacculae are distinctly set off from the rest of the glabella in the region adjacent to the eyes, which are proportionately a little longer at this size. This small cranidium occurs on a large block covered with the remains of *B. tyrannus*. The same block has yielded the large hypostoma (Fig. 5), small and large free cheeks (Figs 9, 10) and many pygidia of *tyrannus* type.

The large free cheek, with an ill-defined border and short genal spines, is like those figured by Salter for *B. tyrannus*, but the small cheek has both a better-defined border and relatively long genal spines. These characters were used by Salter (1866 : 152) to distinguish a second species, *Basilicus peltastes.* It now seems possible that some of the supposed differences between *B. tyrannus* and *B. peltastes* can be accounted for by difference in size. The best specimen used to found *B. peltastes* is a relatively small entire exoskeleton (Salter 1866 : pl. 22, fig. 1; Fig. 11 herein). This is here selected **lectotype.** Salter clearly indicated the lateral inflated areas by the glabella that are here interpreted as bacculae, the same features seen on the supposed small *tyrannus* cranidium described previously. It seems that effacement of dorsal cephalic furrows of these asaphids increases with size, and this applies particularly to the posterior part of the glabella and the cephalic border. The same also applies to the large hypostoma (Fig. 5) which has a poorly-defined middle body and longer fork than the smaller specimen figured by Salter. With free cheeks of length about 5 cm it is possible to find examples with genal spines of various lengths; there may have been intraspecific variation in this character at any one size, as well as a decrease in relative size during ontogeny. The largest free cheek of *peltastes* type is GSM 104306.

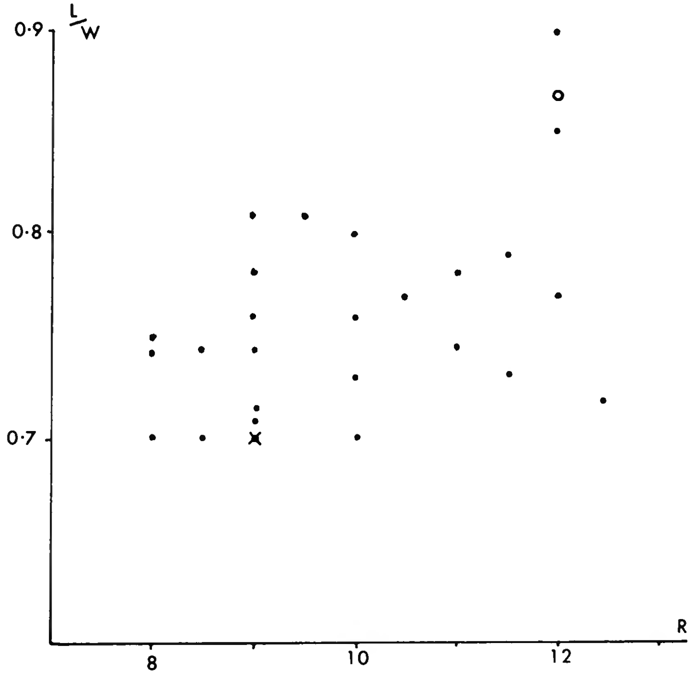

Fig. 12 Graph of length/width ratios of pygidia attributed to *Basilicus tyrannus, sensu lato* against number of pleural ribs, showing broad scatter without discrete grouping. Lectotype of *B. tyrannus* (Fig. 4) is open circle, that of *B. peltastes* (Fig. 11) crossed. Half rib scores obtained when one side of pygidium shows an extra faint rib.

Salter also stressed pygidial differences between *B. peltastes* and *B. tyrannus*, quoting up to 20 axial rings and 12 pairs of ribs on the latter, as against 14–15 axial rings and 9, 10 or rarely 11 pairs of ribs on the former. Counting axial rings or pleural ribs is always problematic, because the posterior ones are invariably faint. On well-preserved specimens of *Basilicus* retaining cuticle there is nearly always a posterior smooth area adjacent to the end of the axis where no ribs are visible. Nine or ten ribs are usually discernable anterior to this area. On some decorticated specimens the most posterior ribs are visible, and these are the ones with as many as twelve (Fig. 6). The best-preserved specimens of pygidia of *Basilicus* from south Wales in the IGS, BM(NH), Sedgwick Museum (Cambridge) and National Museum of Wales show considerable variation in the number of ribs, but 9–10 predominate (Fig. 12). There is no clear break between specimens referred by Salter to *peltastes* and the rest of the *Basilicus* specimens (usually determined as *tyrannus*). Nor does there appear to be any obvious correlation between length/width ratio and number of ribs. Specimens preserved in silty beds usually have the pleural furrows overdeepened. I have been unable to observe more than 17 axial rings on these specimens, and on specimens preserving cuticle there may be as few as nine clearly defined. It seems possible that Salter was confusing annulation with the prominent transverse terracing at the tip of the axis. Smallest pygidia of *B. tyrannus* are about 1 cm long; these are more transverse than larger ones (length/width ratio 0·6–0·7), similar to *Basiliella*.

In summary, it seems that the differences between *B. tyrannus* and *B. peltastes* can be accounted for by ontogenetic changes, or by variation within the population of a single species (*B. tyrannus*). Ontogenetic changes include loss of bacculae and effacement of the posterior cephalic axial furrows. There may yet prove to be changes in the proportions of the population as a whole through the Llandeilo series; for example, the longer pygidia with 12 ribs may prove to be more abundant at higher horizons. This would require statistical examination of precisely localized collections, which are not yet available.

Acknowledgements

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A new Lower Ordovician bivalve family, the Thoraliidae (? Nuculoida), interpreted as actinodont deposit feeders

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Synopsis

A new bivalve family, based on the Lower Ordovician *Thoralia languedociana* (Thoral) gen. nov., is described. It has a shell shape and musculature typical of the Nuculoida but subumbonal cardinal hinge teeth.

Introduction

Material from the early Ordovician (Lower Arenig) of the Montagne Noire of southern France collected by Professor W. T. Dean includes a well-preserved specimen of '*Leda*' *languedociana* Thoral 1935 in which many of the details of the hinge and muscle attachment are preserved.

The species has a shell form typical of mobile protobranch nuculoids but lacks their taxodont teeth. In fact it has a hinge structure having more features in common with the actinodonts than with the nuculoids. This morphology has led me to erect a new genus, *Thoralia*, and family Thoraliidae, for the species. It is tentatively placed in the order Nuculoida, but the family does not fit with any certainty in any of the existing three superfamilies of the Nuculoida. It is among the earliest nuculoid species described where any details of the hinge and muscle attachment are known.

Thoralia languedociana occurs in argillaceous quartz silt sediment where infaunal bivalves form an important part of the fauna. They are associated with bellerophonts, rostroconchs, cephalopods, hyoliths, brachiopods and many trilobites (Thoral 1935 : 329). The fauna is of a more varied nature than those so far described in more inshore facies of the Lower Arenig, especially sands where bivalves predominate. This is true both when the bivalves alone and also when all the Mollusca are considered (Morris 1978 : fig. 25). The nature of the sediment and its fauna suggests an offshore shelf environment.

Orientation

At least three independent characters indicate the correct orientation of *Thoralia*. First, the subrostrate margin, which is interpreted as posterior. Secondly, there is only one possible position in which the ligament could have been situated; this is interpreted as posterior to the umbones. Thirdly, the form and position of the pedal/body attachment muscle scars are closely similar to those in a number of known nuculoids where the orientation is not in doubt.

Nuculoid affinities of *Thoralia*

The shape, ornament and musculature suggest that *Thoralia* is a nuculoid. The shape is very similar to that of a number of genera of Recent Nuculanacea, and it also has some less exact but broad similarities to other Palaeozoic nuculoids, including *Ctenodonta*, *Tancrediopsis* and *Praectenodonta* of the Ctenodontacea and *Palaeoneilo*, *Paleyoldia* and *Phestia* of the Nuculanacea. The only other bivalves that have a remotely similar shape occur within the Tellinacea, the Corbulidae which are in nearly every case more gibbous, and the little known Myophoricardiidae. All of these occur in Mesozoic or younger rocks and I consider them to be offshoots of late Palaeozoic Crassatellacea or just possibly, in the case of the corbulids, the Anomalodesmata.

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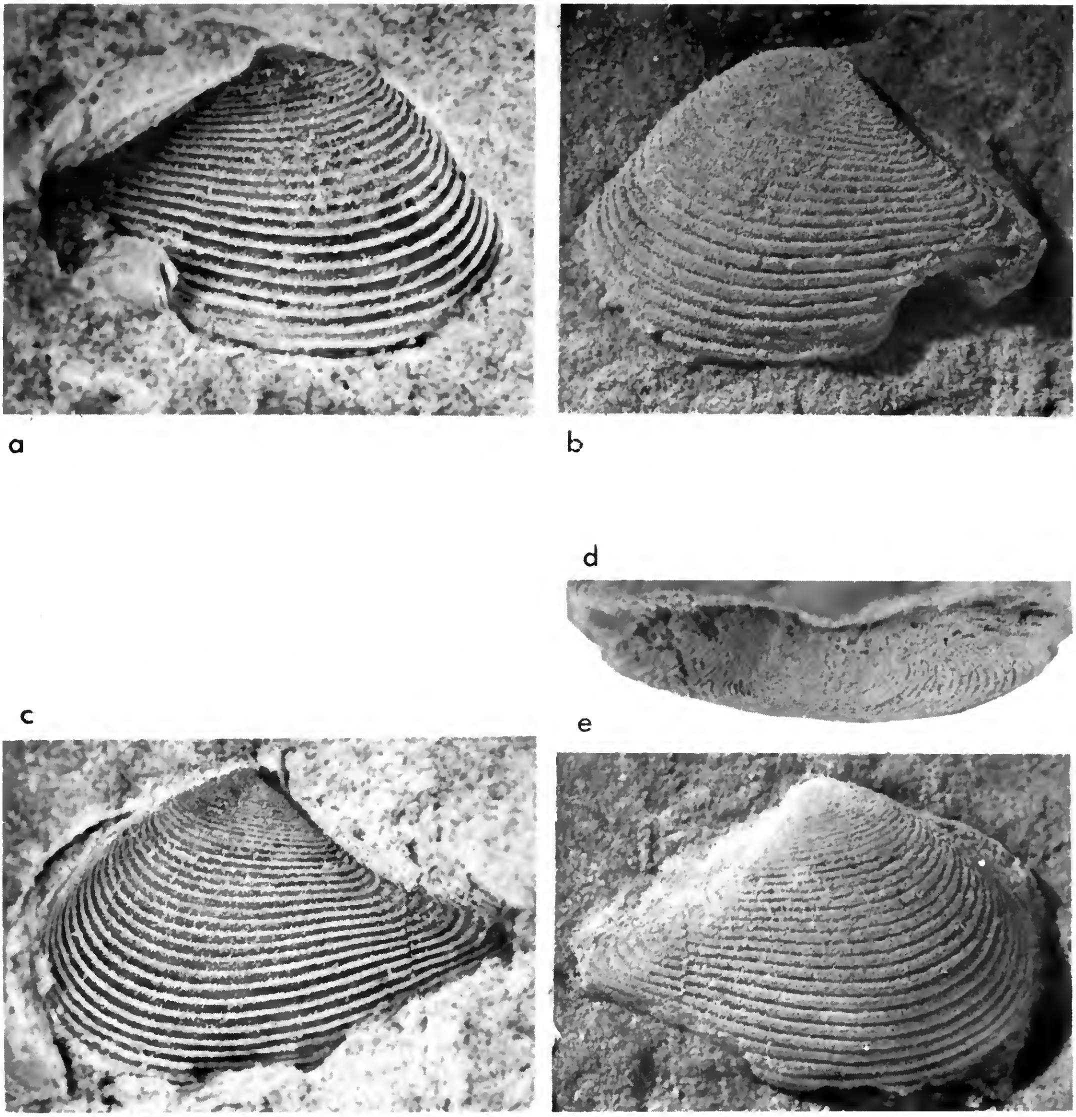


Fig. 1a–e *Thoralia languedociana* (Thoral), L. Arenig, Félines, southern France, all *c.* ×8. a, natural external mould of left valve. b, left valve, latex rubber cast. c, natural external mould of right valve. d–e, right valve, latex rubber cast; d, dorsal view, e, lateral view.

The Tellinacea include secondarily developed deposit feeders whose shape may also be related to their efficient motion through soft sediment.

The elongate shape of *Thoralia* is indicative of good burrowing ability but the relatively thick shell suggests that it did not move rapidly (Stanley 1970).

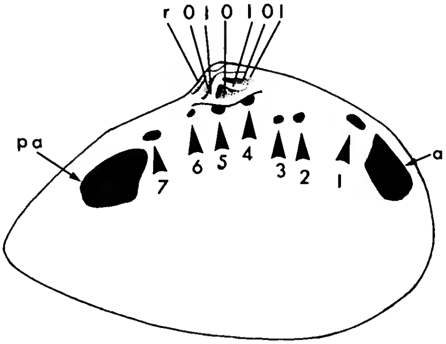
The enlarged illustrations of the shell suggest that it is more coarsely sculptured than is usual for nuculoids, but this is an illusion owing to the small size; *Thoralia* is only 7·8 mm long. The close spacing of the comarginal ribs is of common occurrence in many genera of nuculoids. No pallial line is preserved in *Thoralia* but it is considered unlikely that either a pallial sinus or extensive siphons were present. A pallial sinus is not known in any other Lower or Middle Ordovician nuculoid and it has not been considered that the one possibly sinupalliate Ordovician

Fig. 2 *Thoralia languedociana* (Thoral), steinkern viewed from left side, *c.* ×8.

genus, *Lyrodesma* (Lyrodesmatidae), had particularly extensive siphons. Even in sediments through which oxygenated ground-water may be freely circulating, non-siphonate bivalves such as the Glycymerididae and possibly some Crassatellacea are not known to be deep burrowers. It is therefore very probable that *Thoralia* was also a shallow burrower. The ribbing of the posterior part of the shell is at its most prominent at the rounded carina separating the dorsal area from the shell side and may have served to prevent scouring (Stanley 1977).

Although the specimen of *Thoralia* is very small, seven pairs of pedal/body attachment muscle scars are clearly preserved (Figs 2, 3, 7). They are slightly uneven in their depth of insertion and their disposition along a curving line between the adductor scars. The anterior and posterior pedal retractors (nos 1 & 7) are the most deeply inserted. The two pairs (nos 2 & 3) lying anterior to the umbones occur lower on the flank than the more posterior pairs (nos 4, 5 & 6). Pairs nos 1–4 form a convexly-downward curve on either side, which closely resembles the attachment scars of the wall of muscular tissue surrounding a body cavity in living nuculoids (Heath 1937) and visible in many fossil species (Bradshaw 1978).

Fig. 3 *Thoralia languedociana* (Thoral), reconstruction of left valve, internal view, ×11. I–hinge teeth, O–sockets, r–ligament groove, 1–7 -pedal/body attachment muscle scars, aa–anterior adductor muscle scar, pa–posterior adductor muscle scar.



Evolutionary interpretation of *Thoralia*

Because of the rounded blade-like anterior (*sensu* Stanley 1970) of *Thoralia* and its general similarity in shell shape to living nuculoids, I interpreted this genus as a mobile infaunal deposit feeder (Morris 1979). I also suggested that the inferred existence of early non-taxodont deposit feeders offers some support for the view that deposit feeding may have been a more primitive mechanism than filter feeding within the Bivalvia as a whole (Morris 1979). A plausible model for the evolutionary development of bivalve filter feeding is outlined in Fig. 4.

The existence of this early bivalve with characters of the Nuculoida, except for the number

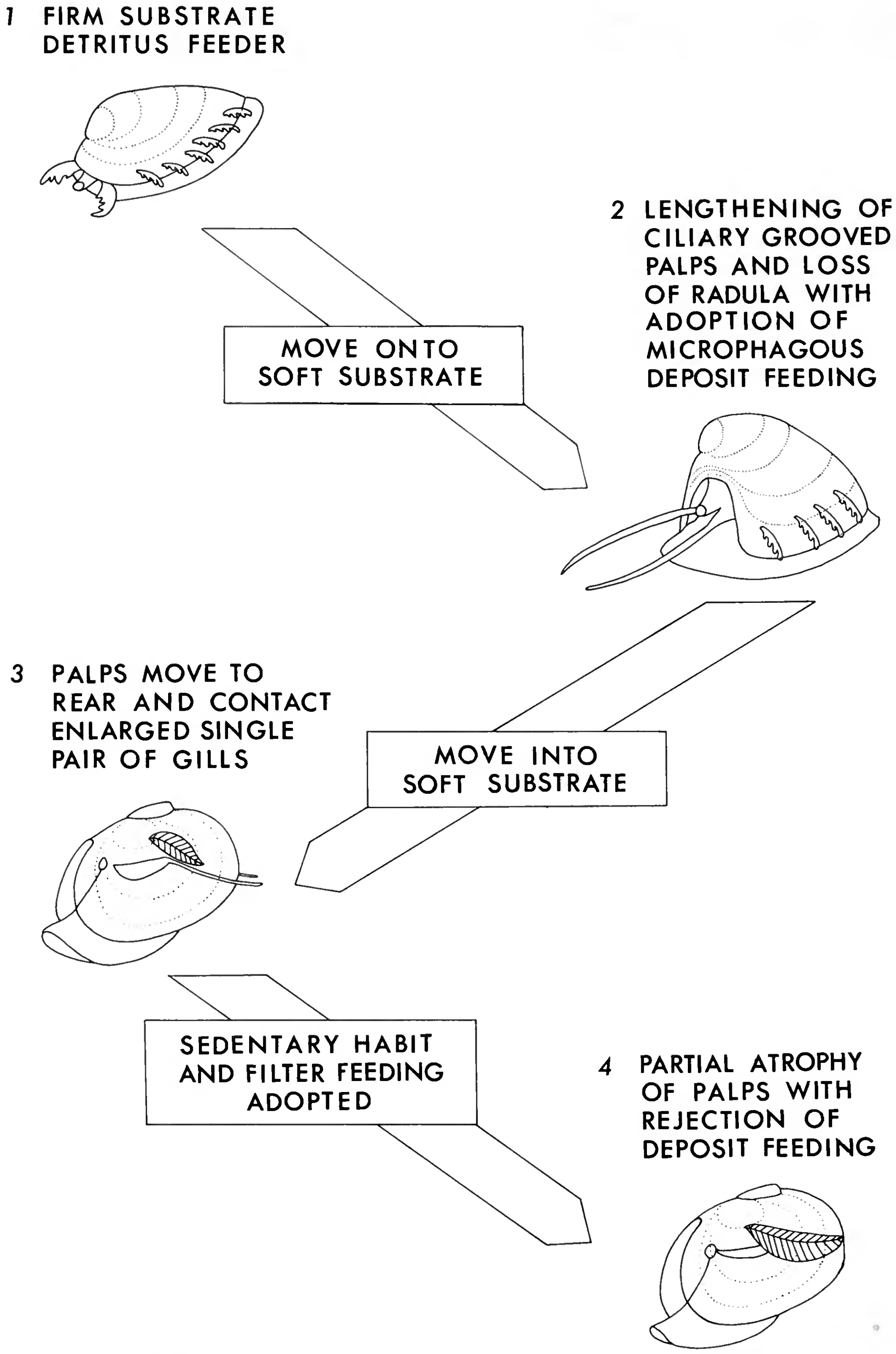


Fig. 4 A hypothetical model for the origin of bivalve filter feeding.

and disposition of the hinge teeth, is consistent with the view that a small, rather than a large, number of hinge teeth is the more primitive condition for the Bivalvia. Other evidence for this includes the distribution in other Lower Ordovician bivalves of hinge teeth types which I previously summarized (Morris 1979), and also the ontogenetic development of the Ordovician nuculoid *Tironucula* (Morris & Fortey 1976, Morris 1979). In addition, in one of the earliest known bivalves, the Lower Cambrian *Fordilla sibirica* Krasilova, the dentition has recently been described (Krasilova 1977, Pojeta 1978). This consists of single interlocking teeth and sockets occurring in front of the umbones, an arrangement comparable to the first-formed teeth of *Tironucula*.

A possible outline of the relationships of *Thoralia* based on these views is shown diagrammatically in Fig. 5.

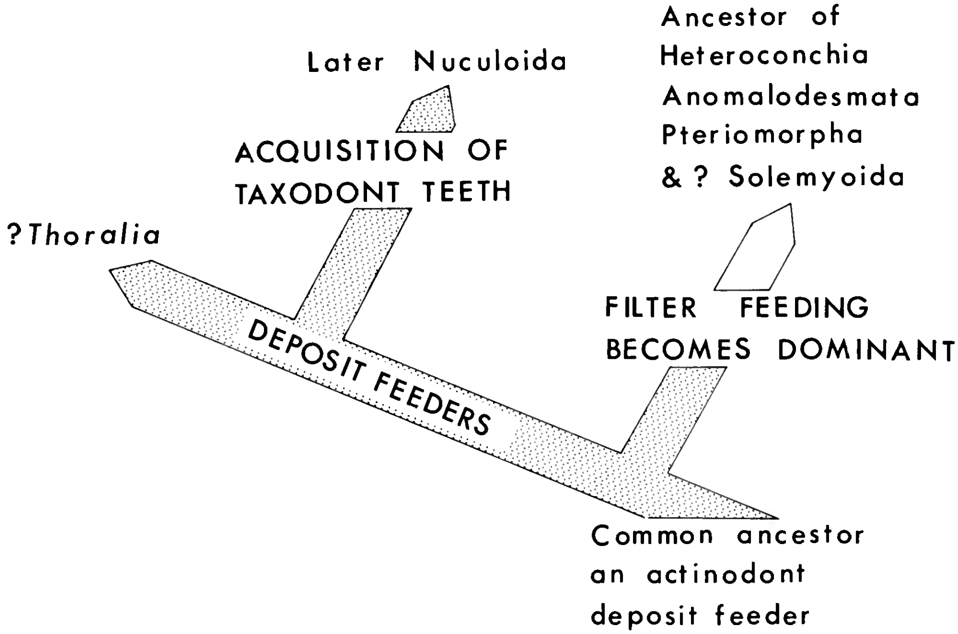


Fig. 5 Suggested relationships of *Thoralia*.

Systematic description

Class **BIVALVIA** Linnaeus, 1758

? Subclass **PALAEOTAXODONTA** Korobkov, 1954

? Order **NUCULOIDA** Dall, 1889

Superfamily uncertain

Family **THORALIIDAE** nov.

FAMILY DIAGNOSIS. Small bivalves of nuculoid shape with four radiating subumbonal cardinal teeth.

REMARKS. This combination of shape and hinge structure distinguishes the Thoraliidae from all other bivalve families.

TYPE and only genus *Thoralia* gen. nov.

Genus *THORALIA* nov.

Diagnosis. As for family.

Type species. *Leda languedociana* Thoral 1935; no other species are known.

Description. As for species.

Thoralia languedociana (Thoral 1935)
Figs 1, 2, 6, 7

1935 *Leda languedociana* Thoral : 164–165; pl. 13, figs 2–3.

Types. A syntypic series described by Thoral (1935) consisting of four specimens in a fine siltstone nodule from the Bois de la Cabosse, north of Assignan (J. Miquel coll. no. 475), and one specimen from a nodule from the Lower Arenig at St Chinian (Villebrun coll.). Thoral thought that all these specimens came from his 'horizon à *Miquelinia miqueli*', which he considered to belong to the Lower Arenig. The specimens are in the collections of the Laboratoire de Paléontologie des Invertébrés, Academie de Montpellier, France.

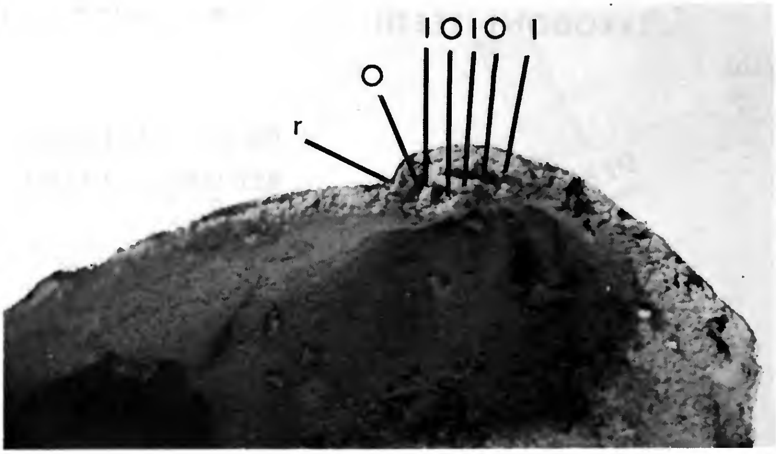


Fig. 6 *Thoralia languedociana* (Thoral). Latex rubber mould of the hinge of the left valve, ×16. I–hinge teeth, O–sockets, r–ligament groove.

Other material. A single specimen with the internal and external mould of both valves in Palaeontology Dept., British Museum (Natural History) (LL 31371), L. Arenig, Vigne, below and west of Rocs de Fayrols, near Camploug, Félines, France (W. T. Dean coll.).

Description. The latter specimen is small and tear-shaped or nuculaniform. The anterior is rounded and the posterior subrostrate. The anterodorsal and ventral margins are subparallel. The umbones are central and opisthogyrate. The posterodorsal area is separated from the flank by a distinct change of angle which forms a rounded edge from the umbones to the posteroventral margins. There is no lunule nor escutcheon.

The sculpture consists of closely packed strong co-marginal rounded ribs separated by narrow slit-like interstices.

There are short, strong hinge plates below the umbones with three small radiating teeth in the left valve (Figs 3, 6). The anterior tooth may be confluent with the dorsal margin. There are four interlocking teeth on the hinge plate of the right valve which is less well preserved. On the articulating surface between the anteriormost tooth of the right valve and the tooth behind it in the left valve there are at least four interlocking denticles, which appear as four oblique striations similar to those of many Cycloconchacea, Trigonidae and Unionidae.

The point of attachment of the ligament is not altogether clear. There is no distinct nymph, but the only position where the ligament could fit is in a very restricted region on the unfortunately obscured dorsal edge of the posterodorsal margin, immediately below and behind the umbones.

The muscle scars (Figs 2, 3, 7) consist of nearly isomyarian adductors, in which no separation into quick and catch is evident, and a series of six pairs of pedal/body attachments which lie between the adductors high on the internal shell surface.

The anterior adductor is moderate-sized, elongate oval, situated close to the anterior margin above its mid-point. The posterior adductor is situated on the posterodorsal area with a rounded posterior and ventral margin. Its dorsal margin runs parallel and close to the dorsal shell margin and it is truncated anteriorly. Because of its position so high in the shell, the scar is set at a considerable angle to the plane of commissure, so that the lower part of the adductor muscle joining the two valves would have been much longer than the upper part.

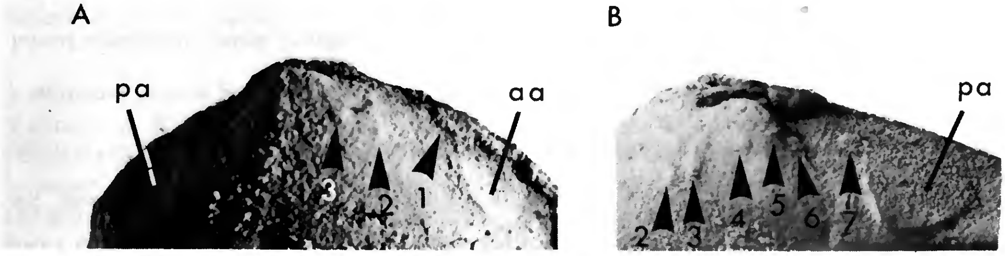


Fig. 7 Muscle attachment scars of *Thoralia languedociana* (Thoral), *c.* ×8; steinkern showing pedal and adductor muscle attachment scars. A, dorsal portion of interior of right valve. B, part of dorsal portion of interior of left valve, oblique view. aa–anterior adductor, pa–posterior adductor, 1–7 – pedal/body attachment muscles.

The anterior pedal retractor (1, Fig. 7) is small, deep-set and rounded and is situated close to the anterior dorsal margin on the umbonal side of the anterior adductor. Pedal scars 2 and 3 are apparently elongate in a dorsoventral direction. Their traces are difficult to separate but this may only be because of imperfect preservation, and their length therefore may be less than appears. They are situated relatively low on the shell side below the anterior part of the hinge plate. Pedal muscle scars 4, 5 and 6 lie close under the umbones. The posterior pedal retractor, 7, lies close to the dorsal shell margin on the umbonal side of the posterior adductor.

DIMENSIONS. Right valve of LL 31371: length 7·8 mm, height 5·48 mm, width 1·66 mm.

DISCUSSION. The elongate teardrop-like shape of this species led Thoral to consider it belonged to the genus *Leda*, in other words to the Nuculanacea of today's classification. But he was not able to see the hinge which, as described here, clearly excludes *Thoralia* from that superfamily. The new family is created here because the particular combination of nuculoid shape and subumbonal cardinal teeth has not previously been encountered.

Thoral compared *T. languedociana* with two species described by Barrande (1881) from the Ordovician of Bohemia which he also placed in '*Leda*'. One of these was *Leda bohemica* Barrande (1881 : pl. 269), but it is an entirely different shape, with posteriorly-placed umbones and the posterior part of the shell taller than the anterior part. It also has taxodont hinge teeth, and so belongs to the family Praenuculidae and possibly the genus *Praeleda*. The other was *Leda incola* Barrande (1881 : pl. 270, fig. 111), which is a more elongate species which Barrande showed to have fine-scale taxodont teeth on a long narrow hinge plate posterior to the umbones. This is apparently an early species of the Malletiidae. Neither species has characters suggesting any close relationship with *T. languedociana*.

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Cretaceous brachiopods from northern Zululand

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Synopsis

Brachiopod specimens collected from Upper Aptian and Albian localities in northern Zululand by W. J. Kennedy and H. C. Klinger are described and their systematic position reviewed in the light of the latest stratigraphical data. Descriptions are given for two new rhynchonellid species, *Cyclothyris africana* and *C. kennedyi*, as well as a new dallinoid brachiopod, *Dzirulina haughtoni*. A lectotype is selected for *Terebratula vanhoepeni* Lang, which is assigned to *Praelongithyris*, and a new species of *Cyrtothyris* is described as *C. ndumuensis*.

Introduction

Kennedy & Klinger (1975) published an account of the stratigraphy of the main Cretaceous outcrops of Zululand and Natal, South Africa in which they proposed the term *Zululand Group* to cover the succession from Upper Barremian to Maastrichtian equivalents. One member of the group, the Mzinene Formation, represents the European equivalent of Albian to Cenomanian rocks and contains a mixed invertebrate fauna of bivalves, gastropods, echinoids, nautiloids, bryozoans, corals and brachiopods. Some brachiopods were collected during the summer expeditions of 1970–71 and these, together with material previously collected by Dr S. H. Haughton and L. N. J. Engelbrecht and now in the collections of the Geological Survey of South Africa, Pretoria, form the subject of the present paper.

The locality and stratigraphical details supplied with the Haughton and Engelbrecht collections is, by present-day standards, somewhat inadequate but a fair match has been possible by comparison with more recently-collected material.

In general, the brachiopod species described here bear a strong resemblance to specimens described and figured by Mme S. Fabre (Fabre *in* Collignon 1949, 1950) from the Albian of Madagascar and are chiefly from northern and northeastern Zululand. While it has been possible to compare external morphologies of some of the terebratulids and rhynchonellids described and figured by Fabre, no material has become available for comparison of internal structures. The transverse serial sections shown here, Figs 1, 2, 4, 6, are taken mainly from duplicate specimens in the Haughton and Engelbrecht collections together with specimens more recently collected by Dr W. J. Kennedy.

Systematic descriptions

Family **TEREBRATULIDAE** Gray, 1840

Subfamily **RECTITHYRIDINAE** Muir-Wood, 1965

Genus ***PRAELONGITHYRIS*** Middlemiss, 1959

Praelongithyris vanhoepeni (Lang)

Figs 1, 8a–c, 9a–c

1937 *Terebratula Van Hoepeni* Lang : 206; pl. 9, figs 13a–f.

EMENDED DESCRIPTION. *Praelongithyris* 25·1 mm long, 23 mm wide and 14·6 mm thick. A short, massive, suberect umbo is truncated by a large circular foramen with a well-developed pedicle

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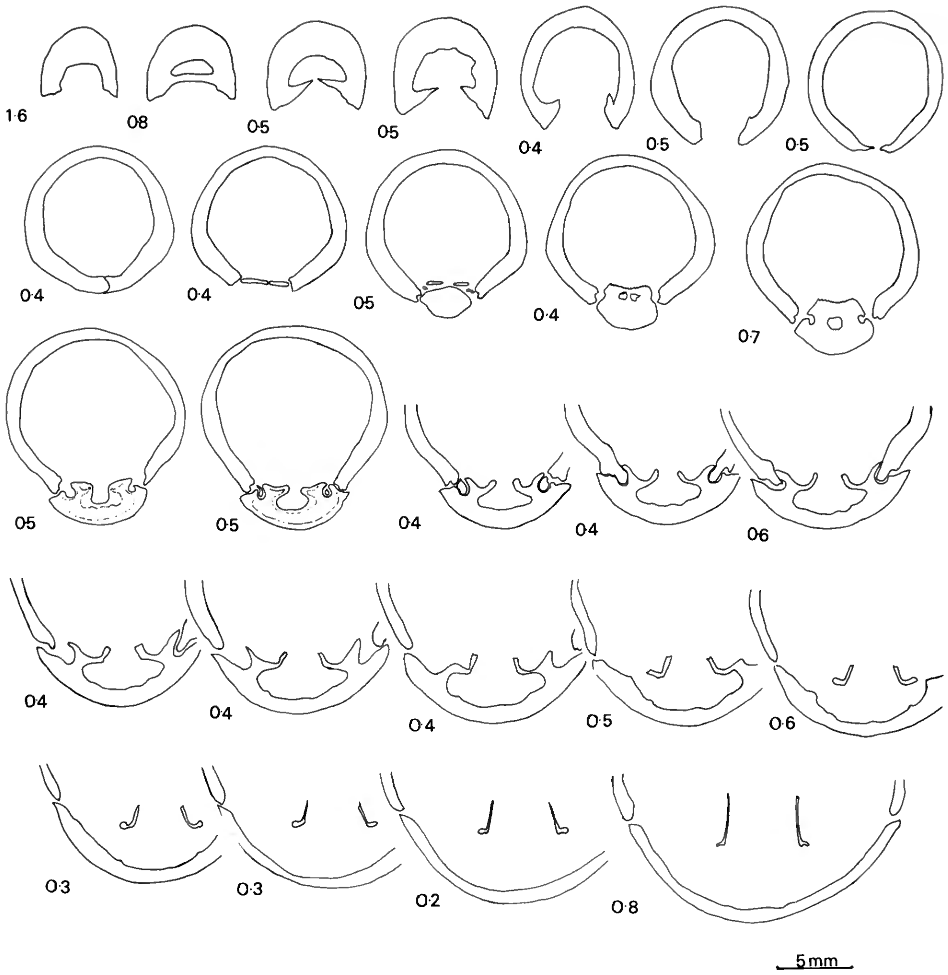


Fig. 1 *Praelongithyris vanhoepeni* (Lang). 26 transverse serial sections through the umbo of a specimen from the Upper Albian, Mzinene Formation, Munywana Creek, northern Zululand. ×2.

collar. Well-defined permesothyridid beak-ridges border a triangular interarea, exposing conjunct deltidial plates. The shell outline is elongate-oval with maximum width at about half the length of the shell. The lateral commissure is acutely deflected ventrally at the anterior end of the shell. The anterior commissure varies from biplicate to sulciplicate, the majority of variants being acutely biplicate. Numerous well-defined concentric growth-lines on the shell surface become closer or more lamellose anteriorly. A faint longitudinal ornament of imbricated striae radiate from the umbonal area of each valve, becoming a little more distinct towards the margins.

Internal characters. The series of 26 transverse serial sections through the umbo of a duplicate specimen of *P. vanhoepeni* shown here (Fig. 1) confirms the assignment of this species to the genus *Praelongithyris*. This is also the opinion of the author of the genus, Dr F. A. Middlemiss (personal communication).

The sections show the characteristic circular transverse outline of the shell cavity, small but thickened cardinal process, virgate and clubbed hinge-plates and extensive or elongated crural processes.

LECTOTYPE. In his original description of the species under the name *Terebratula Van Hoepeni*, Lang (1937 : 206) did not designate a type specimen but mentioned two examples, one of which he figured (pl. 9, figs 13a–f) from the Albian of Ndabana-Umsinene. This specimen, which is here selected as lectotype of the species, was stated to be part of the Stefanini Collection which is in the Istituto Geologico, Universita di Pisa, Italy. The second specimen was said to belong to the Gortani Collection.

MATERIAL AND LOCALITY. Apart from the two specimens already mentioned, nine more were collected from beds considered to be of Upper Albian age, Mzinene Formation at the river cliff, south side of the main southern tributary of Munywana Creek, 1·5 km ESE of the farm Izwehelia, 27°51′36″S, 32°19′41″E (Loc. 64, Kennedy & Klinger 1975 : 289); BM(NH) Palaeontology Dept. BB 81000–8. Two of these are figured here as Figs 8–9.

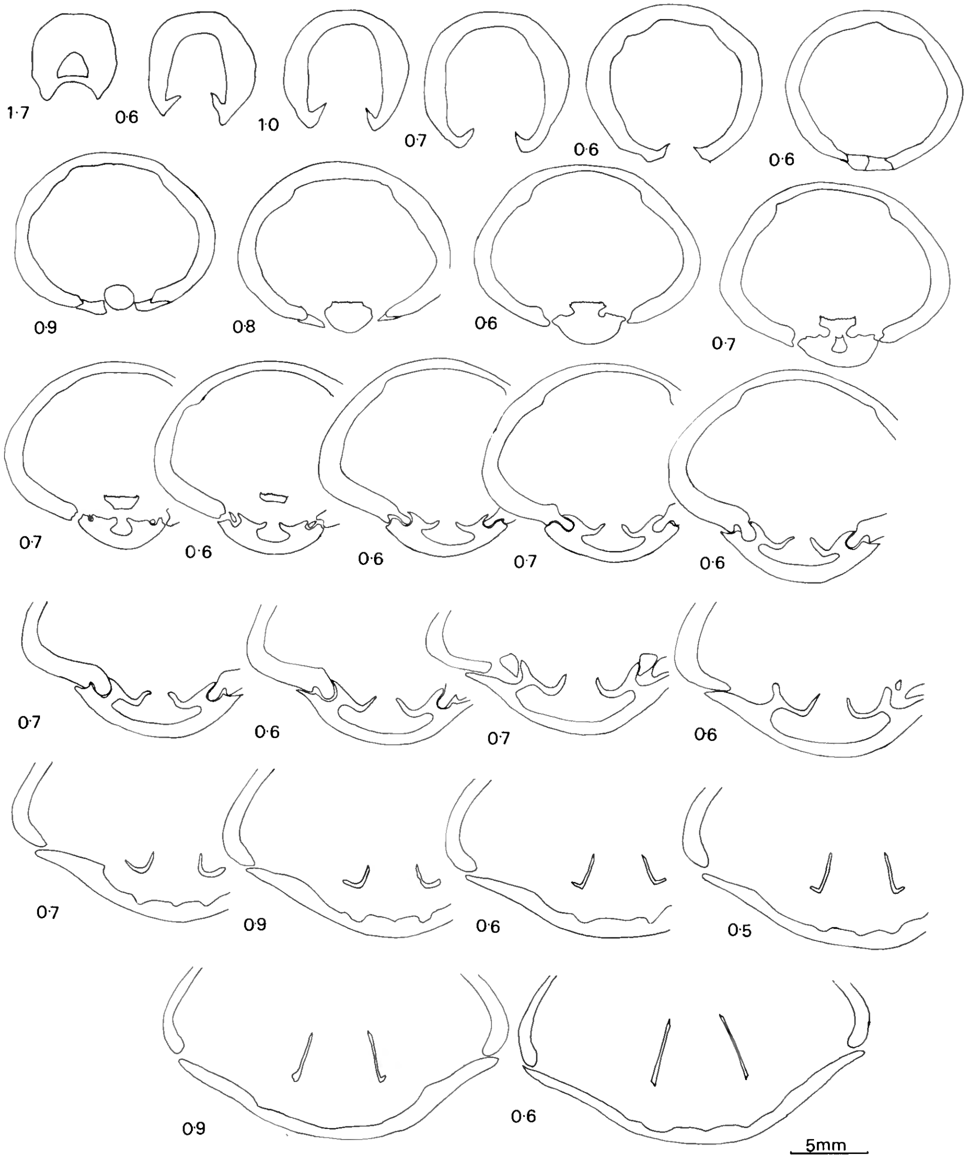


Fig. 2 *Cyrtothyris ndumuensis* sp. nov. 25 transverse serial sections through the umbo of a specimen from the Upper Albian, Mzinene Formation, Ndumu, northern Zululand. ×2.

REMARKS. Fabre (*in* Collignon 1950 : 27; pl. 3, figs 13a–c, 14, 14a) described two Malagasy terebratulids as *Terebratula sella* Sowerby. These specimens show a remarkable similarity to the specimens from Zululand. Although the internal structures of Fabre's specimens are unknown, it seems clear from the external morphology that the specimens which she figured can be assigned to the genus *Praelongithyris*. Furthermore, in her description of the species (1950 : 27), she states that the shell surface has an ornament of fine striae which are clearly visible, a point emphasized by Lang (1937) in his original description of *Terebratula Van Hoepeni* and also noted on examples figured here.

Apart from the occurrence of *Praelongithyris vanhoepeni* in Zululand and possibly in Madagascar, specimens externally similar have been collected, from beds of Upper or Lower Albian age at Kara Bair Dagh, Khorassan, northern Iran, by the Amiranian Oil Company; these were donated to the BM(NH).

Muir-Wood (1953) described and figured a single terebratulid from the Skoenberg Beds, Cenomanian, of Munywana Creek, Zululand, naming the species *manuanensis* and leaving it broadly assigned to *Terebratula*, believing it unrelated to *T. Van Hoepeni* Lang, and pointing out the differences in external morphology which she considered distinguished the two species. In her description of '*Terebratula*' *manuanensis* she mentioned the presence of longitudinal striae on the shell surface, a character which also occurs in *T. Van Hoepeni*. Unfortunately no further material which can be identified as '*T.*' *manuanensis* has since come to light and so the internal characters are still unknown. It is hoped that material will become available for serial sectioning before long.

Genus *CYRTOTHYRIS* Middlemiss, 1959

Cyrtothyris ndumuensis sp. nov.

Figs 2, 10a–c, 11a–c, 12a–c, 13a–c

DESCRIPTION. *Cyrtothyris* elongate-oval to subcircular in general outline. Almost evenly biconvex. Umbo broad, massive, suberect. Foramen large, circular, labiate. Extensive triangular interarea flanked by sharp or clearly-defined mesothyridid beak-ridges. Small, well-exposed symphytium. Shell surface smooth but with well-marked concentric growth-lines, more prominent at the margins. Lateral commissure almost straight. Anterior commissure uniplicate to moderately biplicate.

Internal characters. A series of 25 transverse serial sections (Fig. 2) through the umbo of a duplicate specimen from the type locality show a well-developed pedicle collar, the small, flat cardinal process becoming larger with secondary thickening. Virgate hinge-plates develop anteriorly with extensive inner and outer socket ridges. Long, inwardly-deflected crural processes give rise to strong crural flanges which diminish anteriorly as the brachial loop assumes a broad triangular shape. Transverse band not seen.

HOLOTYPE. The specimen figured here, Fig. 11, from the Mzinene Formation, Upper Albian, 5·5 km SE of the store at Ndumu, northern Zululand. Geological Survey of South Africa Collection. Dimensions, length 29·5 mm, breadth 23·0 mm and thickness 16·9 mm.

MATERIAL AND LOCALITIES. In addition to the holotype, there are the two specimens shown in Figs 12–13 and six others from the same horizon and locality. Three specimens (Fig. 10) considered to be variants are from the low slopes on the western end of Mzinene Pan, also from the Mzinene Formation of Albian age.

REMARKS. *Cyrtothyris ndumuensis* sp. nov. bears a strong resemblance to terebratulid brachiopods figured by Fabre (*in* Collignon 1949 : 11; pl. 1, figs 13a–c, 14, 14a), who briefly described specimens from the Albian of Madagascar as *Terebratula subrotunda* Sowerby. She points out the extreme variability of the species and compares it to a rotund terebratulid described by Stoliczka (1872 : 23; pl. 6, figs 17–23) as *T. subrotunda* Sowerby from the Middle Cretaceous, Trichinopoly Beds of Arialoor, southern India. She mistakenly attributes the variety *subundata* to Stoliczka.

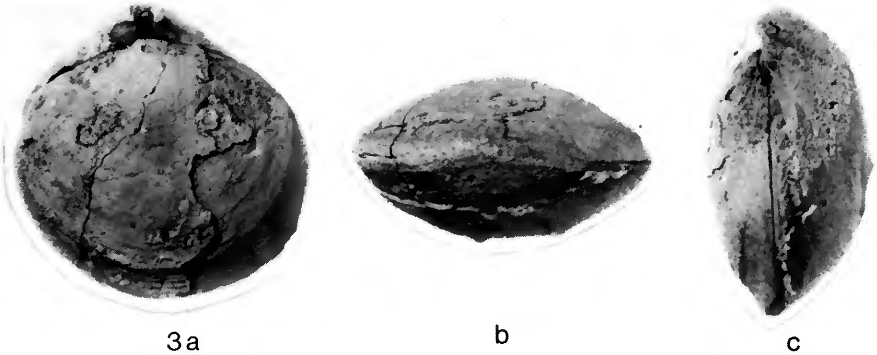


Fig. 3 *Dzirulina haughtoni* sp. nov., from the Upper Aptian, Mfongosi Spruit, northern Zululand. **Holotype.** a, dorsal view. b, anterior view. c, lateral view. ×2. Geological Survey of South Africa coll.

Superfamily **DALLINOIDEA** Beecher, 1893

Family **KINGENIDAE** Elliott, 1948
[*nom. transl.* Owen, 1970]

Subfamily **KINGENINAE** Elliott, 1948

Genus ***DZIRULINA*** Noutsoubidze, 1945

Dzirulina haughtoni sp. nov.
Figs 3, 4

DESCRIPTION. *Dzirulina* 20·5 mm long, 19·8 mm wide and 11 mm in thickness. Evenly biconvex, almost circular in general outline. Broad, massive umbo, well-developed and slightly produced. Beak suberect, beak-ridges sharp, permesothyridid, defining an extensive interarea with well-exposed deltidium and moderately large, circular foramen. Shell surface without ornament except well-marked, evenly spaced concentric growth-lines. Faint longitudinal radiating striae are seen on exposed parts of secondary shell.

Internal characters. From the 19 transverse serial sections (Fig. 4) prepared from a duplicate specimen identified as *Dzirulina haughtoni* from the type locality and horizon it is seen that no cardinal process is developed. Comparatively short, divergent dental lamellae support elongate, peg-like hinge-teeth. The broad, flattened hinge-trough has a central depression or shallow groove which is deeper towards the anterior end of the trough at the point of attachment with the supporting high, well-developed median septum. The descending branches of the brachial loop develop elongate, inwardly curving crural processes and diminish rapidly anteriorly. There is no attachment of descending branches of the loop to the median septum. The conical kingeniform hood is developed from the ascending branches which form an acute Y-shaped angle at the point of attachment to the median septum, approximately mid-way along the septal pillar.

NAME. For Dr S. H. Haughton.

HOLOTYPE. A specimen (Fig. 3) selected from four poorly-preserved but almost whole examples in the Engelbrecht Collection. From Haughton's locality Z2, Mfongosi Spruit, from bluffs along the ridge on the north side of the stream, 700–1200 m ESE of the old drift, 27°21′43″S, 32°09′25″E (Loc. 168; Kennedy & Klinger 1975 : 302).

HORIZON. Haughton (1936 : 301) considered the above locality to have yielded bivalvia of Neocomian age, but there is insufficient ammonite evidence to support his views. He based his assumption on the occurrence of two indigenous bivalves, *Trigonia pongolensis* and *Cardium rogersi*. Kennedy & Klinger (1975 : 301) have suggested an Upper Aptian age for the same section.

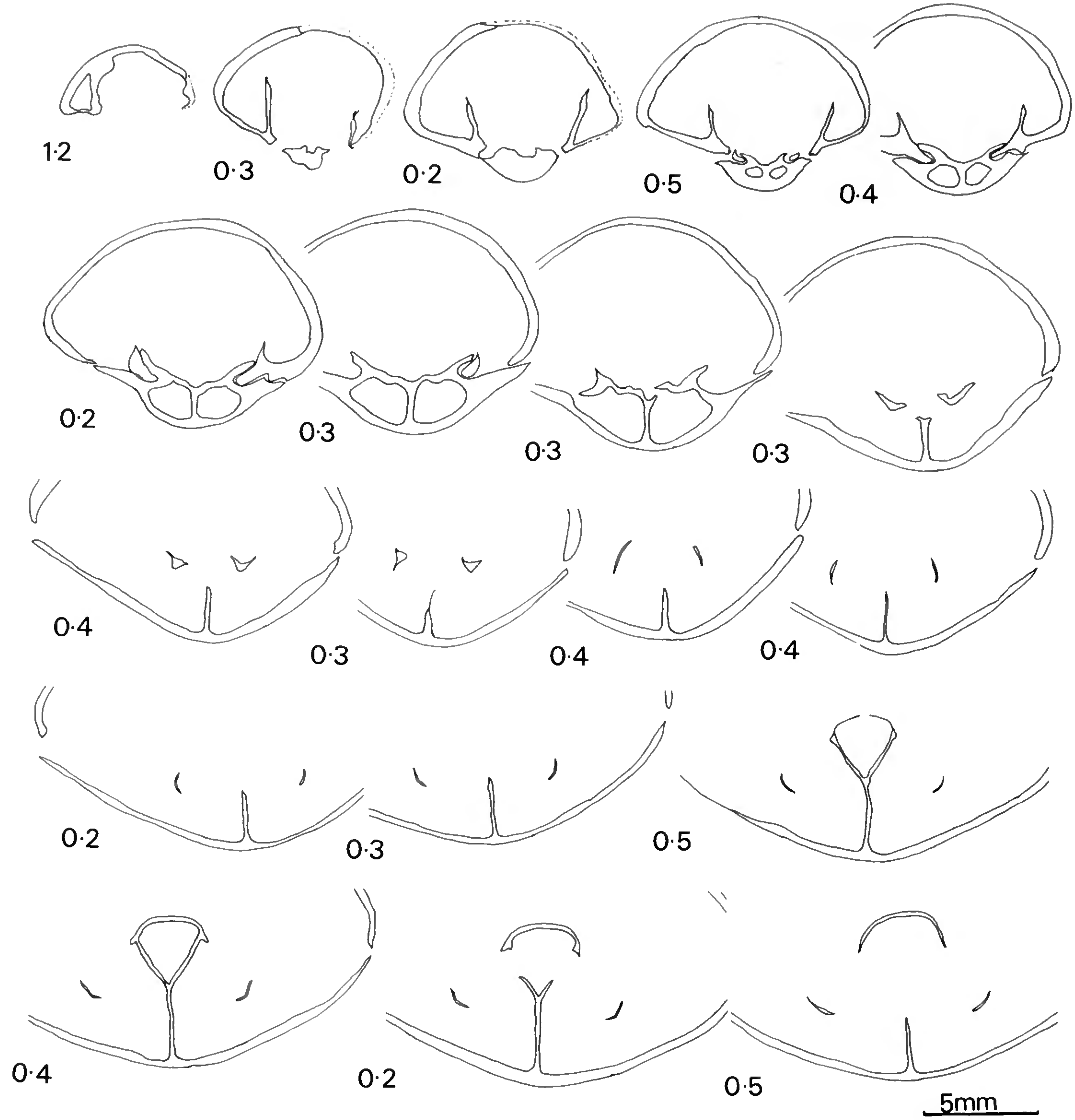


Fig. 4 *Dzirulina haughtoni* sp. nov. 19 transverse serial sections through a specimen from the Upper Aptian of Mfongosi Spruit, northern Zululand. ×3.

REMARKS. Noutsoubidze (1945 : 186) based *Dzirulina* on the Aptian species *Terebratula dzirulensis* Anthula from western Georgia, but was not able to illustrate or describe the internal structures of the type species. In a revision of the genus *Dzirulina*, Kvakhadze (1972) was able to show a series of transverse serial sections through a specimen of *D. dzirulensis* from the type locality, which shows it to be a senior synonym of *Belothyris* Smirnova (1960 : 114), described from the Lower Cretaceous of Beloya, north-western Caucasus. Representative species of this genus are not uncommon in beds of Hauterivian and Barremian age in central and western Europe. Owen (1970) recorded *Belothyris pseudojurensis* (Leymerie) from Hauterivian Beds in Switzerland and eastern France and described a species, *B. nettletonensis*, from beds of possible Hauterivian age at Nettleton, Lincolnshire, England.

Kvakhadze (1972) described a new species under the name *Dzirulina elliptica* from the Barremian of Tskaltsitela River, Kutaisi, Georgia, and this bears a very strong resemblance in shell convexity, general outline and umbonal characters to *D. haughtoni*. The series of transverse serial sections given in Kvakhadze (1972 : fig. 4) accord favourably with those shown here (Fig. 4) for *D. haughtoni*. They are also identical to a series recently made from a specimen of an undescribed species from the ?Aptian of Pezu, Pakistan, now in the BM(NH).

Superfamily **RHYNCHONELLACEA** Gray, 1848

Family **RHYNCHONELLIDAE** Gray, 1848

Subfamily **CYCLOTHYRIDINAE** Makridin, 1955

Genus ***CYCLOTHYRIS*** M'Coy, 1844

Cyclothyris africana sp. nov.

Figs 5, 6

1950 *Rhynchonella sulcata* Dav. var. *paludensis* Jacob & Fallot; Fabre *in* Collignon: pl. 3, figs 11, 11a–c.

DIAGNOSIS. *Cyclothyris c.* 15·1 mm long 19·1 mm wide and 10·9 mm thick. Biconvex, oval in general outline, umbo short, beak suberect, foramen small. Beak-ridges indistinct, interarea short. Brachial valve with acute posterior umbonal inflation and broad, almost imperceptible fold. Pedicle valve with wide, shallow sulcus and trapezoidal linguiform extension.

DESCRIPTION. Both valves are ornamented by *c.* 35–40 fine radiating costae, originating as very fine costellae in the umbonal regions and becoming progressively distinct and more deeply incised towards the shell margins. A low median septum is just visible in the brachial umbo of better-preserved examples.

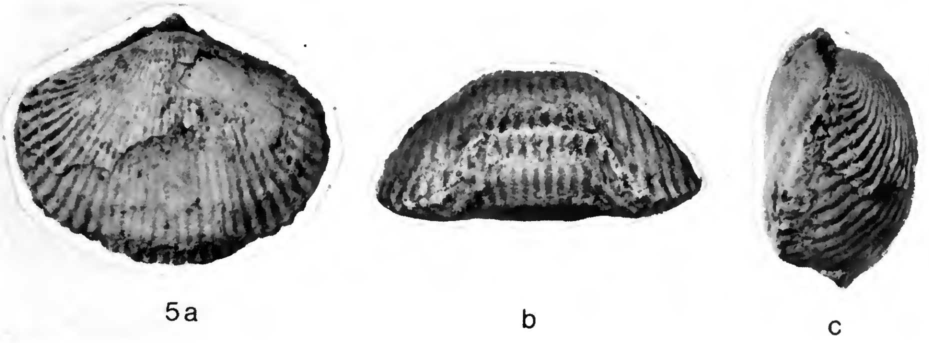


Fig. 5 *Cyclothyris africana* sp. nov., from the Upper Albian, Mzinene Formation, river cliff near Munywana Creek, northern Zululand. **Holotype.** a, dorsal view. b, anterior view. c, lateral view. ×2. Geological Survey of South Africa coll.

Internal characters. The transverse serial sections (Fig. 6) through a poorly-preserved but almost complete specimen confirm that the species belongs to the genus *Cyclothyris*.

The characteristic arrangement of the dorsally deflected hinge-plates, the concave surface of the distal ends of the crura and general transverse outline of the shell are similar to those of the Lower Albian *Cyclothyris deluci* (Pictet) from Perte-du-Rhône, France and its probable junior synonym *C. shenleyensis* (Walker) from Leighton Buzzard, Bedfordshire, England. It also bears a superficial resemblance to the subspecies *C. deluci clavelli* Calzada Badía, 1975, from the Lower Albian of Alcalá de Chivert, Spain. It differs from specimens assigned to *Cyclothyris antidichotoma* (Buvignier) from the Upper Aptian of Upware, Cambridge (Owen 1962 : 48, fig. 5) in having more persistent and less divergent dental lamellae and more acutely curved or dorsally deflected hinge plates.

NAME. 'African'.

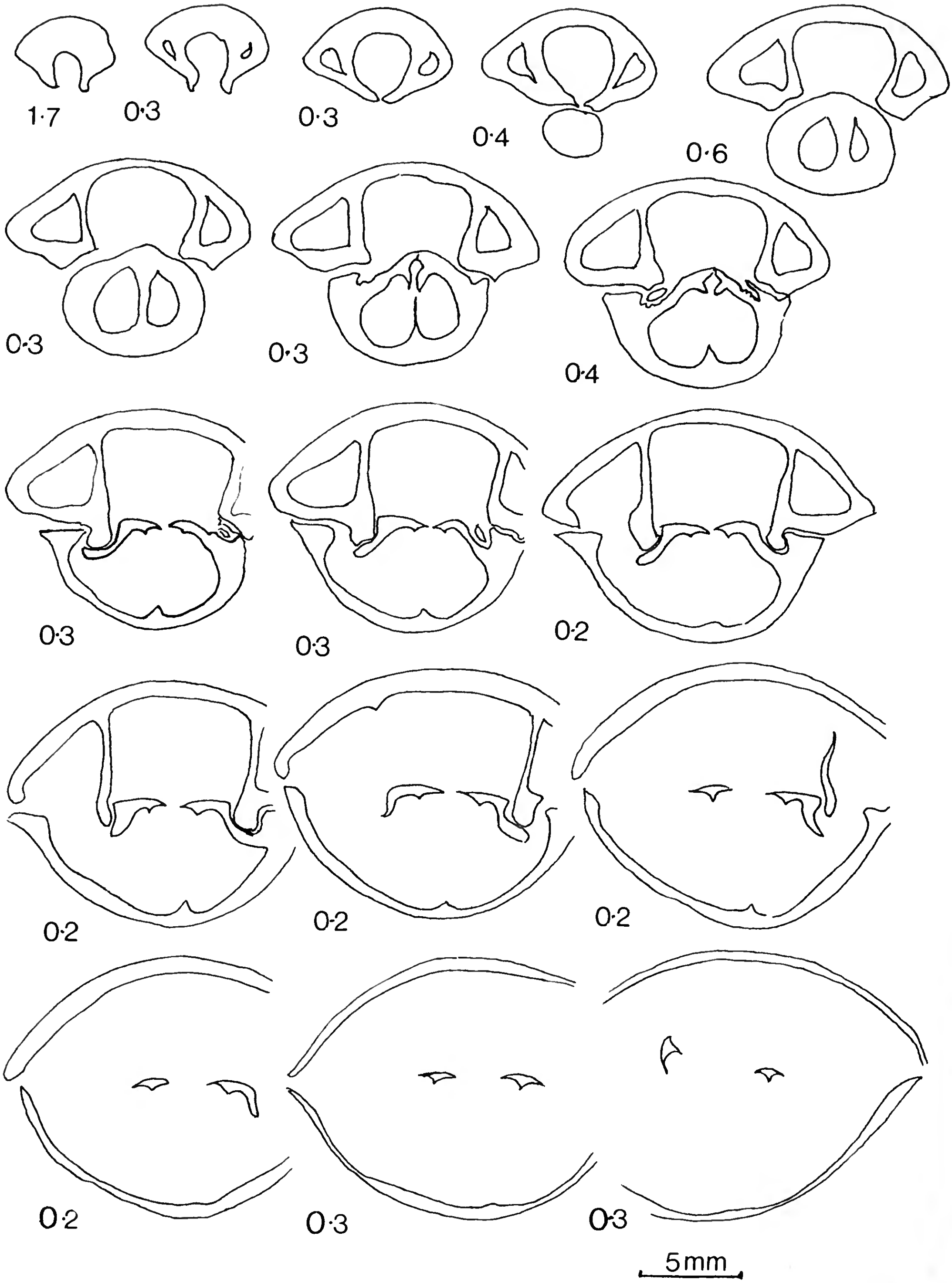


Fig. 6 *Cyclothyris africana* sp. nov. 17 transverse serial sections through a specimen from the Upper Albian, Mzinene Formation, river cliff near Munywana Creek, northern Zululand. ×3.

HOLOTYPE. The specimen figured here (Fig. 5), from the Upper Albian, Mzinene Formation, river cliff on south side of main southern tributary of Munywana Creek, 1·5 km ESE of the farm Izwehlia, northern Zululand (Loc. 64; Kennedy & Klinger 1975 : 289. See p. 275).

MATERIAL. Duplicate specimen from the type locality shown here in transverse serial section (Fig. 6), and two other specimens from the same locality and horizon.

REMARKS. *Cyclothyris africana* is closely related to the European species *C. deluci* from the Albian of Perte-du-Rhône, France. It may also have affinities with a form described and figured from the Upper Aptian (*jacobi* subzone) of Saltwood, near Folkestone, Kent (Owen 1960) as *C. deluci*, but now thought to be distinct.

Fabre (*in* Collignon 1950) described and figured a series of five rhynchonellids from Albian beds of Komihevitra, Madagascar. All five examples can be matched with specimens collected from beds of a similar age from northern Zululand. The specimen figured by Fabre (1950 : pl. 3, figs 11) is thought to belong to *C. africana*. It has similar general outline and costation, similar fold and sulcus and the same degree of inflation of the umbonal region of the brachial valve. It also bears a superficial resemblance to an incomplete rhynchonellid specimen from the ?Aptian–Albian beds of Sheik Budin, Pakistan, BB 18842 in the Department of Palaeontology, BM(NH).

Cyclothyris kennedyi sp. nov.

Fig. 7

DESCRIPTION. Robust, biconvex *Cyclothyris*, more circular in general outline than *C. africana* and with 18–20 coarse, well-incised radiating costae showing well-marked transverse lamellar growth-lines thickening at the shell margins. The hinge-line is broad or slightly extended, with a comparatively wide triangular interarea, large circular foramen and sharp beak-ridges. The median fold on the brachial valve is not clearly defined but the anterior shows a low, shallow sulcation and short, arcuate, linguiform extension.

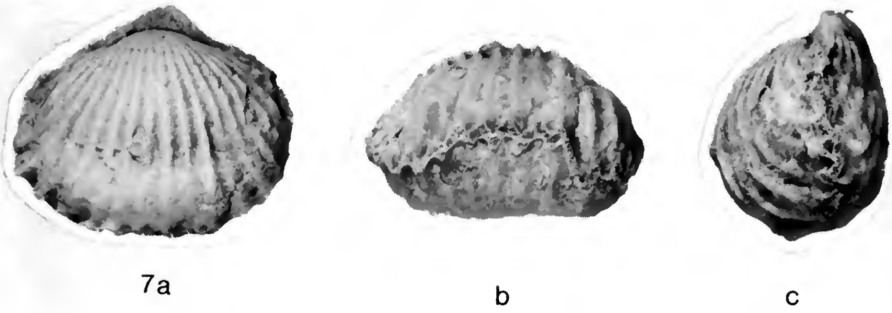


Fig. 7 *Cyclothyris kennedyi* sp. nov., from the Upper Albian, Mzinene Formation, near Ndumu, northern Zululand. **Holotype.** a, dorsal view. b, anterior view. c, lateral view. ×2. Geological Survey of South Africa coll.

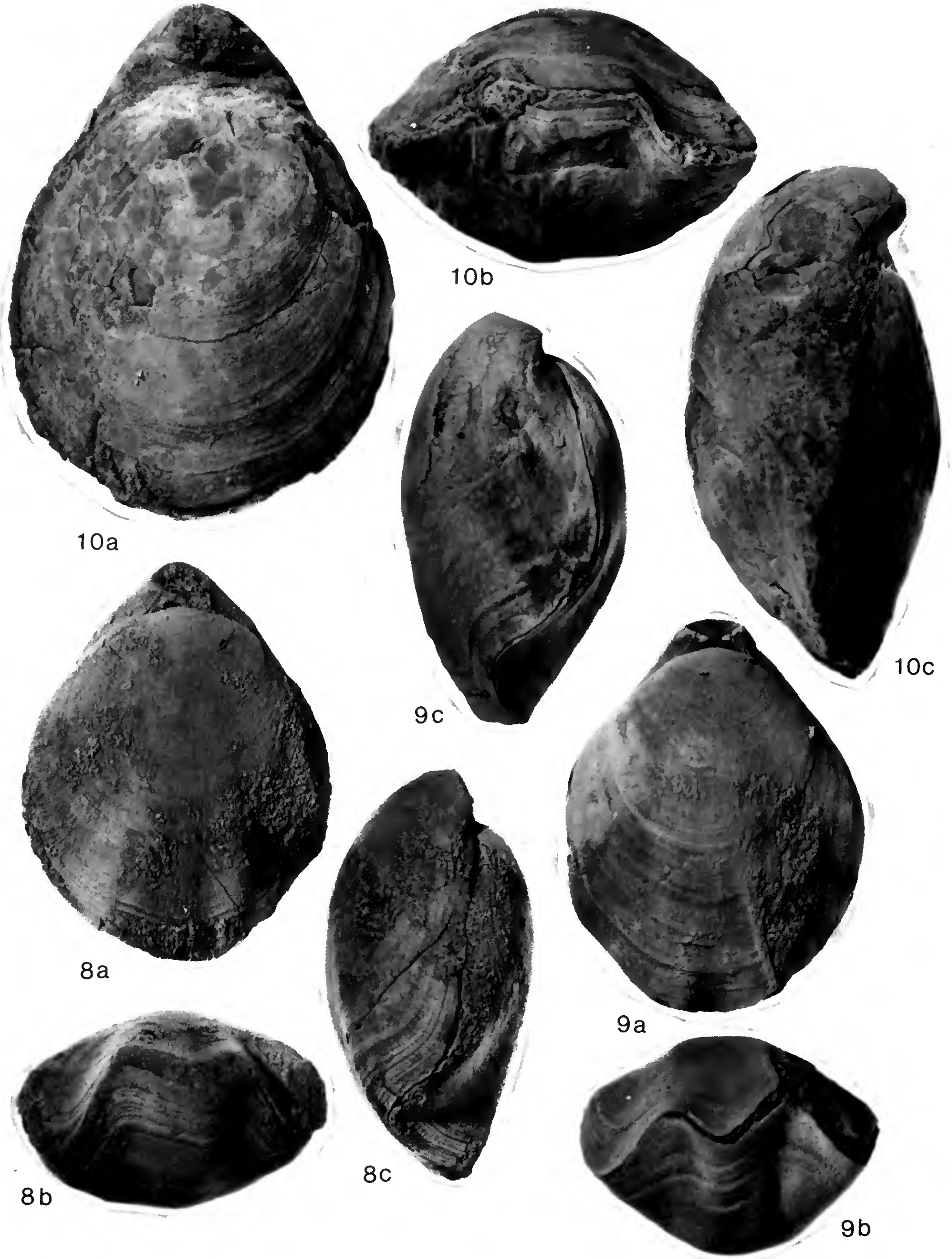
Internal characters. As for *Cyclothyris africana* sp. nov., p. 279.

NAME. For Dr W. J. Kennedy.

HOLOTYPE. From locality L.J.E.549, Upper Albian, Mzinene Formation, 5·5 km SE of the store at Ndumu, northern Zululand. In the collections of the Geological Survey of South Africa, Pretoria.

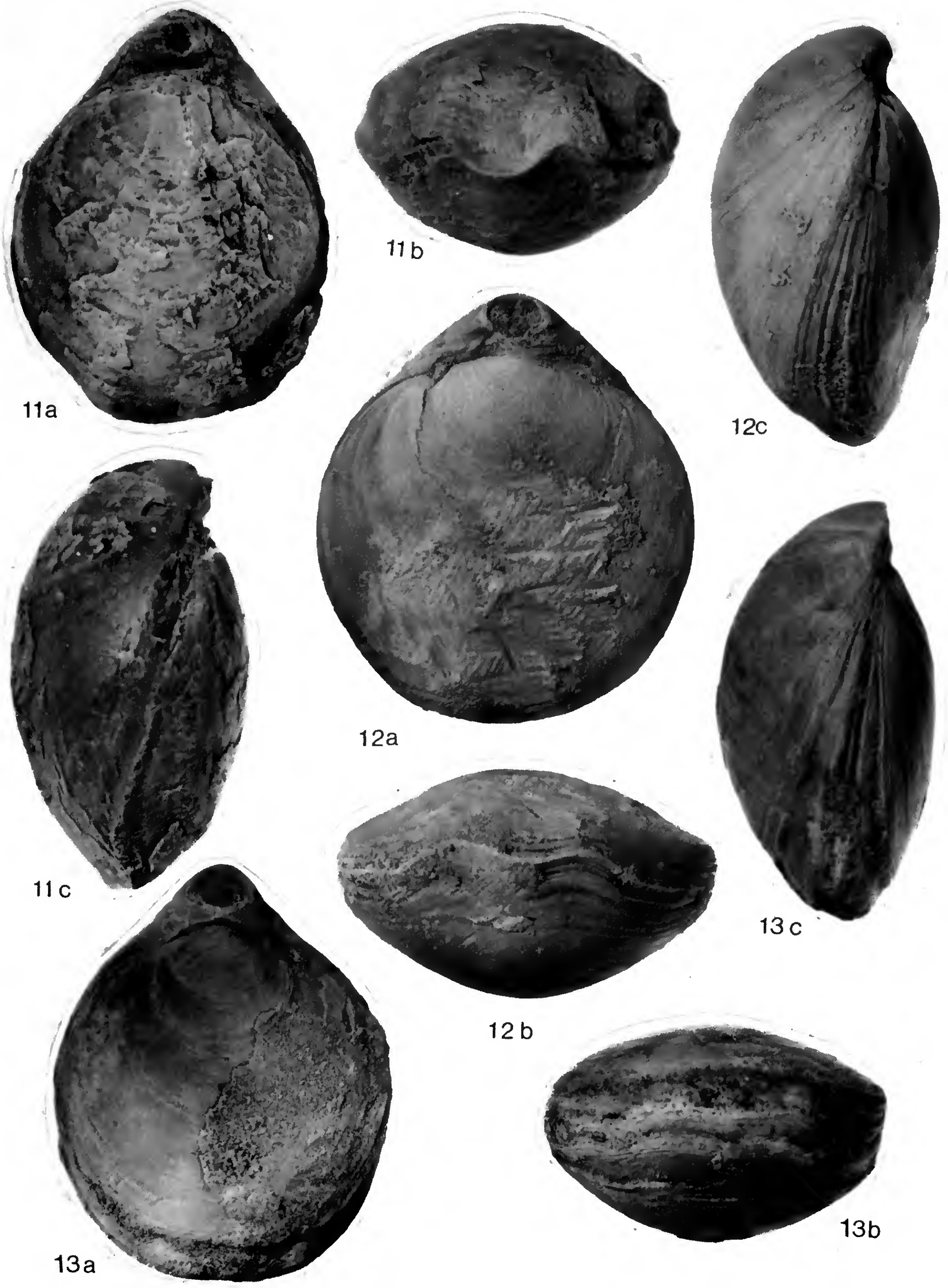
MATERIAL. A further seven specimens from the same locality and horizon.

REMARKS. Once again the species described here as *Cyclothyris kennedyi* strongly resembles a form which occurs in the Albian beds of Madagascar. Fabre (*in* Collignon 1950 : pl. 3, figs 8, 8a)



Figs 8, 9 *Praelongithyris vanhoepeni* (Lang). Figs 8a–c, BB 81006; Figs 9a–c, BB 81004. Both BM(NH) coll., from the Upper Albian, river cliff on south side of main southern tributary of Munywana Creek, northern Zululand. All ×2.

Fig. 10 *Cyrtothyris ndumuensis* sp. nov., from the Upper Albian, Mzinene Formation, Mzinene Pan, northern Zululand. This specimen is considered to be a variant of the species. a, dorsal view. b, anterior view. c, lateral view. ×2. Geological Survey of South Africa coll.



Figs 11–13 *Cyrtothyris ndumuensis* sp. nov., from the Upper Albian, Mzinene Formation, SE of store at Ndumu, northern Zululand. Figs 11a–c, **Holotype.** a, dorsal views. b, anterior views. c, lateral views. All ×2. Geological Survey of South Africa coll.

described and figured a specimen as *Rhynchonella* cf. *polygona* d'Orbigny which agrees with *C. kennedyi* in outline, costation and convexity. Three other specimens shown on the same plate may also be synonyms of *C. kennedyi*; they are named by Fabre as *Rhynchonella sulcata* Dav. (figs 9, 9a–b), *Rhynchonella sulcata* var. *salazacensis* Jacob & Fallot (figs 10, 10a–c) and *Rhynchonella deluci* Pictet (figs 12, 12a–c).

Conclusions

It is generally acknowledged by molluscan workers and others that a strong link appears to exist between the continent of Africa, Madagascar and parts of western Asia in the Aptian and Albian. The additional information from the brachiopod faunas strengthens the link and enlarges our view of the ubiquity of some brachiopod genera and species within a comparatively short time-span. It would be interesting to trace the occurrence of these related faunas still further. As yet the brachiopod facies faunas of the Aptian–Albian of Pakistan and the NW Caucasus are almost unknown and their relationship to similar faunas from central and eastern Europe remains speculative. However, more light is beginning to dawn upon these problems with our greater understanding of internal structures arising from the wider use of transverse serial sections, which tends to broaden our ideas on synonymies.

Acknowledgements

I wish to thank Dr H. C. Klinger and the Director of the South African Geological Survey for the loan of brachiopod material which has been used in this paper. I would also like to thank Dr W. J. Kennedy (Oxford) for his generous help and patience, and Mr J. V. Brown (Photographic Unit, BM(NH)) for the photographs.

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Tupus diluculum sp. nov. (Protodonata), a giant dragonfly from the Upper Carboniferous of Britain

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Synopsis

A description is given of *Tupus diluculum* sp. nov., Insecta, Protodonata, from the Westphalian A (Upper Carboniferous) of Derbyshire.

Introduction

The discovery of a fossil dragonfly with a wingspan of about 200 mm, larger than any living dragonfly, was recently recorded (Whalley 1978a, b, 1979) from a colliery at Bolsover, Derbyshire; it was found some 600 metres below ground. The interest aroused by this insect undoubtedly led to the discovery of a second specimen of a different species in dark grey shale in the same coal mine. The new dragonfly had an estimated wingspan of over 500 mm, making it the largest ever found in Britain. It was found in the same bed and at almost exactly the same height above the coal seam as the previous one, but at some distance from it. Thus it is likely that these two insects were contemporaneous, flying at the edges of the coal forests. The size of the wings makes it unlikely that they flew in thicker parts of the forests and, perhaps like present-day dragonflies, they kept to the margins of fresh water and to the more open parts of woods.

The specimen, which is a hindwing, is broken with some fragments missing, thus precluding an exact measurement of it, but at a conservative estimate the length of one wing was not less than 250 mm. From its venation it is evidently a species of the genus *Tupus* Sellards (Meganeuridae, Tupinae; = Typinae, *sensu* Carpenter 1939 : 37). Species of the subfamily Tupinae are known from the Permian and Upper Carboniferous of Russia and America. The new specimen is extremely similar to *Tupus permianus* Sellards 1906, from the Permian of America (Professor F. Carpenter, *in litt.*), but is much larger. This suggests a remarkable stability of wing venation over 20 million years or more.

Systematics

PROTODONATA, MEGANEURIDAE

Diagnosis. Dragonfly-like insects which lack the nodus, arculus and pterostigma of typical Odonata.

Subfamily **TUPINAE** Handlirsch, 1919

[*nom. correct. & transl.* Whalley, herein (*ex* Typidae Handlirsch, 1919: 572)]

Genus ***TUPUS*** Sellards, 1906

The family-group name Typidae[1] Handlirsch, 1919, was based on the unjustified emendation of the generic name to *Typus*, adopted by Sellards (1909 : 151) and followed by Carpenter (1939, 1960) and many others.

Diagnosis. Rs forks near middle of wing. Subcosta very long.

Tupus diluculum sp. nov.

Diagnosis. Hindwing, maximum width 50 mm. Total length of fragments 235 mm; estimated total wingspan over 500 mm. The costal margin near the base is slightly toothed. The wing

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[1] Application has however been made to the ICZN for conservation of the generic name *Typus* and the family-group name Typidae.

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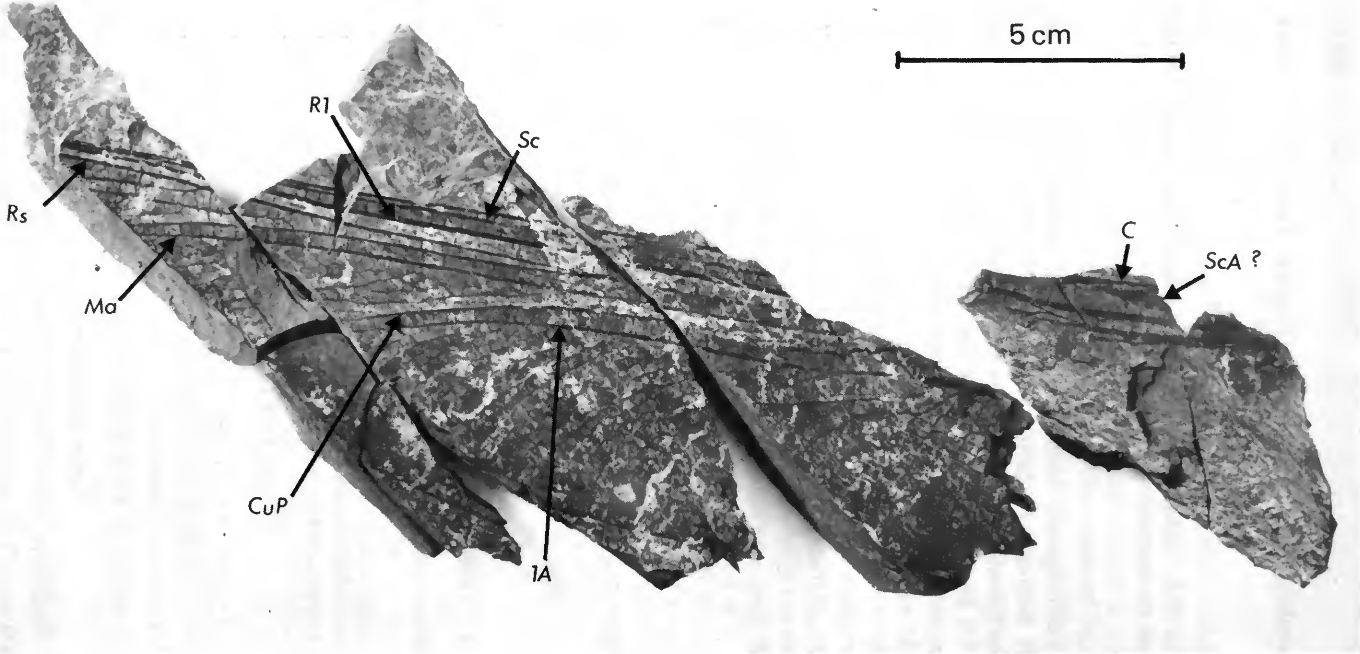

Fig. 1 *Tupus diluculum* sp. nov. Holotype, hindwing. Upper Carboniferous, Westphalian A; Bolsover Colliery, Derbyshire, England. $\times\frac{3}{4}$. 1A, first anal. C, costa. CuP, posterior cubitus. Ma, anterior media. R1, first radial. Rs, radial sector. Sc, subcosta. ScA, anterior subcosta.

impression is preserved upside down (no counterpart). Vein Rs first divides near the middle of the wing. The anterior branch of Ma and posterior branch of Rs run parallel towards the wing margin for most of their length. Similarly CuP and 1A are very evenly separated across the wing. The figure (opposite) shows the veins preserved near the base but it is not possible to determine whether the mark near the base of the costa (ScA ? in the figure) is really a trace of vein ScA.

NAME. Diluculum, Latin, dawn.

HOLOTYPE. Hindwing, Upper Carboniferous, Westphalian A; Bolsover Colliery, Derbyshire, Deep Hard, from roof of seam 15–17 cm above coal, about 600 m deep; coll. G. Ball, 10.8.1978; In.64553 in BM(NH), presented by the National Coal Board.

DISCUSSION. This species can be distinguished from all other *Tupus* by its large size. The subcosta is very long, reaching three-quarters of the way along the costa. *Tupus diluculum* not only extends the geographical range of the genus, species of which are known from Russia and America, but also shows that large size was reached some 10–20 million years before the famous giant fossil dragonflies from Commentry, France (Laurentiaux 1953). Although the species from Commentry are in the same family as the one from Derbyshire, they are currently placed in different subfamilies. *T. diluculum* is the largest known insect from the Westphalian A and certainly the earliest of the giant dragonflies.

Acknowledgements

I am indebted to the National Coal Board for presenting the specimen to the National Collection and to Dr M. Calver for conveying it safely to London. Dr F. Carpenter and Dr J. Kukalová-Peck sent me valuable comments after seeing the photograph; I am most grateful to both. The specimen was prepared and mounted by F. M. P. Howie, Dept of Palaeontology, BM(NH), to whom I offer my thanks.

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Revision of *Plummerita* Brönnimann (Foraminiferida) and a new Maastrichtian species from Ecuador

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Synopsis

Plummerita is emended to include all rugoglobigerinid foraminifera with tubulospinose chambers in the final whorl. The genus, formerly monotypic, now includes *P. hantkeninoides* (Brönnimann) the type-species, *P. reicheli* (Brönnimann) and a new species, *P. kennerleyi*, from Ecuador.

Introduction

Plummerita Brönnimann (1952*a*) was erected as a new name for *Plummerella* Brönnimann, 1952 (*non Plummerella* De Long, 1942). Originally a subgenus of *Rugoglobigerina*, it was raised to generic status by Brönnimann & Brown (1956). Until now it contained but one species and three subspecies, *P. hantkeninoides hantkeninoides*, *P. h. costata* and *P. h. inflata*, defined by Brönnimann (1952) on the degree of inflation of the later-formed chambers of the final whorl and variation in what he termed the 'hantkeninoid' portion of the test; this development of 'spinose' chambers in the axis of coiling readily distinguishing *Plummerita* from *Rugoglobigerina*. The 'spines' of *Plummerita*, however, are more correctly termed tubulospines, as originally defined by Montanaro Gallitelli (1955 : 142) in connection with the genus *Schackoina*. That is, they are hollow, spine-like extensions of the chambers (see Figs 12, 17, p. 293); they are connected internally with the chamber cavity and are not solid as are true spines.

That *Plummerita* and *Rugoglobigerina* are closely related is unquestionable, since both have the same type of surface ornamentation and apparently the same apertural features. In spite of Bolli, Loeblich & Tappan's (1957) original misgivings that the development of chamber elongation and tubulospinosity '. . . were only sufficient to warrant specific separation' (1957 : 44), Loeblich & Tappan (1964) accorded *Plummerita* generic status, as did Masters (1977). The value of tubulospines in the classification of planktonic foraminifera, however, remains uncertain. It is now generally accepted that *Plummerita* is distinct from *Rugoglobigerina*, but on the other hand a new genus based on the only tubulospinose *Globotruncana*, *G. calcarata* Cushman, is not warranted.

Recently a remarkable new species, showing elongation of the chambers in different planes to the axis of coiling and with more than one tubulospine per chamber, has been discovered in the Ecuadorian Andes. These features are unlike anything seen in *Plummerita hantkeninoides* (Brönnimann). Rather than propose a new genus I prefer to emend the diagnosis of *Plummerita* to incorporate all tubulospinose species of *Rugoglobigerina*. The new species is named *P. kennerleyi*. Following the suggestion of Masters (1977), *Rugoglobigerina reicheli* Brönnimann is transferred to *Plummerita*, this species showing radial elongation of the chambers and tubulospines in the final whorl, features not found in any other *Rugoglobigerina*.

Topotypes of *P. hantkeninoides* from the Maastrichtian of Trinidad were studied for comparison with *P. kennerleyi*. The opportunity is taken to illustrate the type species by scanning electron microscopy for the first time, and to show intraspecific variability (Figs 2–10, 16). *P. reicheli* is also re-illustrated from type material (Fig. 11).

Acknowledgements

I am particularly indebted to Professor P. Brönnimann, of the University of Geneva, for his generous help in the preparation of this paper and for supplying the specimens of *Plummerita hantkeninoides* and *P. reicheli* from the Guayaguayare Formation of Trinidad. The assistance in the field

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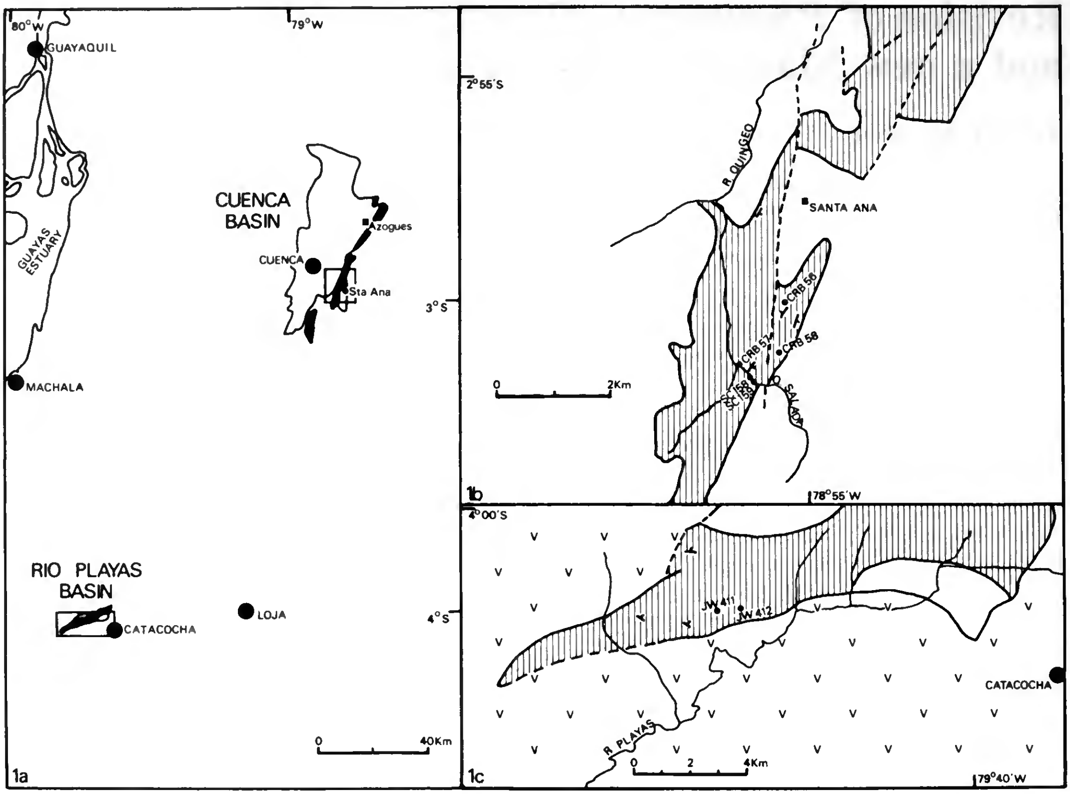


Fig. 1 Locality map. 1a, The Río Playas and Cuenca Basins, south Ecuador; areas shown in detail in Figs 1b, c, are outlined. Figs 1b, c, parts of the Cuenca and Río Playas Basins, respectively. Outcrop of late Cretaceous sediments is indicated by vertical shading; occurrence of *Plummerita kennerleyi* sp. nov. by dots; areas left blank are Tertiary sediments; V = volcanic rocks. (Geology taken from Cariamanga and Gualaceo Sheets, D.G.G.M. 1973–4).

of Dr C. R. Bristow and the late J. B. Kennerley, Institute of Geological Sciences (Overseas Division), London, was much appreciated. My colleagues Dr C. G. Adams and R. L. Hodgkinson are thanked for their critical reading of the manuscript and for their technical assistance, respectively. The SEM photographs were taken by the author and printed by P. P. Lund of the Department of Central Services, British Museum (Natural History). Finally, my wife is thanked for drafting Fig. 1.

Material

All the material illustrated in this paper is housed in the collections of the Protozoa Section, Department of Palaeontology, British Museum (Natural History), London; registered numbers are P 50829–P 50840 inclusive.

Plummerita in Ecuador

Late Cretaceous sediments crop out in several basins within the Ecuadorian Sierra (Andes), in the southwestern Coastal Provinces and in the Oriente to the east of the Andean mountain chain. *Plummerita kennerleyi* sp. nov., however, has only been found so far in the Cuenca and Río Playas Basins (Fig. 1a) described below.

The Cuenca Basin

The Cuenca Basin is the largest Tertiary sedimentary basin of the Ecuadorian Sierra and contains important late Cretaceous sediments which are referred to the Yunguilla Formation (see

Bristow 1973 and Bristow & Hoffstetter 1977, for an explanation of the stratigraphic nomenclature). Most of the recent work in the area has been undertaken by members of the Institute of Geological Sciences (Overseas Division), London (I.G.S.) and three of the samples (CRB 56–58) containing the new species of *Plummerita* were collected in 1972 by Dr C. R. Bristow (I.G.S.). Samples SC 158, 159 came from the collections of the Dirección General de Geología y Minas, Quito, and were collected earlier by a French Technical Aid Mission. Fig. 1b shows these localities in the southeastern part of the Basin just to the south of the small town of Santa Ana. All samples are of black shales from the 'Grupo superior', near the top of the (exposed) Yunguilla Formation, the best material coming from the Quebrada Salada where the shales are particularly friable and the foraminifera easiest to extract. The marine Yunguilla Formation is overlaid unconformably by the Loyola Formation of mid-Miocene age; this and subsequent Tertiary sediments were deposited in brackish or fresh water.

The age of the *Plummerita*-bearing sediments cannot be other than late Cretaceous on the associated foraminifera which include *Gavelinella plummerae* Tappan, *Gavelinella* sp., *Praebulimina joaquinensis* (Martin), *Praebulimina* sp., *Siphogenerinoides revoluta* Stone, *S. parva* Cushman, *S. bramletti* Cushman, *Brizalina* cf. *selmaensis* (Cushman), *Gaudryina laevigata* Franke, and the planktonic species *Heterohelix striata* (Ehrenberg), *H. globulosa* (Ehrenberg), *Hedbergella* spp. and *Rugoglobigerina rugosa* (Plummer). Of these, *Rugoglobigerina rugosa* and *Heterohelix striata* have the shortest stratigraphical range (Santonian to Maastrichtian according to Masters, 1977), although it is probable that the first appearance of the large benthic species *Siphogenerinoides revoluta* is within the Campanian. However, early Maastrichtian ammonites — *Sphenodiscus peruvianus* Gerth and *Solenoceras* sp., identified by Dr M. K. Howarth, British Museum (Natural History) — from the 'Grupo inferior' of the Yunguilla Formation indicate that the age of *Plummerita kennerleyi* in the Cuenca Basin must be either mid or late Maastrichtian.

The Río Playas Basin

This small Andean basin lies some 130 km to the southwest of the Cuenca Basin, just west of Catacocha (Fig. 1c). The sediments, originally studied by Kennerley (1973), are mainly of late Cretaceous age and are very similar in facies and fauna to the Yunguilla Formation farther north. Termed locally the Río Playas Formation, the strata include black shales and some softer, lighter-coloured mudstones with foraminifera. These are in turn overlaid unconformably by brightly coloured freshwater clays and conglomerates of presumed younger Tertiary age (see Bristow & Hoffstetter 1977 : 270). The Río Playas Basin is surrounded by various Cretaceous volcanic rocks.

Two samples, JW 411 and 412, collected by the author in 1974 from the Río Playas Formation, were found to contain *Plummerita kennerleyi*. The localities are shown in Fig. 1c. The associated foraminifera are almost identical to those found with the new species in the Cuenca Basin, and comprise *Gavelinella* sp., *Praebulimina joaquinensis* (Martin), *Siphogenerinoides revoluta* Stone, *S. parva* Cushman, *Anomalinoides* cf. *padella* Jennings, *Brizalina* cf. *selmaensis* (Cushman), *Lenticulina* sp. and the planktonic species *Heterohelix globulosa* (Ehrenberg), *Pseudotextularia elegans* (Rzehak), *Hedbergella* spp. and *Rugoglobigerina rugosa* (Plummer). According to Masters (1977), *Pseudotextularia elegans* is restricted to the Maastrichtian, thus strongly suggesting that *P. kennerleyi* must also be a Maastrichtian species and that the Río Playas specimens are coeval with those from the Cuenas Basin.

Systematics

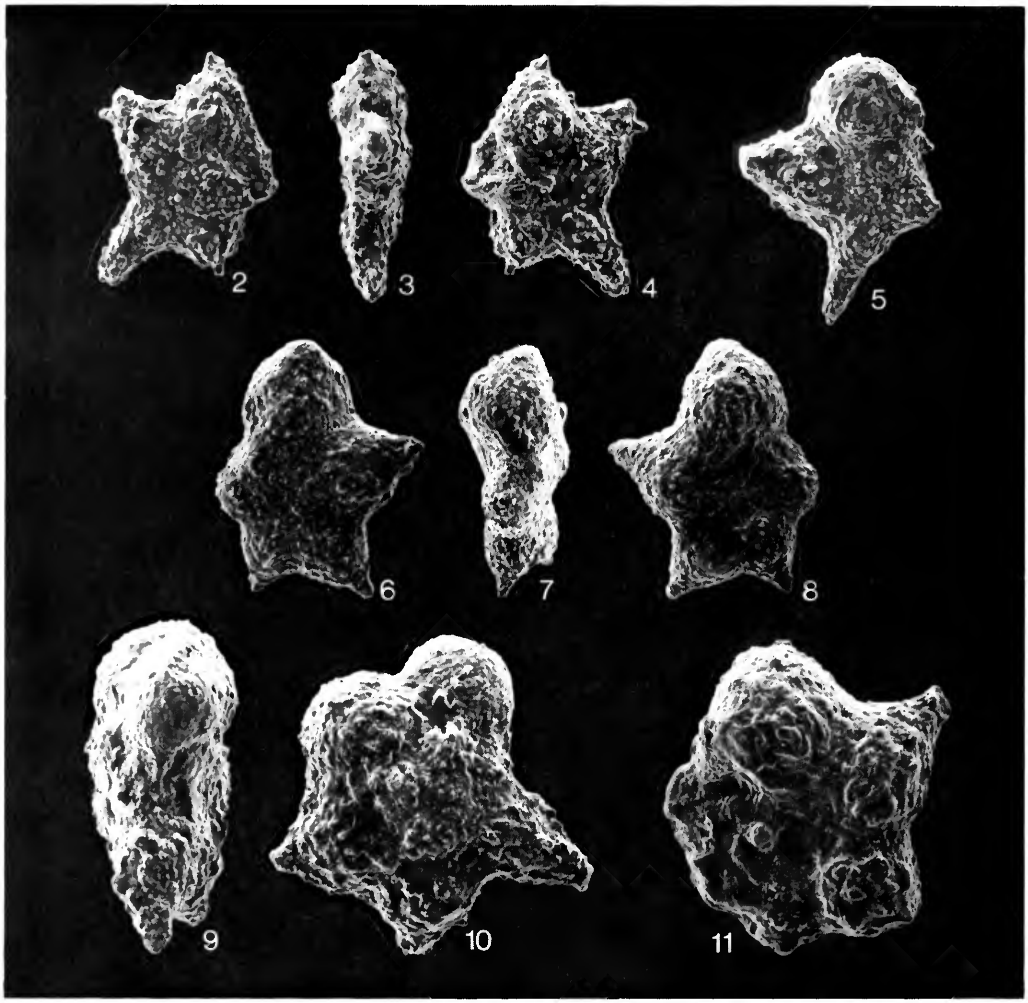
Superfamily **GLOBIGERINACEA** Carpenter, Parker & Jones, 1862

Family **GLOBOTRUNCANIDAE** Brotzen, 1942

Genus ***PLUMMERITA*** Brönnimann, 1952, emend.

TYPE SPECIES. *Rugoglobigerina* (*Plummerella*) *hantkeninoides hantkeninoides* Brönnimann, 1952.

EMENDED GENERIC DIAGNOSIS. Similar to *Rugoglobigerina* in form but with chambers of the last whorl becoming elongate and developing single or paired tubulospines.



Figs 2–10 *Plummerita hantkeninoides* (Brönnimann). Figs 2–8, topotypes, identified by Brönnimann as *P. hantkeninoides hantkeninoides* (Brönnimann), Guayaguayare Formation, SE Trinidad. Figs 2–4, P 50829, spiral, edge (abapertural) and umbilical views; Fig. 5, P 50830, spiral view; Figs 6–8, P 50831, spiral, edge (apertural) and umbilical views. Figs 9, 10, topotypes, identified by Brönnimann as *P. hantkeninoides costata* (Brönnimann), Guayaguayare Formation, SE Trinidad. P 50832, edge (apertural) and spiral views. All specimens × 135.

Fig. 11 *Plummerita reicheli* (Brönnimann). P 50833. Paratype, umbilical view. Guayaguayare Formation, SE Trinidad. × 135.

Description. Test a compressed to moderately inflated low trochospire; outline in spiral and umbilical views lobulate becoming tubulospinate, or tubulospinate throughout; in edge view, periphery rounded or tubulospinose. Chambers of early whorls subspherical, within final whorl becoming elongate either in the plane of coiling or oblique to it with development of single or paired tubulospines. If one tubulospine per chamber, it extends outward from mid-line of each chamber on the periphery; if paired, at opposite margins of the periphery. Terminal and penultimate chambers often inflated and sometimes lacking tubulospines. Surface of test ornamented with meridionally arranged fine to coarse ridges, or lines of course (true) spines or nodes; pores numerous. Tubulospines of various lengths and thicknesses, hollow, with rugose or ridged ornament; perforate. Aperture appears to be a low interiomarginal, umbilical–extraumbilical arch. Umbilicus shallow and usually narrow, tegillum present but rarely preserved.

Plummerita hantkeninoides (Brönnimann)
Figs 2–10, 16

1952 *Rugoglobigerina* (*Plummerella*) *hantkeninoides hantkeninoides* Brönnimann: 37; pl. 3, figs 1–3; text-fig. 17.
1952 *Rugoglobigerina* (*Plummerella*) *hantkeninoides costata* Brönnimann: 39; pl. 3, figs 4–6; text-fig. 18.
1952 *Rugoglobigerina* (*Plummerella*) *hantkeninoides inflata* Brönnimann: 40; pl. 3, figs 7–9; text-fig. 19.
1977 *Plummerita hantkeninoides* (Brönnimann); Masters: 617 (*q.v.* for synonymy).

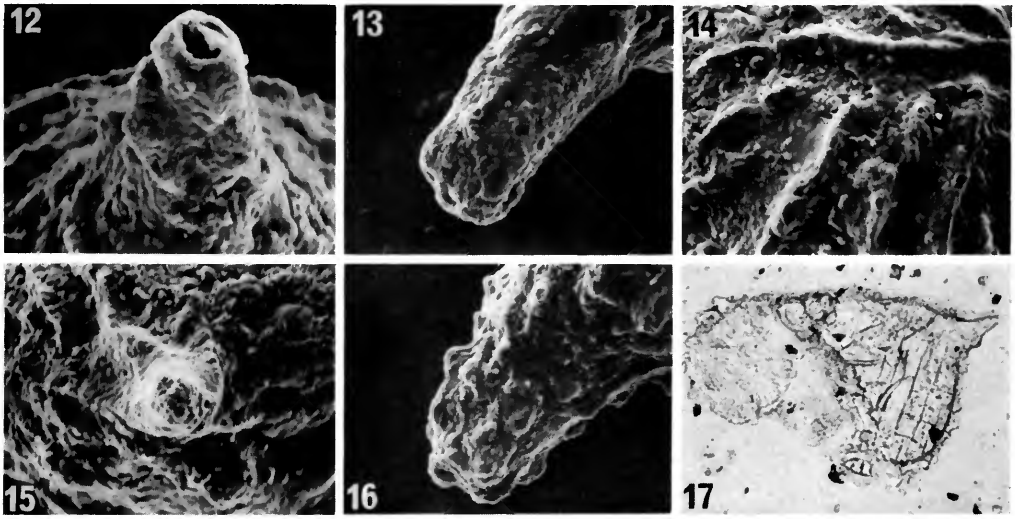
MATERIAL. About 20 topotypic specimens from the Guayaguayare Formation, Guayaguayare Well no. 163, core 19, depth 5588–5598 feet (1703–1706 m), SE Trinidad.

DIMENSIONS. Figured specimens: maximum diameter (including tubulospines) varies between 0·25 and 0·33 mm; greatest width 0·09–0·13 mm.

REMARKS. Nothing new can be added to the original description. The three subspecies occur together, have identical ranges, and are best considered as growth stages within a single species. Topotypes identified by Brönnimann as *P. hantkeninoides hantkeninoides* and *P. hantkeninoides costata* are figured here (Figs 2–8 and 9–10, respectively). Because of their state of preservation, the presence of a tegillum could not be confirmed, although some form of umbilical covering appears to be present in Fig. 4.

DISTRIBUTION. Trinidad (Brönnimann 1952).

RANGE. Late Maastrichtian, according to Masters (1977).



Figs 12–15, 17 *Plummerita kennerleyi* sp. nov. Paratypes, from sample CRB 56, Yunguilla Formation, Cuenca Basin, south Ecuador. Figs 12, 14, P 50836. Fig. 12, tubulospine on final chamber with end broken to show hollow centre, ×655; Fig. 14, detail of final chamber showing pores and well-developed costae, ×380. Figs 13, 15, P 50838. Detail of tubulospines on second and third chambers of final whorl, ×680 and ×380, respectively. Fig. 17, P 50839. Vertical thin section, orientated through one of pair of tubulospines on final chamber, ×135. Note tubulospine is a hollow extension of chamber.

Fig. 16 *Plummerita hantkeninoides* (Brönnimann). P 50829. Topotype, detail of tubulospine, ×425. Guayaguayare Formation, SE Trinidad.

Plummerita kennerleyi sp. nov.
Figs 12–15, 17–31

DIAGNOSIS. A moderately inflated species of *Plummerita* with 4–5 chambers in the final whorl. Tubulospines developed only in last three chambers, paired, one at each angle of the periphery and oblique to the plane of coiling. Ornament of meridionally arranged ridges strongly developed.

NAME. After the late J. Brian Kennerley, former Head of the I.G.S. (Overseas Division) Survey Team in Ecuador.

HOLOTYPE. P 50835, sample SC 159, Yunguilla Formation, Cuenca Basin.

MATERIAL. 71 specimens, samples CRB 56–58, SC 158, 159, Yunguilla Formation, Cuenca Basin; 86 specimens, samples JW 411, 412, Río Playas Formation, Río Playas Basin, S. Ecuador (see Fig. 1).

DESCRIPTION. (Holotype). Test a low trochospire consisting of about two whorls. Outline in spiral and umbilical views lobulate then tubulospinate; five chambers in final whorl, subglobular at first, gradually increasing in size, with last two chambers each produced into two tubulospines at opposite angles to the mid-line of the periphery. Lower periphery rounded in edge view, upper margin tubulospinose. Sutures moderately depressed, curved. Wall calcareous, finely perforate, test surface ornamented by strong, meridionally arranged ridges which extend to the tubulospines. Umbilicus shallow, aperture appears to be an interiomarginal, umbilical–extra-umbilical arch; tegillum not preserved.

DIMENSIONS. Holotype: maximum test diameter (excluding tubulospines) 0·25 mm; (including tubulospines) 0·28 mm; maximum width (including tubulospines) 0·17 mm.

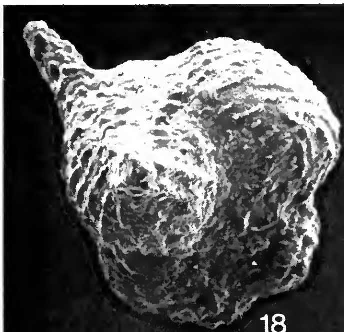
VARIATION. (Paratypes). The maximum test diameter of the four figured paratypes, P 50834 and P 50836–P 50838, varies 0·22–0·33 mm (excluding tubulospines) and 0·25–0·34 mm (including tubulospines); the greatest width (including tubulospines) varies 0·17–0·26 mm. The number of chambers in the final whorl varies between four and five (figured and unfigured paratypes); all specimens have about two whorls.

The paired tubulospines are developed only on the last two or three chambers; their length varies considerably (Figs 18–31) and in extreme cases they become antler-like (Figs 18–20). Four tubulospines occur on the final chamber of one unfigured specimen. The apparent presence of a single tubulospine in some specimens (Figs 28–31) is due to one of the pair being broken off at the base. The last-formed chamber sometimes lacks tubulospines and is globose (Figs 18–20).

REMARKS. *Plummerita kennerleyi* sp. nov. differs from *P. hantkeninoides* (Brönnimann) and *P. reicheli* (Brönnimann) in being much more inflated and in possessing paired tubulospines; the tubulospines in *P. hantkeninoides* and *P. reicheli* are single and are situated in the plane of coiling. *P. kennerleyi* and *P. hantkeninoides* are ornamented by meridionally arranged costae which are longer and much more strongly developed in the former than in the latter, at least in the material available. *P. reicheli* has discrete, coarse blunt spines rather than ridges.

Figs 18–31 *Plummerita kennerleyi* sp. nov., all ×135. Figs 18–23, from sample SC 159, Yunguilla Formation, Cuenca Basin, south Ecuador. Figs 18–20, P 50834. Paratype, spiral, edge (apertural) and umbilical views. Figs 21–23, P 50835. **Holotype,** spiral, edge (apertural) and umbilical views. Figs 24–26, from sample CRB 56, Yunguilla Formation, Cuenca Basin, south Ecuador. P 50836. Paratype, spiral, edge (abapertural) and umbilical views. Fig. 27, from sample JW 412, Río Playas Formation, Río Playas Basin, south Ecuador. P 50837. Paratype, spiral view. Figs 28–31, from same sample as Figs 24–26. P 50838. Paratype, spiral, umbilical and two oblique umbilical views; note possible remains of tegillum in Figs 29–31.

Figs 32–34 *Rugoglobigerina rugosa* (Plummer). P 50840. Spiral, edge (apertural) and umbilical views. Specimen included for comparison with *P. kennerleyi* sp. nov. Sample CRB 56, Yunguilla Formation, Cuenca Basin, south Ecuador. ×135.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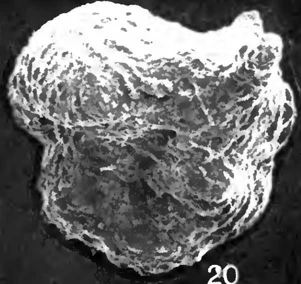
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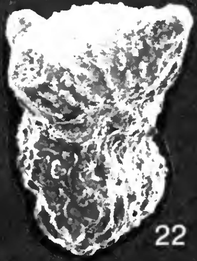
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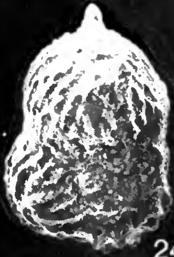
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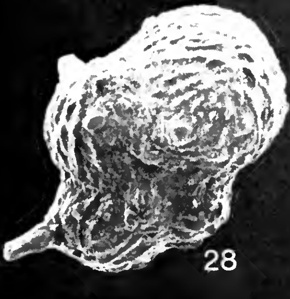
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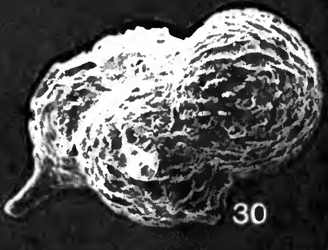
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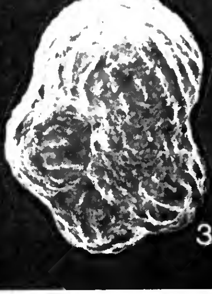
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The tubulospines now shown to occur in *Plummerita* species are closely analogous to those found in another, but not closely related, Cretaceous planktonic genus, *Schackoina*. In this genus are found species which are both single-tubulospinose chambered, such as *S. cenomana* (Schacko), and multi-tubulospinose chambered, such as *S. multispinata* (Cushman & Wickenden). Cushman & Wickenden (1930) proposed several growth stages to account for the varying number of tubulospines in *S. multispinata*. The small forms, with a single tubulospine per chamber, they assumed to be juveniles, while larger individuals with several tubulospines per chamber they regarded as adult or gerontic growth stages. Since *Plummerita hantkeninoides* and *P. kennerleyi* are of similar size and do not occur together it is unlikely that they are growth stages of the same species; furthermore, the latter never possesses chambers which are radially elongate in the plane of coiling, even in very small individuals. The two species must have evolved separately in the Maastrichtian from rugoglobigerine ancestors, probably *Rugoglobigerina rugosa* (Plummer) in the case of *P. kennerleyi* (compare Figs 17–31 with Figs 32–34, both from Ecuador). *P. kennerleyi* may prove to be a geographically restricted form. At present it is not possible to suggest why its curious morphology developed.

A definite tegillum has not been found on any specimens of *P. kennerleyi*. This is, however, thought to be a preservation defect since specimens of *R. rugosa* from the same samples (Figs 32–34) also lack this feature. As the most fragile of apertural coverings, it is generally only preserved in specimens obtained from soft clays and marls (see Smith & Pessagno 1973), and would not be expected to survive extraction from compacted shales.

Distribution. Known only from the Yunguilla Formation (Cuenca Basin) and Río Playas Formation (Río Playas Basin), S. Ecuador.

Range. Maastrichtian (probably mid or late).

Plummerita reicheli (Brönnimann)
Fig. 11

1952 *Rugoglobigerina reicheli reicheli* Brönnimann: 18; pl. 3, figs 10–12; text-figs 4a–m, 5a–i.
1977 *Rugoglobigerina* (?) *reicheli* Brönnimann; Masters: 621 (*q.v.* for synonymy).

Material. Four paratypes from the Guayaguayare Formation, Guayaguayare Well no. 163, core 19, depth 5588–5598 feet (1703–1706 m), SE Trinidad.

Dimensions. Figured specimen: maximum test diameter (including tubulospines) 0·31 mm; maximum width 0·18 mm.

Remarks. Brönnimann (1952) originally described three subspecies of *R. reicheli*, namely *R. reicheli reicheli*, *R. reicheli hexacamerata* and *R. reicheli pustulata*. The second subspecies is now considered a distinct species of its own, while according to Masters (1977) the last-named form is a junior synonym of *R. rugosa* (Plummer).

The species is here placed in *Plummerita* as the paratypes possess radially elongate chambers and tubulospines in the final whorl. Ornament consists of meridionally arranged, coarse, blunt, discrete spines or nodes, rather than ridges as in *P. hantkeninoides* and *P. kennerleyi*. Exceptionally well preserved specimens akin to some forms of this species originally figured by Brönnimann (1952) are illustrated by Smith & Pessagno (1973 : pl. 26); they show that a tegillum does exist in this taxon, and therefore probably in the genus as a whole.

Distribution. Trinidad (Brönnimann 1952); Mexico; Texas and Arkansas, U.S.A. (Pessagno 1967, Smith & Pessagno 1973).

Range. Mid to late Maastrichtian (according to Smith & Pessagno 1973); late Maastrichtian only (according to Masters 1977).

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