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Lower Ordovician Brachiopoda from mid and southwest Wales

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Synopsis

A study of Welsh Lower Ordovician Brachiopoda, especially from rocks of the Llanvirn and Llandeilo Series in the Llandeilo and Builth Wells areas, reveals the presence of 45 species and subspecies of which eight, belonging to the genera *Christiania, Gelidorthis, Glyptorthis, Macrocoelia, Monobolina, Paterula, Schizotreta* and *Trematis,* are new. Representatives of the genera *Plectoglossa, Porambonites, Schmidtites*? and *Torynelasma,* as well as *Conotreta, Gelidorthis* and *Murinella,* were hitherto unknown in Wales; the occurrences of *Christiania, Corineorthis, Gelidorthis, Kullervo, Mcewanella, Murinella, Oxoplecia, Parastrophinella, Paterula, Plectoglossa, Porambonites, Skenidioides, Tissintia, Torynelasma, Trematis* and *Triplesia* constitute the earliest records of these taxa in the Anglo-Welsh Province.

The fauna is reminiscent of the mainly endemic Anglo-Welsh assemblages from the Shelve area, although the indigenous taxa are supplemented by a number of Baltic stocks like *Christiania, Kullervo* and *Porambonites,* and a few of Bohemian affinity, notably *Gelidorthis* and *Paterula.* Correlation between the Shelve and other Anglo-Welsh successions is practicable and demonstrates the widespread distribution of distinctive fossil assemblages dominated by inarticulates in pre-Caradoc argillaceous facies. More precise local correlations based on conspecific forms can be effected between both the argillaceous and arenaceous facies of the Llandeilo and Builth Wells areas.

Introduction

Since the identification of the 'Llandeilo Flags' as the fourth formation of the Silurian System (Murchison 1839: 222), the Ordovician successions of the Llandeilo area have been a source of much controversy. The issues involved are well known and centre on the merits of the Llandeilo Series as an internationally acceptable time-stratigraphical unit. To some extent this debate was generated by the failure of Murchison (1839: 355–357) and others to realise that fossiliferous sandstones associated with the 'Llandeilo Flags' were not Caradoc but Llanvirn or Llandovery in age. Yet even when the stratigraphical succession had been satisfactorily determined (Strahan *et al.* 1907: 12; Williams 1953: 179), the controversy remained alive. In retrospect this was the consequence of not recognizing that much of the Llandeilo Series is coeval with the lower part of the *Nemagraptus gracilis* Zone (Williams *et al.* 1972: 5). This particular shortcoming reflected the inherent difficulties of correlating what was until recently believed to be an exclusively shelly Llandeilo facies with contemporaneous graptolitic shales found in the other parts of Carmarthenshire (Dyfed) and in Shropshire. It also arose from the impoverished nature of the Llandeilo shelly assemblages, the brachiopod constituents of which especially seemed to be mainly pandemic species with wide stratigraphical ranges. Between 1866–1883, for example, Davidson (see Cocks 1978) listed several species of brachiopod from the Llandeilo Flags of Wales, some of which were founded on type specimens from post-Ordovician rocks.

In 1949, one of us (A.W.) described eleven species of Ordovician brachiopods from the Llandeilo–Llangadog area. The study and a later stratigraphical account in 1953 showed that the brachiopod faunas of the Llandeilo Flags and especially those of the varied sediments constituting the underlying Ffairfach Group are more diverse than had been generally acknowledged. The species were poorly illustrated and inadequately defined, but no revision was contemplated until two features of the distribution of Ordovician marine faunas became evident.

The first was the endemic distribution of many of the brachiopod species characteristic of the older Ordovician rocks of Wales and Shropshire. The degree to which these Anglo-Welsh species were distinguishable from contemporaneous taxa in the rocks of Scotland, North America and the Baltic had long been known. But as the Ordovician faunas of Europe and north Africa became more familiar, especially through the admirable researches of Havlíček (1967, 1971, 1977), the endemicity of those from south Britain became more obvious. Indeed factor analyses of such faunas suggested that the Anglo-Welsh assemblages are diagnostic of a marine province which retained its individuality for the greater part of the Period (Williams 1969, 1973). In this context, the unexpected appearances of taxa which are more characteristic of the Baltic, Bohemian or north African successions are records of interprovincial migrations, and their occurrences are important clues to the distribution of tectonic plates during Ordovician times.

A renewed interest in the taxonomy of the older Ordovician faunas of the Builth–Llandeilo area was also prompted by a study of the brachiopod assemblages of the Shelve district in west Shropshire (Williams 1974, 1976: 38–44). These researches showed that the assemblages were relics of three associations of low to moderate diversity, each characteristic of a distinctive type of substrate as indicated by the entombing sediments. The brachiopods recovered from the Shelve successions were obviously closely related to those found in contemporaneous shelly facies in Wales. This circumstance afforded an opportunity to explore the geographic and stratigraphical distributions of the associations and the structure and evolution of their constituent communities in the manner outlined by Lockley (1978). In particular, the varied sediments and pyroclastics associated with the volcanic complexes exposed in the Towy Anticline between Llandrindod Wells and Llandeilo (Fig. 1) were known to contain a relatively diverse brachiopod fauna which may have been the Llanvirn antecedents of some of the associations found in the richly fossiliferous Caradoc Series. The community relationship, if any, between these high-diversity associations and the intercalated restricted faunas of the Llandeilo Series was equally intriguing.

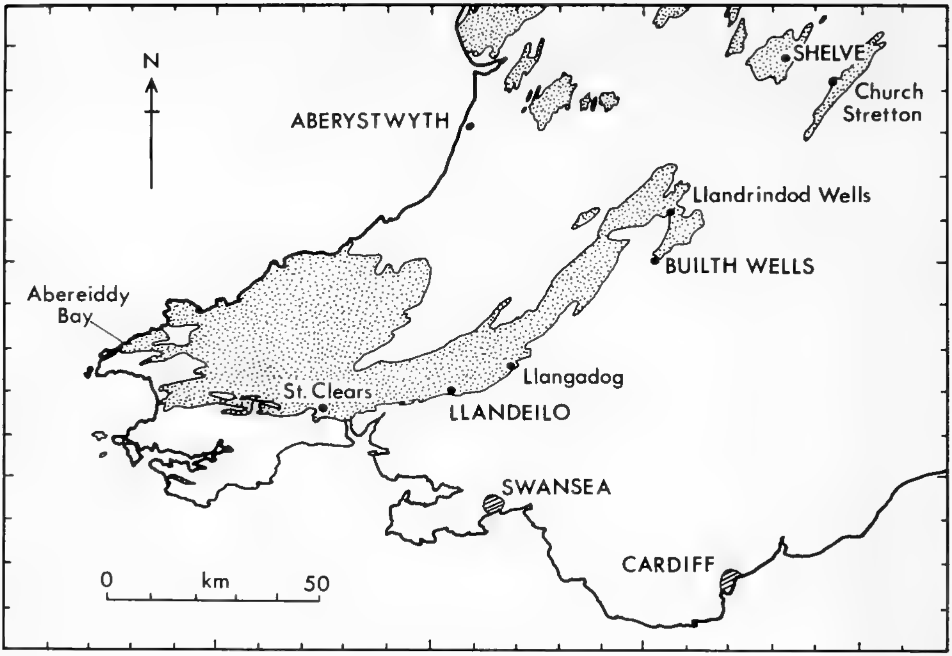


Fig. 1 Map of south Wales and the Welsh Borders, showing key localities and outcrop of Ordovician rocks (stippled).

In an attempt to unravel these relationships, collections from the Llanvirn and Llandeilo rocks of Powys and Dyfed were made by Dr J. M. Hurst and Dr C. J. Wilcox as well as the authors. Systematic sampling was limited to comparatively few, albeit the most representative and best exposed, stratigraphical sections. About 500 kg of rock were collected from the type section of the Ffairfach Group and these have yielded over 7500 brachiopods and numerous representatives of several other phyla. Another 130 kg of coeval sediments and ashes from the Coed Duon and Longwood sections, respectively about 4 km SE and SW of Llangadog, provided nearly 3000 brachiopod specimens. In contrast over 1300 kg of Llandeilo rocks, collected by Dr Wilcox especially from Dynevor Park, Pont-bren–Araeth Dingle and the type section along the Cennen, yielded fewer than 6000 brachiopods; these he kindly placed at our disposal for this study.

From the viewpoint of clarifying the relationship between the fossil faunas of the Shelve and Llandeilo areas, those occurring in the Ordovician sediments and ashes of the Builth–Llandrindod Inlier are crucial. We were fortunate to have access to brachiopods from collections made by Mr P. R. Sheldon, obtained mainly from the Carneddau Hills north of Builth Wells and sections along the Howey Brook and near Bwlch-y-cefn Banc, both within 5 km east of Llandrindod Wells, which were invaluable supplements to our own samples. In all, the impressions of over 5000 brachiopods retrieved from the Inlier were available for systematic appraisal.

The classic areas of Builth Wells and Llandeilo were, of course, well known to those indefatigable fossil collectors who provided eminent palaeontologists of the last century, like Davidson, M'Coy and J. de C. Sowerby, with so much material for study. In the course of our own researches we have examined as many relevant specimens featured in publications as we have been able to unearth. In this task, we have been aided by Dr L. R. M. Cocks' Review of British Lower Palaeozoic Brachiopods (1978). Such specimens are housed in the British

Museum (Natural History), the Geological Survey Museum, the National Museum of Wales and the Sedgwick Museum; their whereabouts are identified by the prefixes B or BB, GSM, NMW and SM respectively. New numbers assigned to specimens during this study fall within the sequences BB 92265–499, BB 94036–77 and BB 94216–48, and SMA 104410–9, SMA 104446–65 and SMA 105827–36.

Table 1 Stratigraphical distribution of brachiopod species according to 'subseries' occurrence. L1 and L2 represent the *Didymograptus bifidus* Shales and Ffairfach Group of the Llandeilo area. L3, L4 and L5 represent the Lower, Middle and Upper Llandeilo of the Llandeilo area, respectively. B1 and B2 represent the *D. bifidus* and *D. murchisoni* Beds, and B3 and B4 the *Glyptograptus teretiusculus* and *Nemagraptus gracilis* Beds of the Builth area. Brackets denote uncertainty about the horizon at which a taxon occurs. Six of the 45 described taxa, which are not listed here, originate from isolated localities referred to in the text.

Species	L1	L2	L3	L4	L5	B1	B2	B3	B4
Christiania elusa sp. nov.							*		
Corineorthis pustula Williams			*						
Corineorthis cf. *pustula* Williams								*	*
Corineorthis sp.		*							
Dalmanella parva Williams		*	*	*	*		*	*	
Gelidorthis cennenensis sp. nov.		*							
Glyptorthis cf. *viriosa* Williams			*	*			*		
Glyptorthis viriosa Williams *tumida* subsp. nov.		*							
Hesperorthis dynevorensis Williams		*					*		
Horderleyella convexa Williams		*							
Horderleyella sp.		*	*	*					
Kullervo sp.		*							
Lingulella cf. *displosa* Williams							*	*	
Macrocoelia llandeiloensis (Davidson)		*	*	*			*		
Macrocoelia llandeiloensis (Davidson) *elongata* subsp. nov.							*		
Mcewanella berwynensis MacGregor			*				*		
Monobolina crassa sp. nov.								*	*
Murinella sp.		*							
Oxoplecia cf. *nantensis* MacGregor		*	*	*					
Palaeoglossa attenuata (Sowerby)		*	*	*			*	*	*
Parastrophinella cf. *musculosa* Williams			(*)						
Parastrophinella parva MacGregor			*				*		
Paterula cf. *bohemica* Barrande		*	*						
Plectoglossa sp.			(*)						
Porambonites sp.							*		
Pseudolingula granulata (Phillips)		*	*				*		
Rostricellula triangularis Williams		*	*						
Salopia turgida (M'Coy)		*					*		
Schizocrania cf. *salopiensis* Williams		*	*		*		*	*	*
Schizotreta cf. *transversa* Williams			*						
Schizotreta transversa Williams *ffairfachensis* subsp. nov.		*							
Schmidtites ? *micula* (M'Coy)					(*)		*	*	*
Skenidioides sp.		*							
Sowerbyella antiqua Jones		*	*	*			*		
Tissintia immatura (Williams)		*	*	*	*				
Tissintia plana (Williams)		*	*						
Tissintia prototypa (Williams)	*	*				*	*		
Tissintia sp.									*
Triplesia edgelliana (Davidson)		*							

Faunal distribution

In the wake of current palaeoecological studies, the traditional faunal list showing the stratigraphical range and frequency of occurrence of fossil species may be misleading. A lithostratigraphical unit as comprehensive as a Group or a Formation may contain a number of benthic associations which are more or less exclusive of one another. In the varied sediments and ashes composing the Ffairfach Group, for example, there are as many as eight distinctive faunal assemblages; and, although some of them may have been ecotones, the majority must have been fully independent associations. It may, therefore, seem pointless to present an introductory list of species recorded from, say, the Ffairfach Group. Yet there are two benefits from doing so which prompt us to continue the tradition.

The first is that if there are two or more benthic associations in a stratigraphical unit, they are likely to reflect an orderly sequence of events affecting the palaeoenvironment and will, through such facies relationships, impart a diagnostic pattern on the faunal list for the entire unit. Such sequences of associations are well seen in the Ffairfach Group and will be discussed elsewhere. Meanwhile it is noteworthy that part of the sequence identified at Ffairfach is found in the Upper Llanvirn sediments and ashes of the Builth area which, of course, accounts for the similarities in the two faunal lists.

Secondly the changing nature of fossil associations also contributes to their general usefulness when they are used to compile faunal lists. Throughout geological time, associations have evolved by replacement of their constituent taxa, by speciation and by assimilation of immigrant stocks. Since such changes commonly occurred, a particular climax association is normally diagnostic of a short segment of geological time. The exceptions appear to be some low diversity associations like those characteristic of the Middle and Upper Llandeilo successions. Even these, however, are informative if only for palaeoecological purposes.

As the list in Table 1 shows, 45 brachiopod taxa have been identified in the Llanvirn–Llandeilo rocks of mid-Wales, with 16 species belonging to the Inarticulata, 18 to the Orthida, 2 to the Triplesiidina, 5 to the Strophomenida, 3 to the Pentamerida and 1 to the Rhynchonellida. Their stratigraphical distribution is also given.

In both the Llandeilo and Builth Wells areas, the pattern of distribution is essentially the same. The Lower Llanvirn *(Didymograptus bifidus)* successions are dominated by the opportunistic articulate species *Tissintia prototypa.* Thereafter diversity dwindles from a maximum in the variable sediments and ashes of Upper Llanvirn age where articulate species may outnumber inarticulates by 6 or 7 to 1. Reduction in diversity resulted from an elimination of articulate species which although dominant in the Lower and Middle Llandeilo successions of the type area were no more numerous than the inarticulates in the Upper Llandeilo, while in the Builth area they had almost entirely disappeared by the end of Lower Llandeilo times (*Nemagraptus gracilis* Zone). As for the endemicity of the faunas, the study has confirmed the dominance of the Anglo-Welsh stocks, but sporadic immigrant genera from the Baltic province are well in evidence in late Llanvirn times when volcanic activity briefly provided shallow belts of clean-washed pyroclastics and derived sediments for colonization by *Christiania, Hesperorthis, Kullervo* and *Triplesia.*

Stratigraphical terminology

The stratigraphical nomenclature used in the systematic section is based almost entirely on the stratigraphy proposed by Williams (1953) for the Llandeilo region and by Elles (1939) and Jones & Pugh (1941, 1948, 1949) for the Builth district. In both areas the existing nomenclature may be lithostratigraphical, biostratigraphical and chronostratigraphical and in the Builth district is complex and in some respects repetitive.

At Llandeilo the *D. bifidus* shales are overlain by the Upper Llanvirn Ffairfach Group which was divided by Williams (1953: 180) into five lithostratigraphical units, referred to here as formations. In the overlying Llandeilo Series, which consists of a biostratigraphically based chronostratigraphical sequence of stages (Lower, Middle and Upper), the succession can be further subdivided into distinctive lithostratigraphical and biostratigraphical units (Williams 1948) which have been used in the descriptions of the range of some species.

In the Builth–Llandrindod area, the 'stratigraphical and palaeontological succession' of zones proposed by Elles (1939: 389), largely on the basis of graptolite biostratigraphy, included only one lithologically-based unit, the Main Volcanic Series. This was subsequently subdivided by Jones & Pugh (1941, 1949), who recognized four volcanic series and numerous laterally variable or impersistent lithostratigraphical units in the succession as a whole. The terminology proposed by these authors remained essentially unchanged except for minor modifications introduced by Hughes (1969) until, with the publication of the Geological Society Special Report no. 3 on the Ordovician (Williams *et al.* 1972) and the 1976 I.G.S. map of the 'Llandrindod Wells Ordovician Inlier', the stratigraphical terminology of this area was modified to conform to modern lithostratigraphical practice (e.g. Elles' *D. murchisoni* 'zone' is now the Upper and Lower *D. murchisoni* Shales). Some confusion arises in the classification adopted for the I.G.S. map, which has modified the lithostratigraphical terminology established by Jones & Pugh in such a way that the lower part of the Builth Volcanic Series becomes the 'Main tuff group' while the Grey Felspar Sands and Pyritous Felspar Sands become amalgamated equally informally into the 'Coarse felspathic sandstones'. Although the nomenclatorial modifications incorporated in the I.G.S. map have been accepted for identifying the successions from which the described taxa have been recovered, we prefer a formalized classification (i.e. Main Tuff Group) and we adhere to the chronostratigraphy proposed by Williams *et al.* (1972).

Systematic methods

The procedure adopted in the taxonomic study of the fossil collections at our disposal has been governed by the need to define all taxa as precisely as possible in preparation for palaeoecological researches on the older Ordovician brachiopod faunas throughout Wales and the Welsh borderland. The work has necessarily involved rectifying a number of nomenclatural errors, some of which have been perpetrated by an author of this monograph. The major commitment, however, has been to conduct taxonomic surveys of large samples collected at closely-spaced intervals. Thus in the type section of the Ffairfach Group, which consists of about 100 m of nearly continuous exposures including the mainly unfossiliferous basal Grit Formation (>20 m), 77 samples, each yielding an average of almost 100 identifiable brachiopod remains, were taken from these outcrops at a mean stratigraphic interval of 85 cm. The commonest fossil was *Dalmanella parva*, which constituted more than half of all the brachiopods recorded in 36 out of the 64 samples in which it occurs. It would have been too daunting a task to subject every collection of *Dalmanella parva* to an exhaustive series of statistical tests. Instead spot checks were carried out to confirm the morphological homogeneity of the stock throughout the entire range of its occurrence, and having found this to be so, one of the better-preserved samples was chosen to represent the Ffairfach populations in statistical comparisons with *Dalmanella* from other localities. When, as was true of *Sowerbyella*, a genus appeared to be represented by morphologically distinguishable populations within a section, an appropriate number of samples were comprehensively compared so as to define the variation.

The statistical procedures adopted here conform to those outlined by one of us (Williams 1962: 69–79) and permit direct comparisons with data presented subsequently (e.g. Williams 1974) which were also derived from analyses conducted in a similar or identical manner. Economy precludes publication of the 103 statistical tables on which our systematic studies have been based. The tables, laid out according to standard format and arranged in the taxonomic sequence of this paper, have been deposited in the Palaeontology Library of the British Museum (Natural History) and are available for consultation. In addition, the means, variances and numbers of measurements taken for all quantified characters are incorporated in the following systematic descriptions. Where a bivariate estimate of a feature had been calculated, a coefficient of correlation (r) is also given. These parameters should prove sufficient to enable readers to carry out the standard univariate and bivariate statistical tests. In particular, they can be used for the calculations of the rate of growth (a), the index of residual shape (b) and even the natural logarithms of means (variances) when allometric effects of shell growth can be demonstrated (Kermack & Haldane 1950).

The abbreviations used in the text for presentation of these statistics identify certain vectors of measurement expressed in millimetres. They are: l, length; $\bar{l}$, mean maximum length; w, width; $\bar{w}$, mean maximum width; $\overline{th}$, mean maximum depth; $\overline{lsc}$, mean maximum length of a muscle scar; $\overline{ls}$, mean maximum length of the median (or compound) septum; $\overline{dl}$, mean maximum length of dental lamellae; $\overline{lc}$, mean maximum length of the dorsal cardinalia (brachiophore bases unless otherwise stated); and $\overline{lsr}$, the mean maximum length of the dorsal socket ridges. The variances (var) are always given with these statistics, as are the mean maximum length and variance of the complete valve, i.e. $\bar{l}$ mm (var l), and the coefficient of correlation (r) when the relative growth of a valve or one of its features is being described.

Taxonomic descriptions

Under 'material' all measurements given are in mm; p.v. = pedicle valve, b.v. = brachial valve.

Lectotypes were mainly selected by Cocks (1978).

Class **INARTICULATA** Huxley, 1869

Order **LINGULIDA** Waagen, 1885

Superfamily **LINGULACEA** Menke, 1828

Family **OBOLIDAE** King, 1846

Subfamily **OBOLINAE** King, 1846

Genus ***SCHMIDTITES*** Schuchert & Le Vene, 1929

Schmidtites ? ***micula*** (M'Coy), emended
(Figs 2–10)

1851 *Siphonotreta micula* M'Coy : 389
1852 *Siphonotreta micula* M'Coy; M'Coy *in* Sedgwick & M'Coy : 188; pl. 1H, fig. 3.
1866 *Siphonotreta micula* M'Coy; Davidson : 76; pl. 8, figs 2–6.
1974 *Schmidtites* ? *simplex* Williams : 26; pl. 1, figs 11–15.
1978 *Helmersenia* ? *micula* (M'Coy) Cocks : 29.

Diagnosis. Subequally biconvex, circular obolids with valves almost as wide as long and 13% as deep as long ventrally, ornamented by concentric fila, fine overlapping lamellae and microscopic radial striations; pseudointerareas narrow, obscure, dorsal interior with fine median ridge.

Description. Suboval, gently biconvex obolids with obtuse posterior beaks subtending an angle of about 120° and rounded anterior margins; shells averaging between 92 and 99% as wide as long in 5 samples (e.g. 33 valves from Pen Cerrig: $\bar{l}$ mm (var l) 3·31 (0·314), $\bar{w}$ mm (var w) 3·25 (0·350), r 0·967) and averaging 13% as deep as long ventrally in 2 samples (e.g. 21 valves from Pen Cerrig: $\bar{l}$ mm (var l) 3·32 (0·188), $\overline{th}$ (var th) 0·43 (0·011), r 0·359); ornamented by strong closely-spaced fila, finely-developed overlapping lamellae and very fine striations; valves with narrow arcuate divided pseudointerareas; brachial valve interior with a low variably-developed median ridge up to 50% of valve length.

MATERIAL		length	width
Lectotype, exterior of p.v.	SM A.45444	3·6	3·6
Articulated valves	BB 92473	2·5	2·6
"	BB 92470	1·5	(1·4)
"	SM A.44903	4·7	4·5
Exterior of p.v.	GSM 16457	4·1	4·1
"	GSM 16472	3·0	2·9
"	SM A.104456	5·0	4·4
Internal and external mould of b.v.	BB 92301	3·0	2·7
Internal mould of b.v.	SM A.104419	(5·5)	5·0

HORIZONS AND LOCALITIES. SM A.44879–90 and A.45441–57 from the black Llandeilo shales (probably high *Glyptograptus teretiusculus* or low *Nemagraptus gracilis* Zones) of Pen Cerrig, 2·5 km north of Builth Wells, (National Grid ref. SO 042540); SM A.44891–927 from the olive shales belonging to *N. gracilis* Zone exposed in Harper's Quarry, Wellfield, 2 km north of Builth Wells (SO 037534); BB 92301–6 and BB 92470–3 from Upper *Didymograptus murchisoni* Shales exposed in Howey Brook, 4 km east of Howey, NW of Builth Wells (SO 091592); GSM 16456–8 from the black Llandeilo Flags of Wyeford, Builth Wells; GSM 16469–73 from an unknown horizon and locality in the 'Upper Llandeilo of the Llandeilo area'; NMW 68.376.G.167–70 from Upper Llanvirn shales exposed in stream 600 m SW of Shaky Bridge, 2 km east of Llandrindod Wells (SO 079609); SM A.44838–9, A.44858, 104419 and 104453–6 from basal *N. gracilis* Shales exposed in Gwern-y-fed-fach quarry, 1·5 km north of Builth (SO 030526).

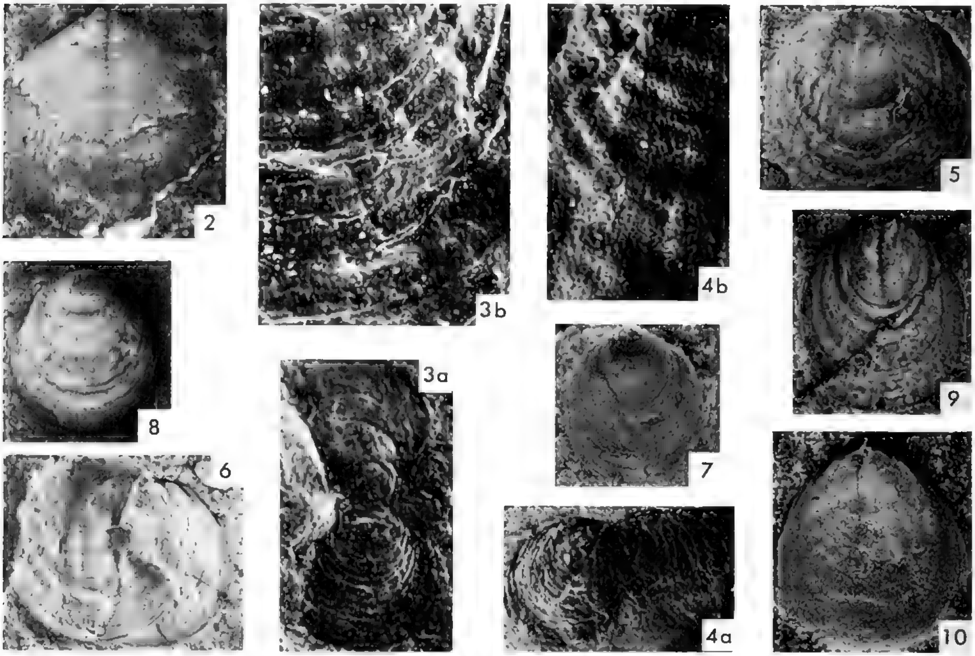
DISCUSSION. The observation that *Schmidtites* ? *simplex* Williams (1974) and *Siphonotreta micula* M'Coy (1851) are synonyms highlights a problem of taxonomic classification which can only be resolved by establishing whether the morphological characteristics of the samples used in this review of the species are of lingulacean or siphonotretacean affinity.

An examination of the lectotype (SM A.45444) and paralectotypes from Pen Cerrig near Builth indicates that the shell ornament consists only of concentric growth-lines devoid of spine bases, and fine microscopic radial striations which are best seen under the scanning electron microscope. Occasionally, specimens show a finely granular ornament in association with concentric growth lines. Specimens from the olive shales of Wellfield are similarly characterized by strong concentric growth lines with some individuals displaying in addition a coarsely granular to pustulose relief on both the internal and external surface of valves. This extra 'ornamentation' is attributable to a microscopic rucking of the entombing shales. The shells of all specimens are very thin and often crumpled or split peripherally, particularly posteromedially as in the lectotype. Williams (1974 : 27) noted a similar 'transverse or even radiating' wrinkling of the shells of *Schmidtites* described by him from the Shelve area. Indeed a symmetrical posteromedian splitting of the shell is such a common phenomenon, particularly in the Pen Cerrig sample, that it has almost certainly been mistaken for a pedicle groove and must account for the fanciful reconstructions of Sedgwick & M'Coy (1852: pl. 1H) and Davidson (1866: pl. 8).

The presence of an internal dorsal median ridge, divided interarea and microscopic radial striations indicates that these thin-shelled inarticulates have clear lingulacean affinities and can therefore be assigned with some confidence to the genus *Schmidtites*.

Comparisons between the Stapeley, Rorrington, Meadowtown, Pen Cerrig, Wellfield, Wyeford, Howey Brook and Shaky Brook samples reveals that the Stapeley subspecies, identified here as *Schmidtites* ? *micula subcircularis* Williams, is different from all seven other samples in being significantly more elongate ($p>0{\cdot}05$, $p>0{\cdot}05$, $p>0{\cdot}001$, $p>0{\cdot}001$, $p>0{\cdot}01$, $p>0{\cdot}05$ and $p>0{\cdot}005$ respectively). Comparisons of the remaining samples reveal that they are all essentially identical. Only the Rorrington and Howey Brook samples differ significantly at the 5% level ($0{\cdot}05<p<0{\cdot}04$). Clearly the species group *S. ? micula* (M'Coy) shows limited variation in space and time, a conservative evolutionary characteristic often ascribed to the lingulaceans.

GSM specimens 16469–73 represent the only specimens of *S. ? micula* (M'Coy) known from the Llandeilo of the type area; they are reported from an unknown locality in the 'Upper Llandeilo' of Llandeilo.



Figs 2–10 *Schmidtites ? micula* (M'Coy). Fig. 2, lectotype SM A.45444, exterior of a pedicle valve × 10, from Llandeilo shales, Pen Cerrig, Builth. Figs 3a, b, BB 92470, matching valves × 15, with detail of growth lines × 70; Figs 4a, b, BB 92473, matching valves × 8, with detail of punctae × 300; both from Llanvirn shales, Howey Brook, Llandrindod. Fig. 5, GSM 16457, latex impression of exterior of a pedicle valve × 8, from Llandeilo shales, Wyeford, Builth. Fig. 6, SM A.44903, matching valves × 6, from Llandeilo shales, Wellfield, Builth. Fig. 7, BB 92301, external mould of a pedicle valve × 8, from Llanvirn shales, Howey Brook, Llandrindod. Fig. 8, GSM 16472, exterior of a pedicle valve × 8, from Llandeilo shales, Llandeilo. Fig. 9, SM A.104456, exterior of a pedicle valve × 6; Fig. 10, SM A.104419, internal mould of a brachial valve × 6; both from Llandeilo shales, Gwernyfed, Builth.

Subfamily **LINGULELLINAE** Schuchert, 1893

Genus ***LINGULELLA*** Salter, 1866

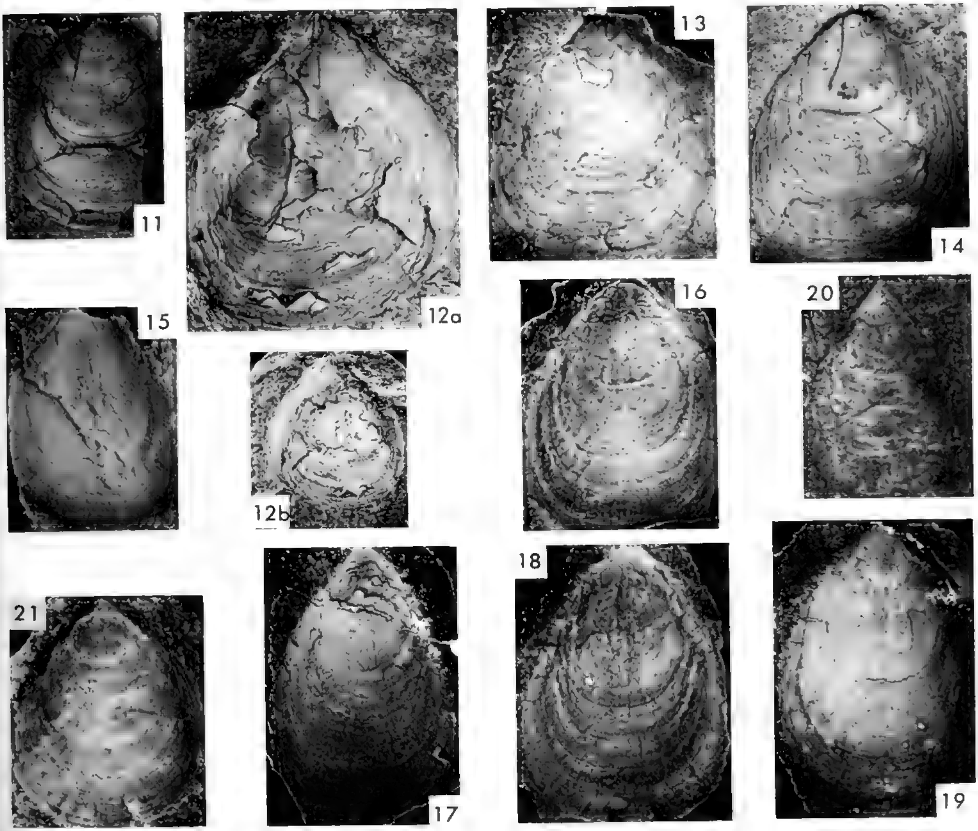
Lingulella cf. ***displosa*** Williams
(Figs 11–14)

cf. 1974 *Lingulella displosa* Williams : 28; pl. 2, figs 2–8.

DESCRIPTION. Ventribiconvex, elongately oval to subtriangular lingulellinids with a pedicle valve averaging 84% as wide as long ($\bar{l}$ mm (var l) 11·15 (5·32), $\bar{w}$ mm (var w) 9·35 (4·16), r 0·946 for 8 valves from Bach y Graig) with striated pseudointerarea divided by pedicle groove into two propareas; exterior ornamented by slightly irregular concentrically disposed impersistent lamellae.

FIGURED MATERIAL		length	width
Matching valves	SM A.104460	11	9·0
Exterior of p.v.	SM A.104410	16	(14)
,, ...	SM A.104465	8·8	7·7
,, ...	SM A.104464	10	8·5

HORIZONS AND LOCALITIES. SM A.104410, A.104459–65 and A.46523 from uppermost *Didymograptus murchisoni* to lower *Glyptograptus teretiusculus* shales exposed in the stream section east of Bach y Graig, 1·5 km east of Llandrindod Wells (SO 072610); SM A.44862 from the 'Llandeilo Limestone' (*Nemagraptus gracilis* Zone) of Harper's Quarry, Wellfield, 2 km north of Builth (SO 037534).



Figs 11–14 *Lingulella* cf. *displosa* Williams. Fig. 11, SM A.104410, exterior of a pedicle valve ×2; Figs 12a, b, SM A.104460, matching valves ×4 and latex impression of same ×2; Figs 13–14, SM A.104464–5, latex impressions of exteriors of pedicle valves, both ×4; all specimens from Llanvirn shales, Bach y Graig, Llandrindod.

Figs 15–21 *Palaeoglossa attenuata* (J. de C. Sowerby). Fig. 15, BB 92265, internal part of exfoliated pedicle valve ×2·5; Figs 16–19, latex impressions of partially exfoliated pedicle valves GSM 16600, 16542, 16598 and 16599, respectively, all ×2·5; all from Lower Llandeilo Flags, Coed Shôn, Llangadog. Fig. 20, SM A.104411, dorsal view of matching valves ×4, from Llanvirn shales, Upper Gilwern, Builth. Fig. 21, SM A.16678, latex cast of external mould of a pedicle valve ×4, from Llandeilo Flags, Wellfield, Builth.

DISCUSSION. The material described here closely resembles the Shelve *L. displosa* Williams in its broadly triangular outline, length : width ratio $(0{\cdot}5 < p < 0{\cdot}4)$ and distinctive lamellose ornament. Where good material is available *Lingulella* can be distinguished from the closely related lingulellinid *Palaeoglossa* both by its ornament and shape. However, although *Palaeoglossa* is apparently more widespread than *Lingulella* in the successions of mid Wales and the Welsh Borderland further material is needed to establish the stratigraphical and geographical distribution of these two closely related genera more fully.

Genus ***PALAEOGLOSSA*** Cockerell, 1911 emended Williams (1974)

Palaeoglossa attenuata (J. de C. Sowerby)

(Figs 15–21)

1839 *Lingula attenuata* J. de C. Sowerby *in* Murchison : 641; pl. 22, fig. 13.
1866 *Lingula attenuata* J. de C. Sowerby; Davidson : 44; pl. 3, figs 18–23, 26, 27, 33 *only*.
1974 *Palaeoglossa attenuata* (Sowerby) Williams : 32; pl. 3, figs 2–13.

DESCRIPTION. Biconvex, elongately oval lingulids with acute beaks subtending an angle of about 60° and slightly curved lateral and anterior margins; pedicle valve about two-thirds as wide as long and about 10% as deep as long and evenly convex in transverse and longitudinal profile; shell ornamented by growth lines, fine concentric fila (up to 10 per mm) and very fine radial striations.

FIGURED MATERIAL		length	width
Matching valves	SM A.104411	8·0	5·0
Exterior of p.v.	GSM 16599	11·0	7·5
,,	GSM 16598	17·0	12·5
,,	GSM 16542	18·0	11·5
,,	GSM 16600	17·0	13·0
,,	SM A.16678	9·0	7·5
,,	BB 92265	14·0	10·0

HORIZONS AND LOCALITIES. BB 92265 and GSM 16542, 16598–600 from the Lower Llandeilo *Lloydolithus lloydi* Flags exposed in Coed Shôn Quarry (SN 712256), 2·5 km south of Llangadog; SM A.16678 from 'calcareous flags' exposed at Wellfield (probably Harper's Quarry), 2 km north of Builth (SO 036534); A.104411 from Llanvirn shales exposed in small quarries 550 m east of Upper Gilwern (SO 092582).

DISCUSSION. Since Williams (1974 : 31–35) described the Lower Llandeilo *P. attenuata* (Sowerby) from the Meadowtown Beds, an examination of historical records and further collecting have revealed the relatively widespread occurrence of this species in contemporaneous successions in the Builth and Llandeilo regions.

GSM specimens 16542 and 16598 figured by Davidson (1866 : pl. 3, figs 19 and 20 respectively), together with GSM 16599, 16600 and BB 92265 from Coed Shôn Quarry, average 71% as wide as long in five pedicle valves. The relevant statistics, $\bar{l}$ mm (var l) 15·40 (8·30), $\bar{w}$ mm (var w) 10·90 (4·925), r 0·926, show no significant difference in shape $(p < 0{\cdot}9)$ from the smaller-sized topotypes. Although specimen SM A.16678 (also figured by Davidson 1866 : pl. 3, fig. 33) is similar to the topotypes it exhibits radial striations and may prove to be a *Lingulella*.

Sporadic records of *P. attenuata* in the *Didymograptus bifidus* and lower *Didymogr. murchisoni* shales have been given by Elles (1939 : 394–403). Shales of Upper *D. murchisoni* to early *Nemagraptus gracilis* age yielded nearly all the preserved Builth specimens. This suggests that the majority of *P. attenuata* in the Builth area are found in late Upper Llanvirn to Middle Llandeilo sediments, and are therefore coeval with most of the specimens from the Llandeilo area including B 23276 and SM A.44834 from contemporaneous horizons, at Llandeilo and Ffairfach respectively, and BB 92283 from Dynevor Park (Wilcox 1979 : 177). A single poorly preserved external mould (BB 92283), from the argillaceous lower part of the

Flags and Grits Formation of the Ffairfach Group at the type section (SN 628611), is tentatively assigned to *P. attenuata* and may represent the earliest record of the species in the Llandeilo area.

The observation that shells of *Palaeoglossa* are characterized by fine radial striations serves to emphasize its close relationship to *Lingulella* and we reiterate an earlier observation (Williams 1974 : 31) that it may eventually prove to be a junior synonym of the latter.

Subfamily **GLOSSELLINAE** Cooper, 1956

Genus ***PSEUDOLINGULA*** Mickwitz, 1909 emended Williams (1974)

Pseudolingula granulata (Phillips)

(Figs 22–29)

1848 *Lingula granulata* Phillips *in* Phillips & Salter : 370; pl. 25, fig. 1.
1866 *Lingula granulata* Phillips; Davidson : 36; pl. 2, figs 15–18.
1974 *Pseudolingula spatula* Williams : 36; pl. 4, figs 6–14; pl. 5, fig. 1.

Diagnosis. Subequally biconvex, subquadrate *Pseudolingula* with brachial valves between two-thirds and nine-tenths as wide as long in relation to increasing size and the angles subtended at the beaks changing from an acute 80° to as much as 125° in larger specimens; ornamented by strong fila laterally and anterolaterally with a wavelength of 0·2 mm; adnate ventral muscle platform and dorsal median ridge both extending forward for about half the length of the valve.

Description. Subequally biconvex, subquadrate *Pseudolingula* with parallel lateral and obtusely rounded anterior margins and slightly acute to obtuse beaks subtending an angle of between 80° and 90° in 4 smaller specimens and 115° and 125° in 2 larger adult ones; 3 pedicle valves are between 64% and 77% as wide as long; both valves subcarinate posteriorly, flattening anteriorly and laterally; exterior surface ornamented by growth lines and strongly developed fila with a wavelength of about 0·2 mm laterally, fine radial striations numbering about 20 per mm are well developed in the median sector of valves and probably represent a radial ornamentation developed on the inner layers of the shell; variably developed granules are found sporadically in large shells at the intersections between radial striae and concentric growth lines.

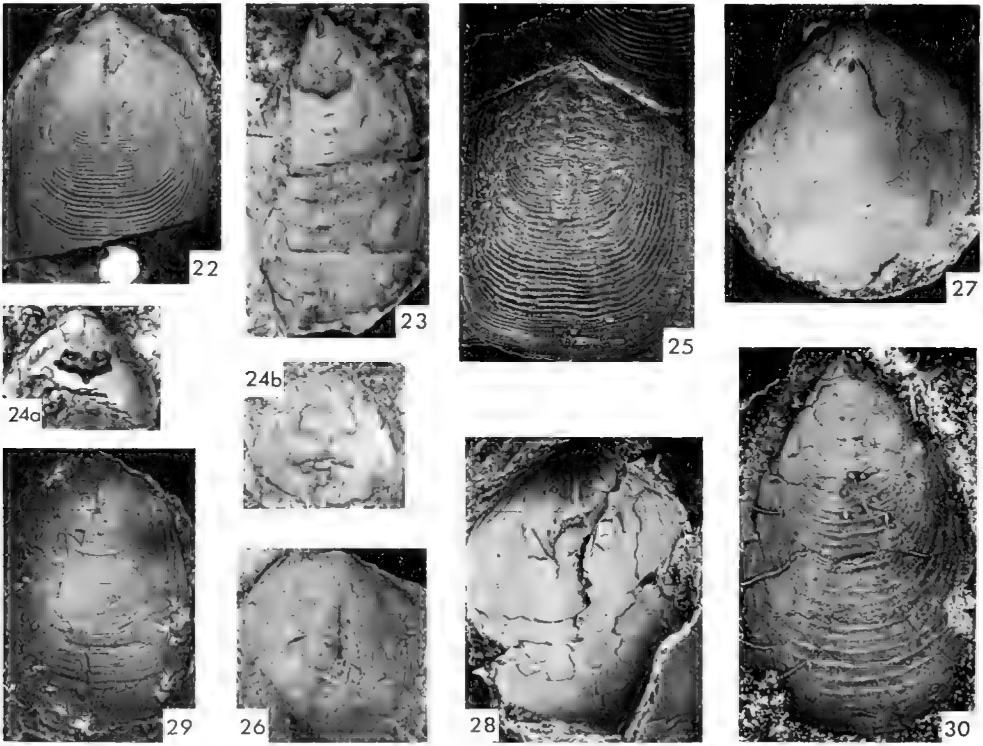
Ventral interior characterized by broad anteromedially protruding platform heavily rutted by growth lines and extending forward from the beak for half the length of the valve.

Dorsal interior characterized by sporadic coarse pitting and a well-developed median septum arising near the beak and extending forward for about half of valve length, to attain its maximum height at the anterior end.

Figured material		length	width
Lectotype, internal part of exfoliated b.v. .	GSM 8460	(20)	15
Internal part of exfoliated b.v.	SM A.45419	23·5	17·5
„	BB 92271a	—	(15)
Internal part of exfoliated p.v.	BB 92269a	12	(8)
Internal and external parts of exfoliated b.v. .	BB 92285a, b	21	19
„ .	SM A.104417	23	14
Internal mould and external shell of matching valves	BB 92284	12	10
Internal and external parts of exfoliated p.v. .	BB 92267a, b	—	(6)

Horizons and localities. Lectotype (GSM 8460) from unknown horizon and locality in 'Llandeilo Limestone' of Dynevor Park; BB 92284–5 and 92293 from the Flags and Grits in the middle part of the Ffairfach Group, Ffairfach railway cutting (SN 628211); BB 92266–70 from Middle Llandeilo Flags exposed in old trackway 50 m NW of St Tyfei's Church, Dynevor Park, Llandeilo (SN 622233); BB 92271 from Lower Llandeilo (*Corineorthis* Beds) in old quarry 75 m SE of St Tyfei's Church (SN 622222); SM A.45419 from an unknown locality in the 'Llandeilo Beds' of the Llandeilo area and A.44840 from an unknown horizon in the Ffairfach railway cutting south of the station; SM A.104417 from Lower Llanvirn shales exposed in Camnant Brook near The Court Farm 7 km NE of Builth (SO 088576).

Discussion. When Williams (1974 : 36) erected the species *spatula* for a distinctive *Pseudolingula* occurring sporadically throughout the Lower Ordovician successions of the Shelve area, he overlooked the long-established but little-known *Lingula granulata* Phillips. This taxon was effectively founded on one brachial valve from the 'Llandeilo Limestone' of Dynevor Park in the type area, but there is no doubt that the species is a *Pseudolingula*. Moreover recent collecting throughout the Ffairfach Group and the Llandeilo Series in the type area yielded a sufficient number of valves assignable to *P. granulata* to provide some



Figs 22–29 *Pseudolingula granulata* (Phillips). Fig. 22, holotype GSM 8460, exfoliated brachial valve ×2, from Lower Llandeilo limestones, Dynevor Park, Llandeilo. Fig. 23, BB 92269, exfoliated pedicle valve ×4; Figs 24a, b, BB 92270, internal and external parts of exfoliated pedicle valve ×4; both from Middle Llandeilo Flags, Dynevor Park, Llandeilo. Fig. 25, SM A.45419, exfoliated brachial valve ×2, from Llandeilo Limestones, Llandeilo. Fig. 26, BB 92271, internal part of an exfoliated brachial valve ×2, Lower Llandeilo, Dynevor Park. Fig. 27, BB 92285a, internal part of an exfoliated brachial valve, ×2; Fig. 28, BB 92284, external part of exfoliated matching valves (view of dorsal valve) ×4; both from Flags and Grits, Ffairfach Group, type section. Fig. 29, SM A.104417, latex impression of an exfoliated brachial valve ×2, from Llanvirn shales, Camnant Brook, Builth.

Fig. 30 ? *Plectoglossa* sp. B 3474, latex cast of an exfoliated pedicle valve ×8, from Llandeilo Beds, Llandeilo.

indication of the variability of the species. Despite the fact that the Llandeilo specimens tend to be relatively broader than those comprising the sample on which *P. spatula* was founded (Williams 1974 : 37), the difference is evidently related to the smaller size of the Shropshire shells. The Shelve species is, therefore, regarded by us as a junior synonym of *P. granulata.*

The changes in outline which the valves of *Pseudolingula* underwent during growth also complicate comparisons between samples from the Ffairfach Group and the Llandeilo Limestone. Llandeilo shells differ from the larger Ffairfach forms in being relatively longer and in exhibiting a more acute beak in smaller forms and a more variable beak generally; there are also slight differences in ornamentation. The morphological differences between the three Llanvirn specimens and the eight Llandeilo ones available for comparison are restricted to shape and ornament and are probably size-related. The three Llanvirn brachial valves are especially characterized by obtuse beaks subtending an angle of about 110° and are between 83% and 90% as wide as long. The inner radial striae and external fila are coarser also, but the sample is too small for the differences to warrant taxonomic recognition.

Specimen SM A.46529 from Llanvirn shales exposed at Hendy Bank, south of Llandegley Rocks 7 km ESE of Llandrindod (SO 125595 approx.), is a pedicle valve of *P. granulata* collected by Elles. She correctly identified this specimen and presumably therefore others which she assigned to the species from neighbouring localities (Elles 1939 : 394–399).

Genus ***PLECTOGLOSSA*** Cooper, 1956

? ***Plectoglossa*** sp.

(Fig. 30)

A single specimen (B 3474) of the external part of an exfoliated pedicle valve from the 'Upper Llandeilo' of an unknown locality in the Llandeilo area is a glossellinid and is provisionally assigned to the genus *Plectoglossa.* The specimen is 7·5 mm long and 4·5 mm wide with an acute beak subtending an angle of 70° and evenly convex longitudinal and transverse profiles. The ornament is highly distinctive with prominent, elevated, evenly spaced, concentric growth lines numbering 4 per mm over the post-neanic surface of the valve. The specimen almost certainly comes from beds of the Llandeilo Series, since it is associated with a marrolithinid. Although the Llandeilo Glossellinae are represented almost exclusively by *Pseudolingula granulata* (Phillips) it is considered improbable that this small specimen might be a juvenile representative of that species. No individuals of comparable size show such evenly curved lateral margins, the same prominent elevated growth lines, or are characterized by a lack of a ventral platform.

Family **ELKANIIDAE** Walcott & Schuchert, 1908

Genus ***MONOBOLINA*** Salter, 1865

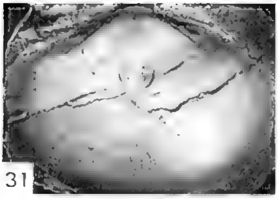
Monobolina plumbea (Salter)

(Figs 31–34)

1859 *Lingula plumbea* Salter *in* Murchison : 50; foss. 8, fig. 1.
1859 *Lingula Ramsayi* Salter *in* Murchison : 55; foss. 10, fig. 20.
1868 *Obolus? plumbea* (Salter) var. *plicata* (Hicks MS) Davidson : 311; pl. 16, fig. 6, *non* fig. 7.
1875 *Dinobolus? Hicksii* Davidson *in* Hicks : 188; pl. 10, fig. 6.

Since the type species of *Monobolina* was redescribed by one of us (Williams 1974 : 38) we have observed a further detail of dorsal morphology in the form of socket ridges about one-quarter as long as wide and about one-sixth as long as the valve (Fig. 31).

Cocks (1978 : 19) has suggested that *Lingula ramsayi* Salter probably belongs in the genus *Monobolina* and selected lectotypes for *M. plumbea, M. plumbea* var. *plicata* and *M. ? ramsayi.* We agree that the lectotype (GSM 8439) and particularly the paralectotypes (GSM 8434 and B 14404) of *M. ? ramsayi* belong to the genus *Monobolina,* although there is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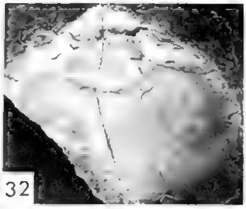
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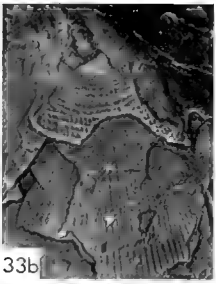
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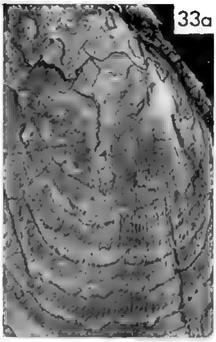
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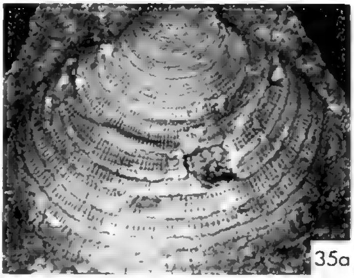
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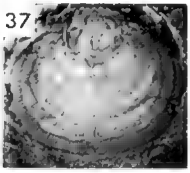
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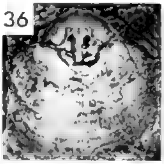
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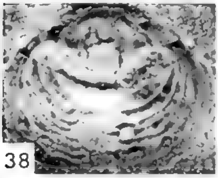
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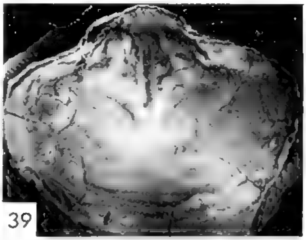
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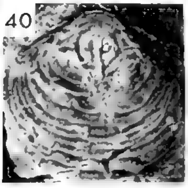
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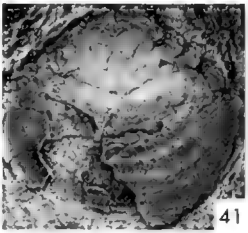
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Figs 31–34 *Monobolina plumbea* (Salter). Fig. 31, paralectotype B 5917, latex cast of internal part of exfoliated brachial valve × 2·5; Fig. 32, lectotype GSM 16909, latex cast of internal part of exfoliated pedicle valve × 2·5; both from Mytton Flags, White Grit Mine, Shropshire. Figs 33a, b, BB 14404, partially exfoliated valve × 3, and detail of ornament × 8, from Llanvirn Beds, Abereiddy Bay, Dyfed. Fig. 34, B 14376, latex cast of external mould of a ? pedicle valve × 4, from Arenig Beds, Tremanhire, St David's, Dyfed.

Figs 35–41 *Monobolina crassa* sp. nov. Figs 35a, b, B 5918, latex cast of external mould of a pedicle valve × 4, with detail of ornament × 8, from Llandeilo shales, Wellfield, Builth. Figs 36–38 and 40, GSM 16902, 16918, 16901 and 16900 respectively, internal moulds of brachial valves all × 2, from Llandeilo shales, Wyeford, Builth. Fig. 39, **holotype** SM A.104412, latex cast of internal mould of a brachial valve × 2, from Llandeilo shales, Pen Cerrig, Builth. Fig. 41, SM A.44850, exterior of a pedicle valve × 2, from *Nemagraptus gracilis* shales, Gwern-y-fed, Builth.

no evidence to suggest that the specimens are distinguishable from the type species. The large, thick-shelled paralectotypes are better preserved than the lectotype and exhibit 7 and 9 costellae respectively at 5 mm anteromedially of the umbones; B 14404 also exhibits the distinctive concentric fila characteristic of the type species. Indeed, having examined over 150 recognizable *Monobolina* specimens in an old Geological Survey collection from Abereiddy Bay, we have selected twelve specimens (GSM Zs 6259–70) which exhibit the outline, ornament and ventral muscle platform impressions characteristic of the type species *M. plumbea*. The lectotype (B 14376) of *M. plumbea* var. *plicata* which Davidson

(1868 : 312) and Hicks suggested was 'a small variety of *O. plumbea*' has 9 costellae per mm, 5 mm anteromedially of the umbo; the internal mould figure by Davidson (1868 : pl. 16, fig. 7) is no longer known.

Lingulella ? hicksii (Davidson), which comes from approximately the same horizon and locality as the specimens of *M. ? ramsayi*, should be regarded as a *nomen dubium* (Cocks 1978 : 15). The holotype B 5943 (by monotypy), although poorly preserved, is large and apparently transverse in outline with distinguishable thickened growth lines and platelike shell layers, all of which indicate that it might be a *Monobolina*.

MATERIAL		length	width
Lectotype, internal part of an exfoliated p.v. exterior	GSM 16909	13	16
Paralectotype, external part of an exfoliated b.v.	B 5917	12	17
External part of a partially exfoliated valve .	B 14404	(17·5)	(14)
External mould of a valve	B 14376	7·5	6·5

HORIZONS AND LOCALITIES. GSM 16909 and B 5917 from the Mytton Flags (Arenig), White Grit Mine, west of Stiperstones, Shropshire (*c.* SJ 335002); B 14404, GSM 8434, 8439, Zs 6259–70 and SM A.44841–9 and 97723 from rocks of Llanvirn age, Abereiddy Bay, Dyfed (*c.* SM 798307); B 14376 from Arenig Beds, Tremanhire, St Davids, Dyfed (*c.* SM 827263).

Monobolina crassa sp. nov.
(Figs 35–41)

1866 *Obolella plumbea* (Salter); Davidson : 61 pars; pl. 4, fig. 23, *non* figs 20–22, 24–27.
1871 *Obolus? plumbeus* (Salter); Davidson : 341 pars; pl. 50, fig. 24, *non* figs 22–23.

DIAGNOSIS. Large thick-shelled *Monobolina* with well-developed anteromedian extension to the internal dorsal platform and a short ventral platform about one-fifth as long as valve.

NAME. 'Thick'.

DESCRIPTION. Large, transverse, subelliptical, thick-shelled biconvex *Monobolina* with valves averaging about four-fifths as long as wide ($\bar{l}$ mm (var l) 13·46 (6·808), $\bar{w}$ mm (var w) 16·40 (14·30), r 0·995 for 5 specimens) and up to one-quarter as deep as long with obtuse umbones; shell thick, up to 0·8 mm in larger specimens and consisting of platelike lamellae inclined obliquely to the shell surface; exterior ornamented by irregular concentric fila in densities, 5 mm anteromedially of the umbones, of 4 fila per mm in one specimen and of 6, 7, 8 and 9 costellae per mm in 1, 2, 3 and 1 valves and with low concentric rugae with a wavelength of about 1 mm on the postneanic shell; ventral interior with posterior muscle platform about one-fifth as long as valve and about as wide as long; dorsal interior with well-developed, diamond-shaped posterior platform (p) averaging 53% as long as valve in 4 specimens ($\bar{l}$ mm (var l) 13·58 (8·989), $\bar{l}p$ (var lp) 7·15 (4·097), r 0·984) and impressed by a pair of outside lateral and elongate, submedian muscle scars with prominent muscle tracks on either side of a longer median groove which extends forward to the pointed anterior margin of the platform and is divided anteromedially by a fine, low ridge.

MATERIAL		length	width
Holotype, internal and external parts of exfoliated b.v.	SM A.104412	18	23
Paratype, exterior of p.v.	SM A.44850	16	19
Paratype, internal mould of b.v.	GSM 16918	11·5	14
"	GSM 16900	12·8	15
Paratype, external mould of p.v.	B 5918	10·3	12·5
Paratype, internal mould of b.v.	GSM 16901	13	16·5
"	GSM 16902	12	(14)

Horizons and localities. B 5918 from 'Llandeilo Flags' (probably *Glyptograptus teretiusculus* Zone) of Wellfield, Builth; SM A.104412 and A.104451–2 from *G. teretiusculus* shales exposed in the stream section east of Pen-Cerrig, 3 km north of Builth (SO 048537); SM A.104446–8 and GSM 16547 from *G. teretiusculus* shales exposed in the Trecoed stream section, 4 km north of Builth Wells (SO 054552); SM A.104449 from *G. teretiusculus* shales exposed in Dulas Brook, 5·5 km north of Builth Wells (SO 059566); GSM 16900–2 and 16918 from Llandeilo Shales of Hellpool, Wyeford, Builth; SM A.44850 (2 specimens) from *Nemagraptus gracilis* shales exposed in Gwern-y-fed quarry, 1·5 km north of Builth (SO 030526).

Discussion. *Monobolina crassa* sp. nov. differs from *M. plumbea* Salter in its greater biconvexity, well-developed posteromedian dorsal platform and relatively small ventral platform, and therefore must be regarded as specifically distinct from the older Shelve species. Although Davidson (1866 : 61) stated that 'in the Museum of the Geological Survey some specimens are labelled Hellpool, Wyeford Builth. This is "Upper Llandeilo" and it may be a mistake', it is now certain that *Monobolina* occurs sporadically in the Llandeilo successions of the Builth area (i.e. *G. teretiusculus* to *N. gracilis* Zones). This means that the genus, represented by the type species *M. plumbea* (Salter) in the Arenig rocks of the Shelve area and the related form described here, does not have such a restricted stratigraphical and geographical range as previously considered (Rowell *in* Williams *et al.* 1965 : H270, Williams 1974 : 39).

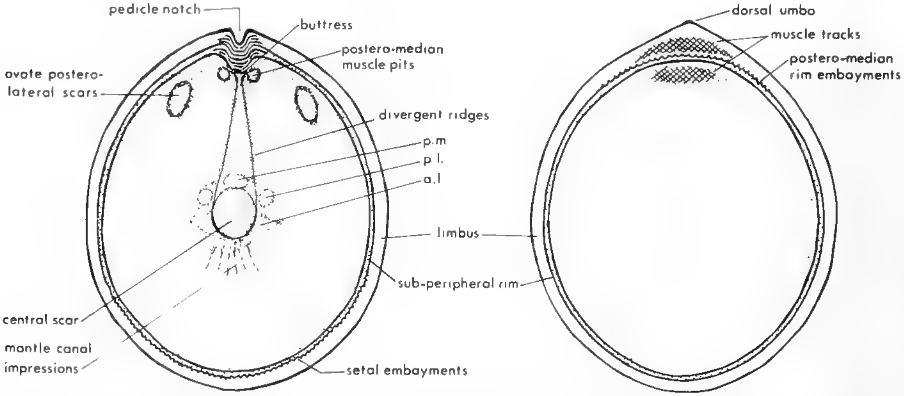


Fig. 42 Diagrammatic views of the interiors of the brachial (right) and pedicle (left) valves of *Paterula fissura* [Addison ms] sp. nov., showing the posteromedian (p.m.), posterolateral (p.l.) and anterolateral (a.l.) components of the central muscle scar.

Family **PATERULIDAE** Cooper, 1956

Genus ***PATERULA*** Barrande, 1879

Paterula cf. ***bohemica*** Barrande
(Figs 43–45)

cf. 1879 *Paterula Bohemica* Barrande : 110; pl. 95 (1–3); pl. 152, fig. 1 (1–9A).
cf. 1974 *Paterula* cf. *bohemica* Barrande; Williams : 40; pl. 6, figs 2–11.

Description. Dorsibiconvex subcircular to suboval *Paterula* with a slightly truncated to rounded posterior margin and a rounded anterior one; brachial valve with a mean width relative to length of 90% (range 86–93% in 4 valves) and a mean depth relative to length of 16% (range 14–17% in 3 valves); limbus well-defined, about 0·1 mm wide representing 5–7% of valve length and enclosing subperipheral rim; dorsal beak situated immediately forward of posterior arc of limbus; concentric ornament fine, with up to 40 fila per mm; ventral interior characterized by grooves diverging from beak to bound posteromedian sector of about 20° and to extend anteriorly for about one-third of valve length; dorsal interior featureless.

FIGURED MATERIAL

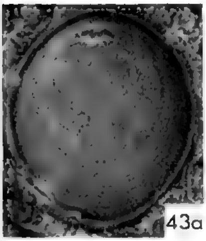
		length	width
Internal and external parts of exfoliated b.v.	BB 92286	1·5	1·4
,,	BB 92287	1·5	1·4
Internal part of exfoliated b.v.	BB 92272	2·1	1·8

HORIZON AND LOCALITIES. BB 92286–9 from the calcareous upper part of Flags and Grits in the middle of Ffairfach Group, Ffairfach railway cutting (SN 628211); BB 92272 from the Lower Llandeilo *Marrolithus inflatus maturus* Limestones exposed 100 m downstream from waterfall in Pontbren Araeth Dingle (SN 622237); SM A.44835 from an unknown horizon and locality in the Llandeilo area.

DISCUSSION. *Paterula* from the Llandeilo area compares very closely with the type species *P. bohemica* Barrande from the Llanvirn Sárka Formation of Czechoslovakia, as does the contemporaneous stock from the Shelve area of Shropshire (Williams 1974 : 40). The species is especially distinguishable in the full development of the limbus around the entire margin of the shell and the submarginal location of the dorsal beak. Although the Welsh forms have a less sharply truncated margin than the Shropshire specimens, the difference does not warrant any formal recognition.

Paterula fissura [Addison MS] sp. nov.
(Figs 42, 46–49)

DIAGNOSIS. Elongately oval *Paterula* with submarginal beaks and deep, tapering pedicle notch from which radiate grooves on interior of pedicle valve enclosing a central circular muscle scar.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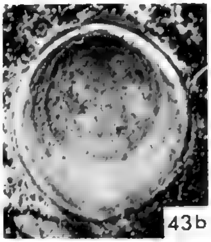
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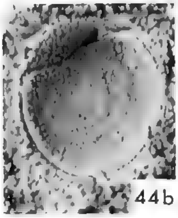
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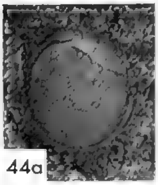
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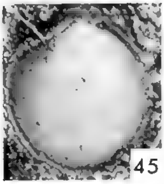
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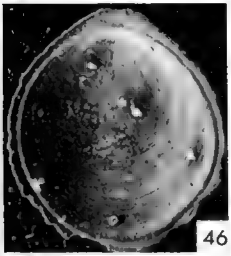
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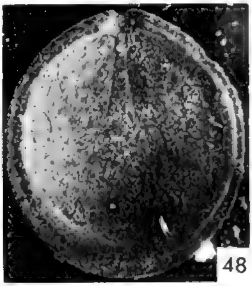
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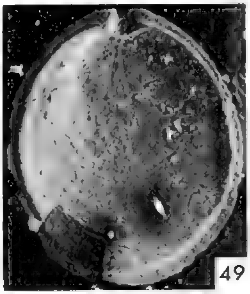
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Figs 43–45 *Paterula* cf. *bohemica* Barrande. Figs 43a, b, BB 92272a, b, internal part of exfoliated brachial valve and latex cast of same, both × 16, from Lower Llandeilo limestones, Pontbren Araeth, Llandeilo. Figs 44a, b, BB 92287, internal and external parts of an exfoliated brachial valve, both × 12; Fig. 45, BB 92286, internal part of an exfoliated brachial valve × 16; all from the Flags and Grits, Ffairfach Group type section.

Figs 46–49 *Paterula fissura* [Addison MS] sp. nov. Fig. 46, paratype BB 36121, a brachial valve × 24; Fig. 47, paratype BB 36124, a pedicle valve (external view) × 20; Fig. 48, **holotype** BB 36120, a pedicle valve, × 20; Fig. 49, paratype BB 94065, a pedicle valve × 20; all from Upper Llandeilo limestones, St Clears, Dyfed.

NAME. 'A cleft or slit'.

DESCRIPTION. Small dorsibiconvex, suboval *Paterula* with both pedicle and brachial valves averaging 86% as wide as long (e.g. $\bar{l}$ mm (var l) 1·45 (0·076), $\bar{w}$ mm (var w) 1·24 (0·061), r 0·978 for 20 brachial valves) and respectively averaging 11% and 13% as deep as long (e.g. $\bar{l}$ mm (var l) 1·44 (0·084), $\overline{th}$ (var th) 0·19 (0·004), r 0·933 for 18 brachial valves); transverse profiles evenly convex with longitudinal profile characterized by submarginal umbonal apices attaining maximum height just anterior of the slightly pointed posterior umbones.

Ventral interior with flat marginal limbus enclosing a subperipheral rim deeply embayed by posteriorly tapering pedicle notch which is about 10% as wide as valve at the rim and 5% as wide as valve at posterior extremity of umbo; long, narrowly divergent grooves arising at posterior embayment in subperipheral rim extend anteriorly for about half of valve length to meet tangentially and enclose a central circular muscle scar which is about 10% as wide as valve.

Dorsal interior also with subperipheral rim enclosed by marginal limbus which is enlarged and slightly pointed posteromedially.

FIGURED MATERIAL		length	width
Holotype, p.v.	BB 36120	2·0	1·7
Paratypes, b.v.	BB 36121	1·6	1·4
Paratype, p.v.	BB 94065	2·0	1·6
,, ...	BB 36124	1·6	1·4

HORIZON AND LOCALITY. BB 36120–4 and BB 94065 from the Upper Llandeilo Bryn Glas Limestone of the Narbeth succession exposed in the old quarry 400 m north of Lower Court Farm, St Clears, Dyfed (SN 307152).

DISCUSSION. This species was studied, but not formally published, by Addison (1974 : 139) with the aid of a scanning electron microscope, which allowed the observation of minute morphological detail. In addition to those features described above, he noted a small posteromedian buttress connecting the pedicle notch and the divergent grooves and recorded two sets of ventral posterolateral muscle scars and three sets of scars comprising the central scar complex (Fig. 42, p. 18). He also noted fine radiating anteromedian mantle canal markings and minute embayments which probably accommodated setae in the outer edge of the anterior part of the subperipheral rim. Both the dorsal umbonal cavity and posterior sector of the limbus were shown to be covered by a fine network of muscle tracks with small muscle pit embayments in the outer posterior sector of the subperipheral rim.

We support Addison's contention that *P. fissura* resembles *P. perfecta* Cooper in many respects. Like him, however, we regard differences, such as the configuration of the ventral muscle scar complex and the extent of the development of mantle canal markings, as indicative of specific differences between these two forms.

Order **ACROTRETIDA** Kuhn, 1949

Superfamily **ACROTRETACEA** Schuchert, 1893

Family **ACROTRETIDAE** Schuchert, 1893

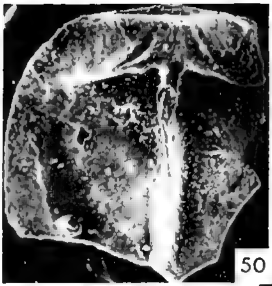
Subfamily **ACROTRETINAE** Schuchert, 1893

Genus ***CONOTRETA*** Walcott, 1889

? ***Conotreta*** sp.

(Figs 50–52)

DESCRIPTION. Acrotretinid brachial valve with a subcircular to subquadrate outline and a convex profile, almost as long as wide with well-developed transverse proparea, one-fifth to one-quarter as long as valve, bounded anteriorly by prominent hinge line and short anacline interarea; cardinal scars divergent, developed as wide, deep grooves in propareas which are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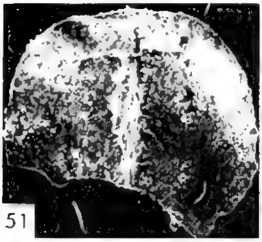
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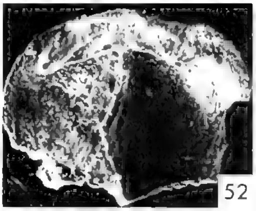
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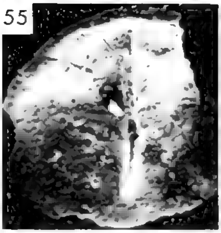
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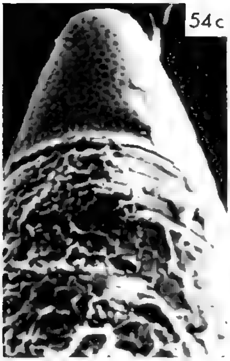
54b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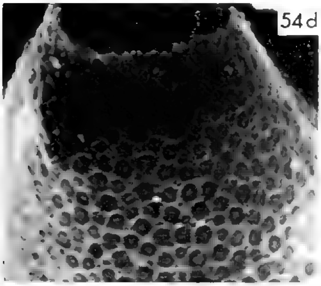
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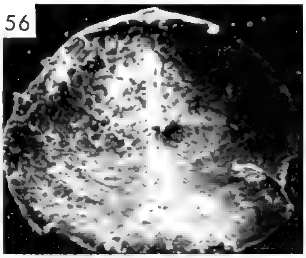
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58

Figs 50–52 ? *Conotreta* sp. BB 94049, 94054 and 94052, three brachial valves × 36, × 32 and × 24 respectively, all from Upper Llandeilo limestones, St Clears, Dyfed.

Figs 53–56 *Torynelasma* sp. Fig. 53, BB 94044, a pedicle valve × 56; Figs 54a–d, BB 94045, a pedicle valve with details of growth lines (and punctae), protegulum and foramen, × 56, × 850, × 250 and × 600 respectively; Figs 55–56, BB 94046–7, two brachial valves × 40 and × 56; all specimens from Upper Llandeilo limestones, St Clears, Dyfed.

Figs 57–58 ? Acrotretid indet. Figs 57a, b, BB 94056, a pedicle valve × 16, with detail of foramen × 180; Fig. 58, BB 94057, a pedicle valve (apical view) × 95; both from Upper Llandeilo limestones, St Clears, Dyfed. (See p. 23).

indented medially at the posterior margin where the thick median septum arises steeply to form a prominent triangular keel incorporating upper and lower anteroventrally projecting rods; radial lines developed sporadically on valve floor; dorsal exterior and ventral valve unknown.

FIGURED MATERIAL		length	width
Brachial valve	BB 94049	(1·0)	1·25
"	BB 94052	(1·2)	1·5
"	BB 94054	(1·1)	1·25

Horizon and locality. BB 94049–55 from Upper Llandeilo Bryn Glas Limestone strata of Narbeth succession exposed in old quarry 400 m north of Lower Court Farm, St Clears, Dyfed (SN 307152).

Discussion. This material is almost certainly representative of a hitherto unknown acrotretinid, but in the absence of a pedicle valve we can make no conclusive statements about its taxonomic affinity. It resembles *Conotreta* in having well-developed propareas, cardinal scars and a posteriorly arising median septum.

Subfamily **TORYNELASMATINAE** Rowell, 1965

Genus ***TORYNELASMA*** Cooper, 1956

Torynelasma sp.

(Figs 53–56)

Description. Small torynelasmatinid with acutely conical pedicle valve at least half as long and half as wide as deep, with obscure pseudointerarea and prominent asymmetrically conical 'bubble raft' protegulum, about one-sixth as deep as valve and extending furthest from the apex on the posterior side of the valve, apical foramen about 30 μm in diameter in 2 specimens; larger protegular pits averaging 3·46 μm in diameter ($n = 50$, var 0·636); the non-protegular shell is punctate with encircling evenly-spaced growth lines between 6 and 8 μm apart; brachial valve flat to slightly convex and transversely subelliptical ranging between 83 and 94% as long as wide in three valves, pseudointerarea short anacline bounded posteriorly by obtuse umbo and anteriorly by straight hinge, median septum long extending almost to anterior commissure, with maximum height towards anterior but no transverse plate- or rod-like structures; obscure posteromedian muscle scars occur on either side of the median septum and faint concentric growth lines mark the valve floor; dorsal exterior unknown; pedicle valve interior structurally featureless.

FIGURED MATERIAL		length	width	depth
Pedicle valve . . .	BB 94044	0·4	0·4	0·75
" . . .	BB 94045	0·4	0·4	0·7
Brachial valve . . .	BB 94046	1·0	1·2	—
" . . .	BB 94047	0·65	0·7	—

Horizon and locality. Upper Llandeilo Bryn Glas Limestone strata of the Narbeth succession exposed in the old quarry 400 m north of Lower Court farm, St Clears, Dyfed (SN 397152).

Discussion. The ventral morphology is essentially identical to the *Torynelasma* type species *T. toryniferum* Cooper (1956 : 257), though it apparently has larger protegular pits (cf. Biernat & Williams 1970 : 494). It is also similar to the Siluro-Devonian genus *Caenotreta* (Cocks 1979 : 93). The dorsal interior of the Llandeilo *Torynelasma* does not bear the spoon-like transverse septal plate of the type species, or rods as in *Caenotreta*, but this may be because of imperfect preservation. If further suitable material becomes available it will be important to establish whether the septal development seen in specimen BB 94047 is representative of a complete undamaged structure; if this were the case, the species would be better considered representative of a new generic stock within the Torynelasmatinae.

We note that despite differences in protegular structure, *Opsiconidion* Ludvigsen (1974), Scaphalasmatinae, and *Caenotreta* are virtually identical in all other respects and also would probably be best accommodated in the Torynelasmatinae.

In addition to the acrotretaceans discussed here, the Bryn Glas Limestone residues have yielded miscellaneous faunal elements including the 'acutely conical valves' (BB 94056–7) illustrated (Figs 57–58). These exceptionally conical valves, although exhibiting no recognizable protegular ornament, show a discernible change in cone slope near the apex and a well-developed apical foramen. With our present imperfect knowledge of acrotretacean faunas we tentatively consider that these valves may also be related to the Torynelasmatinae.

Genus indet

Material and Discussion. An assemblage of small acrotretids recovered from basal *G. teretiusculus* shales exposed just east of Welfield Lodge (SO 044528) represents the first authentic record of this order from the Builth area. The specimens, SM A.105827–36, exhibit acutely conical pedicle valves about twice as deep (up to 3·5 mm) as long (1·5–2·0 mm) and subcircular slightly convex brachial valves with a median septum of unknown profile. They are unlike *Conotreta* or *Apsotreta* from the Shelve area (Williams 1974) and may ultimately prove to be more closely related to the Torynelasmatinae.

Superfamily **DISCINACEA** Gray, 1840
Family **TREMATIDAE** Schuchert, 1893

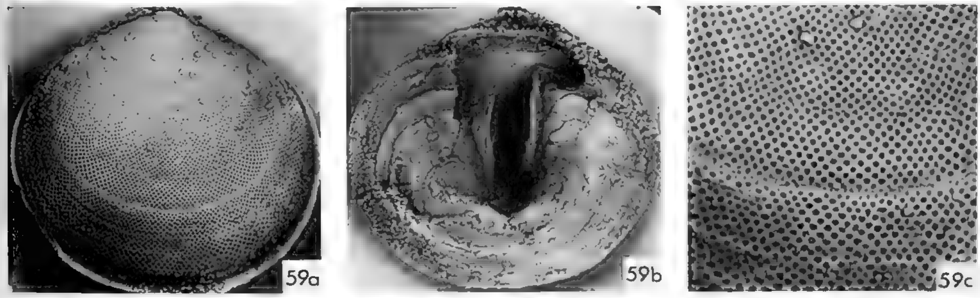
Genus ***TREMATIS*** Sharpe, 1848

Trematis evansi [Addison MS] sp. nov.
(Figs 59a–c)

Diagnosis. Subcircular, biconvex *Trematis* with pedicle notch about three-fifths as long as valve, situated in broad posteromedian sector; ornament quincuncial with 12 concentric pit rows betwen 4 and 5 mm anteromedially of dorsal umbo and 7 pits per mm in each row at this point.

Name. For D. C. Evans, who in 1906 published his pioneering work on the Ordovician rocks of western Carmarthenshire.

Description. Subcircular biconvex *Trematis* with valves slightly wider than long and about one-quarter to one-fifth as deep as long; pedicle valve with broad posteriomedian sulcus extending from the apex, just anterior to the mid-point where the maximum depth is observed, to the posterior margin with sides enclosing a sector of almost 90°; median pedicle notch, about three-fifths as long and one-eighth as wide as valve with sides of notch concave towards mid-line; listrum small apically but well-developed along each side of the pedicle fissure as longitudinal plates about one-third as wide as notch and characterized by fine radiating lines; brachial valve evenly convex with maximum depth just anterior of the mid-point, umbo obtuse, interarea simple, about one-tenth as long as valve. Ornament of small quincuncially arranged pits, numbering 7 per mm 5 mm anteromedially of the dorsal umbo,



Figs 59a–c *Trematis evansi* [Addison MS] sp. nov. **Holotype** BB 36126, dorsal view × 4, ventral view × 4 and detail of dorsal ornament of conjoined valves × 10, from Upper Llandeilo limestones, St Clears, Dyfed..

has 12 alternately arranged concentric pit rows between 4 and 5 mm anteromedially; pit size, pit and pit row spacing increase progressively from umbo to anterior margin with quincuncial pattern consistent over entire valve surface except where growth pauses result in minor attenuations.

Interiors of both valves incompletely known except for pair of rounded dorsal muscle scars on either side of an obscure low median ridge.

HOLOTYPE. Complete specimen, BB 36126; length 11·0 mm, width 12·3 mm.

HORIZON AND LOCALITY. Upper Llandeilo Bryn-glas Limestone, exposed in old quarry 400 m north of Lower Court Farm near St Clears (SN 307152).

DISCUSSION. Addison (1974 : 144, not formally published) reviewed the affinities of *T. evansi*, showing that amongst quincuncially-ornamented *Trematis* it can only be considered to resemble *T. parva* Cooper and *T. melliflua* Reed in density and style of ornament. Both these poorly-known species, however, have sulcate brachial valves and are distinguishable from *T. evansi* at least in this respect.

Genus *SCHIZOCRANIA* Hall & Whitfield, 1875

Schizocrania cf. ***salopiensis*** Williams
(Figs 60–65)

1866 *Discina crassa* Hall?; Davidson *pars* : pl. 6, fig. 6, *non* fig. 7.
cf. 1974 *Schizocrania salopiensis* Williams : 44; pl. 6, figs 22–26.

DIAGNOSIS. *Schizocrania* with subcircular to suboval outline and a broadly triangular pedicle opening, about one-third as deep as long dorsally with a posteriorly placed umbo and dichotomizing capillae developed with variable density; ventral ornament of concentric growth lines.

DESCRIPTION. Pedicle valve subcircular to transversely suboval with broadly triangular pedicle opening with straight sides and a well-developed listrum; brachial valve subcircular to suboval, between 85% and 91% as long as wide in 5 specimens, with an evenly convex transverse profile, longitudinal profile asymmetrically convex with posterior umbo overhanging smoothly rounded posterior margin; ventral exterior ornamented by concentric growth lines surrounding the central point at the anterior apex of the triangular pedicle opening and extending onto listrum; dorsal exterior ornamented by sporadically occurring faint growth lines and prominent capillae disposed radially from umbo and numbering 9 to 15 per mm at the anterior margin in a sample of small shells, and between 10 and 16 per mm at 5 mm anteromedially in a group of larger shells; capillae reflexed posterolaterally.

Dorsal interior with well-defined slightly divergent posterior adductor scars extending forward for about one-fifth of valve length and separated by a median ridge; radial mantle canals number 6 and 7 per mm, 5 mm anteromedially of the umbo, in 4 and 1 specimens from Penddol with each canal therefore corresponding to about two external capillae; ventral interior unknown.

FIGURED MATERIAL

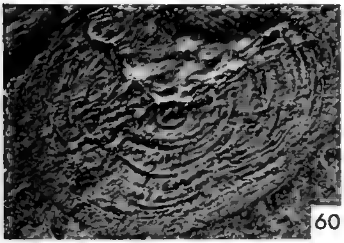
		length	width
Exfoliated exterior part of b.v.	BB 92277	4·1	4·5
Internal mould of b.v.	BB 92300	4·2	4·6
External mould of b.v.	SM A.46560	10·5	11·5
„	SM A.44861	11	12
Internal part of exfoliated b.v.	SM A.104418	8	10·5
External mould of p.v.	SM A.104413	(6·5)	(9·0)

HORIZONS AND LOCALITIES. BB 92492–4 from Flags and Grits of the Ffairfach Group exposed at Coed Duon, Llangadog (SN 709256); BB 94248 from Flags and Grits, Ffairfach Group type section (SN 628211); BB 92275–7 from Upper Llandeilo Flags exposed in dingle 200 m south of Crûg, Llandeilo (SN 627229); BB 92278 from Lower Llandeilo

Sowerbyella Limestones exposed in old trackway SW end of Deer Park, Dynevor Park, Llandeilo (SN 609223); BB 92298–300 from the grey shelly sandstones ('Pebbly Felspar Ash' of the Main Tuff Group) 200 m SW of Carn peak, Carneddau Hills, 1·25 km ESE of Newmead Farm near Builth Wells (SO 065539); SM A.44861 from the 'Llandeilo Limestone' (*Nemagraptus gracilis* Zone) of Harper's Quarry, Wellfield, 2 km north of Builth (SO 037534); SM A.46560 from Llanvirn *Didymograptus murchisoni* shales exposed in Howey Brook (SO 090592); SM A.104418 from *Glyptograptus teretiusculus* shales exposed in the stream section east of Pen Cerrig (SO 948537). SM A.104413 from *G. teretiusculus* to *N. gracilis* Zone shales exposed at Penddol Rocks, in the Wye river section 1 km NW of Builth (SO 031522); GSM 16762 from the 'Llandeilo flags of Builth', probably the same horizon, precise locality unknown.

DISCUSSION. The specimens, including GSM 16762, SM A.44850, A.46560 and A.51157 from localities in the Builth region, allow us to add information on the species' ventral morphology and the variability of its dorsal ornament to the existing description (Williams 1974 : 44). The small Llandeilo and the usually larger Builth specimens exhibit more variable dorsal capillae densities than apparently conspecific brachial valves from Shelve. Such pronounced variability in ornament may be indicative of specific variation in the Welsh stock.

The stratigraphical range of *Schizocrania* cf. *salopiensis* in the Builth region and in the Llandeilo area (Bassett *et al.* 1974 : 9; Wilcox 1979 : 42) falls within that of the Shelve stock which is known from Upper Llanvirn, Llandeilo and basal Caradoc rocks.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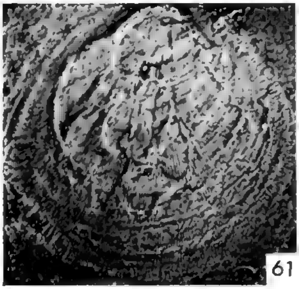
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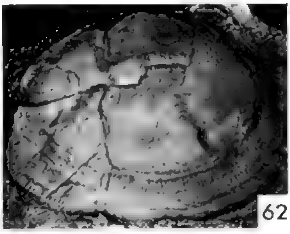
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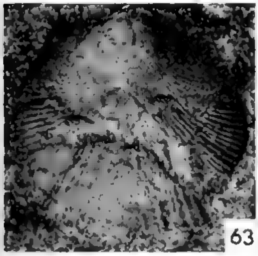
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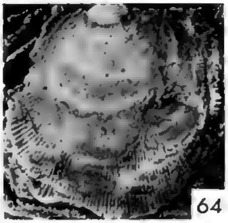
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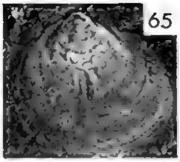
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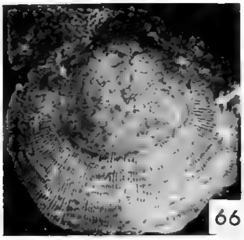
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Figs 60–65 *Schizocrania* cf. *salopiensis* Williams. Fig. 60, SM A.104413, internal mould of a pedicle valve × 6, from Llandeilo shales, Penddol, Builth. Fig. 61, SM A.46560, latex cast of an external mould of a brachial valve × 8, from Llanvirn shales in Howey Brook, Llandrindod. Fig. 62, SM A.104418, internal part of an exfoliated brachial valve × 4, from Llandeilo shales, Pen Cerrig, Builth. Fig. 63, BB 92277, a partially exfoliated brachial valve × 8, from Upper Llandeilo shales, Llandeilo. Fig. 64, BB 92300, exterior of a brachial valve × 8, from Llanvirn sandstones, Newmead, Builth. Fig. 65, SM A.44861, latex cast of external mould of a brachial valve × 2, from Llandeilo shales, Wellfield, Builth.

Fig. 66 *Schizocrania multistriata* (Reed). Holotype SM A.34039, exterior of a brachial valve × 2, from Lower Caradoc limestones, Lampeter Velfrey, Dyfed.

Schizocrania multistriata (Reed), emended
(Fig. 66)

1905 *Trematis multistriata* Reed : 446; pl. 23, figs 1–1a.

DESCRIPTION. Subcircular to transversely suboval *Schizocrania* with brachial valve about nine-tenths as long as wide and one-fifth as deep as long, dorsal transverse profile evenly convex, longitudinal profile unevenly convex with maximum depth posterior to midline; ornament of a few indistinct concentric growth lines and prominent radial capillae numbering 10 per mm at 5 mm anteromedially of the dorsal umbo, capillae reflexed posterolaterally. Interior of brachial valve and pedicle valve unknown.

HOLOTYPE. Exterior of brachial valve, SM A.34039; length 16·5 mm, width 18·5 mm.

HORIZON AND LOCALITY. The only known specimen is from the Lower Caradoc Bryn Banc Limestone exposed in old quarry 250 m NW of Lampeter Velfrey Church (SN 153146).

DISCUSSION. This species, of which the holotype is still the only specimen known, resembles *S. salopiensis* Williams in its external dorsal morphology and may prove to be a senior synonym of the Shelve species. Meanwhile it is transferred to the genus *Schizocrania,* to which it undoubtedly belongs.

Family **DISCINIDAE** Gray, 1840

Subfamily **ORBICULOIDEINAE** Schuchert & Le Vene, 1929

Genus ***SCHIZOTRETA*** Kutorga, 1848

Schizotreta cf. ***transversa*** Williams
(Fig. 70)

cf. 1974 *Schizotreta transversa* Williams : 47; pl. 7, figs 2, 3, 7.

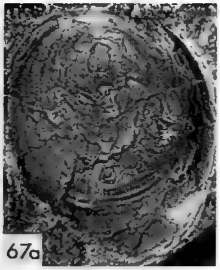
A single external mould of a *Schizotreta* pedicle valve (BB 92274) from the Lower Llandeilo *Lloydolithus lloydi* Flags exposed in the old quarry in Castle Wood, Dynevor Park, Llandeilo (SN 615217), compares most closely with the contemporaneous Shelve species *S. transversa* Williams. The similarity in the relatively transverse outline and lack of well-developed fila is especially noteworthy in view of the distinctive form from the Ffairfach Group described below.

Schizotreta transversa Williams ***ffairfachensis*** subsp. nov.
(Figs 67–69)

DIAGNOSIS. Suboval *Schizotreta* slightly longer than wide, with a surface ornament consisting of well-developed fila.

NAME. From Ffairfach.

DESCRIPTION. Subcircular to suboval *Schizotreta* with truncated posterior margin and pronounced concentric ornamentation consisting of strongly-developed fila numbering 5–6 per mm in the anterior and lateral parts of the valve and with fine, closely spaced radial striations over the whole shell; pedicle valve subconical, almost as wide as long (averaging 95% in three specimens) and 20% as deep as long in 2 valves, with a well-developed pedicle track occupying median portion of the valve posterior to apex which is situated medially 29% of valve length anterior of posterior margin; brachial valve 88% as wide as long ($\bar{l}$ mm (var l) 7·64 (1·413), $\bar{w}$ mm (var w) 6·44 (4·798), r 0·968 in 5 valves) and 13% as deep as long ($\bar{l}$ mm (var l) 7·64 (1·413), $\overline{th}$ (var th) 0·98 (0·137), r 0·966 in 5 valves) with apex situated at 14% of valve length forward of the posterior margin.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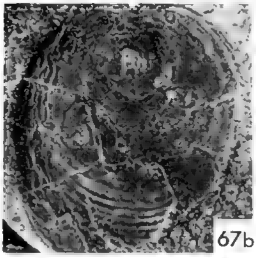
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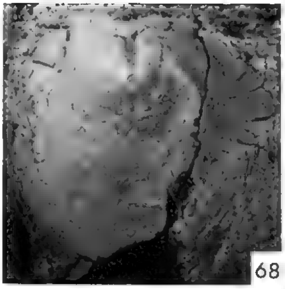
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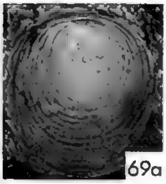
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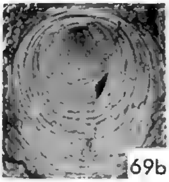
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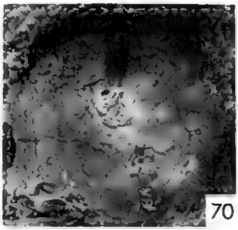
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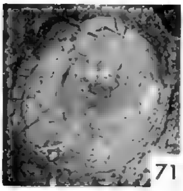
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Figs 67–69 *Schizotreta transversa ffairfachensis* subsp. nov. Figs 67a, b, **holotype** BB 92290a, b, internal and external parts of an exfoliated brachial valve × 4; Fig. 68, paratype BB 92292, internal part of an exfoliated pedicle valve × 4; Figs 69a, b, paratype BB 92291a, b, internal and external parts of an exfoliated brachial valve × 4; all from Flags and Grits, Ffairfach Group, type section.

Fig. 70 *Schizotreta* cf. *transversa transversa* Williams. BB 92274, exterior of a pedicle valve × 8, from Lower Llandeilo Limestones, Dynevor Park, Llandeilo.

Fig. 71 *Schizotreta transversa transversa* Williams. B 21766, latex cast of external mould of a pedicle valve × 4, from Llandeilo Flags, Shelve, Shropshire.

TYPE MATERIAL

		length	width
Holotype, external and internal parts of exfoliated b.v.	BB 92290	10·0	9·0
Paratype, internal part of an exfoliated p.v.	BB 92292	11·0	10·5
Paratype, internal and external parts of exfoliated b.v.	BB 92291	6·5	5·9

HORIZON AND LOCALITY. All specimens are from the argillaceous lower part of the Flags and Grits of the Ffairfach Group, Ffairfach railway cutting, Llandeilo (SN 628211).

DISCUSSION. The Ffairfach *Schizotreta* differs from the smaller form *S. transversa* Williams (1974 : 47) from the Shelve area in its more elongate shape and particularly in the strong development of concentric fila. These features are considered important enough to warrant subspecific recognition of the Llanvirn form. The recognition of *Schizotreta* in the Arenig (Williams 1974 : 48) and Llanvirn Series reveals an extended stratigraphical range for the genus and indicates that the characteristic elongately suboval shape of Scottish and American stocks like *S. corrugata* (Cooper) and *S. medioradiata* (Reed) was also typical of early Anglo-Welsh forms.

An examination of specimen B 21766 (Fig. 71) from the 'Llandeilo Flags' of Shelve, referred to by Davidson (1866 : pl. 7) as *Orbiculoidea forbesi* Davidson and since referred to *Orbiculoidea* sp. by Cocks (1978 : 176), reveals that it can be assigned to *S. transversa transversa* Williams.

Class **ARTICULATA** Huxley, 1869

Order **ORTHIDA** Schuchert & Cooper, 1932

Suborder **ORTHIDINA** Schuchert & Cooper, 1932

Superfamily **ORTHACEA** Woodward, 1852

Family **DOLERORTHIDAE** Öpik, 1934

Subfamily **HESPERORTHINAE** Schuchert & Cooper, 1931

Genus ***HESPERORTHIS*** Schuchert & Cooper, 1931

Hesperorthis dynevorensis Williams, emended
(Figs 72–80)

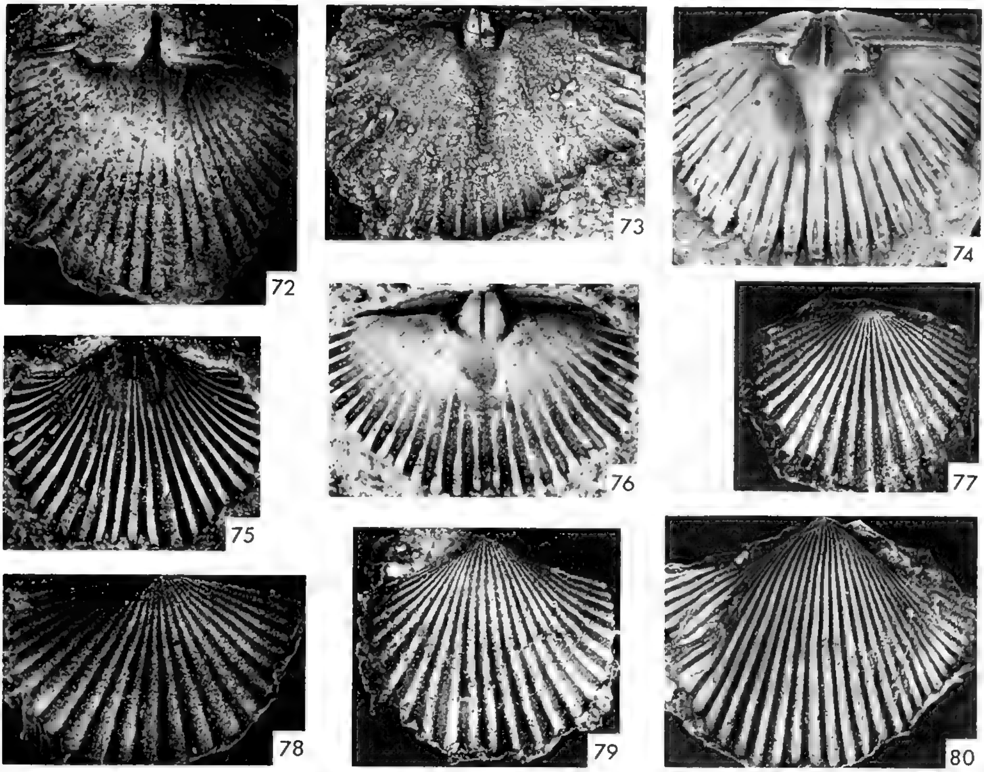
1949 *Hesperorthis dynevorensis* Williams : 226; pl. 11, figs 1, 2.

Diagnosis. Planoconvex to ventribiconvex *Hesperorthis* with up to 34 regularly spaced costae, numbering 2 per mm at 5 mm anterior of the umbones, and a ventral muscle scar averaging 38% as long as pedicle valve.

Description. Planoconvex to ventribiconvex *Hesperorthis* with suboval outline and slightly obtuse cardinal angles; pedicle valve averaging 82 to 89% as long as wide and 24 to 28% as deep as long (e.g. $\bar{l}$ mm (var l) 9·08 (5·778), $\overline{th}$ (var th) 2·18 (0·325), r 0·738 in 13 valves from Newmead) in three samples; brachial valve averaging 74 to 84% as long as wide (e.g. $\bar{l}$ mm (var l) 11·14 (18·842), $\bar{w}$ mm (var w) 14·28 (27·855), r 0·980 in 30 valves from Llanelwedd) and 14 to 17% as deep as long in same three samples (e.g. $\bar{l}$ mm (var l) 14·75 (4·175), $\overline{th}$ (var th) 2·33 (0·351), r 0·826 in 6 valves from Llanelwedd); ventral interarea curved apsacline and up to one-quarter as long as valve with narrow delthyrium defined by parallel to slightly divergent boundaries subtending an angle of up to 30°; dorsal interarea flat, anacline and up to 15% as long as valve with well-developed fine transverse growth lines numbering 10–15 per mm; notothyrium open with divergent boundaries forming an angle of about 60°; exterior ornamented by up to 35 regularly spaced rounded costae depending on size; mean amplitude of costae 0·5 mm at 5 mm anteromedially of umbones of 9 valves; counts of 25, 26, 27, 28, 29, 30, 31, 32, 33, 34 and 35 costae were recorded in 1, 0, 0, 1, 3, 4, 6, 4, 1, 0 and 2 valves of specimens from the type horizon at Llandeilo compared with 2, 3, 6, 7, 6, 2, 1, 0, 0 and 0 valves from the Builth area (see Table 2, p. 30).

Ventral interior with deep delthyrial cavity bounded by dental lamellae supporting small teeth about 20% as long as interarea with maximum anterior extension at lateral margins of tooth; ventral muscle scar slightly raised, averaging between 37 and 39% as long as valve (e.g. $\bar{l}$ mm (var l) 9·65 (4·563), $\overline{lsc}$ (var lsc) 3·54 (0·605), r 0·865 in 11 valves from Newmead) and 65 to 83% as wide as long in three samples (e.g. $\bar{l}$ mm (var l) 3·54 (0·550), $\bar{w}$ mm (var w) 2·93 (0·424), r 0·885 in 12 valves from Newmead); paired adductor scars, thin and long, represented anteriorly by fine ridges separated and bounded by fine grooves extending beyond the anterior margin of diductor scars to link with *vascula media*.

Dorsal interior with simple low, thin plate-like cardinal process narrowing posteriorly and dividing a broad, low, smooth notothyrial cavity; brachiophores short divergent about 30% as long as interarea, with bases averaging 19 to 22% as long as valve (e.g. $\bar{l}$ mm (var l) 11·11 (17·501), $\overline{lc}$ (var lc) 2·38 (0·791), r 0·947 in 30 valves from Llanelwedd) and 78 to 86% as long as wide (e.g. $\bar{l}$ mm (var l) 2·45 (0·738), $\bar{w}$ mm (var w) 3·41 (1·901), r 0·951 in 18 valves from Llanelwedd); sockets deep; adductor scar pattern quadripartite with anterior adductors smaller than more deeply impressed posterior pair and extending forward for about 60% of the length of the valve, entire field about two-thirds as wide as long and one-third as wide as valve.



Figs 72–80 *Hesperorthis dynevorensis* Williams. Fig. 72, BB 92308, latex cast of the internal mould of a pedicle valve × 2; Fig. 73, BB 92307, internal mould of a brachial valve × 2; both from Pebbly Sandstones, Ffairfach Group, type section. Fig. 74, BB 92313, latex cast of internal mould of a brachial valve × 4; Fig. 75, BB 92314, internal mould of a pedicle valve × 3; Fig. 76, BB 92312, internal mould of a brachial valve × 4; all from Upper Llanvirn sandstones, Newmead, Builth. Figs 77–78, NMW 68.376.G.153–3, latex casts of external moulds of two brachial valves, both × 2; Fig. 79, NMW 68.376.G.151–1, latex cast of external mould of a pedicle valve × 2; all from Llanvirn Sandstones, Tan y Craig, Builth. Fig. 80, BB 92475, latex cast of external mould of a pedicle valve × 2, from Upper Llanvirn Ashes and Lavas, Coed, Duon, Llangadog.

FIGURED MATERIAL		length	width
Internal mould of b.v.	BB 92307	19	26
,, ...	BB 92312	8	12
Latex cast of internal mould of p.v.	BB 92308	24	24
Latex cast of external mould of p.v.	BB 92475	20	26
,, . . .	NMW 68.376.G.151-1	17	19
Latex cast of external mould of b.v.	NMW 68.376.G.153-3	15	22
,, . . .	NMW 68.376.G.153-3	13	16
Latex cast of internal mould of b.v.	BB 92313	11	13·5
Internal mould of p.v.	BB 92314	11	13·5

HORIZON AND LOCALITIES. BB 92307–11 from the upper part of the Pebbly Sands Formation of the Ffairfach Group, Ffairfach railway cutting, Ffairfach, Llandeilo (SN 628211);

BB 92312–4 from the lower to middle part of the Main Tuff Group with Lower *Didymograptus murchisoni* Shales, outcrop SW of cairn on Carneddau Hills 1 km ESE of Newmead Farm (SO 065539); BB 92474–5 from rhyolitic conglomerates in the Ashes and Lavas Formation of the Ffairfach Group exposed at Coed Duon, 3 km south of Llangadog (SN 709256); NMW 68.376.G.150–61 from tuffaceous sandstones exposed in quarry east of Tan y Grait 1 km north of Llanelwedd, north of Builth Wells (SO 047528).

Discussion. Comparisons between penecontemporaneous *Hesperorthis* from Ffairfach, Newmead and Llanelwedd are affected by the restricted size range of individuals composing the samples and by the fact that the Ffairfach specimens are, on average, more than twice as big as those from Newmead. Consequently, if allometric changes had occurred during growth, tests of significance might show the samples to be different. However, the Ffairfach and Llanelwedd samples show no significant difference in the eight characters tested and the Newmead sample differs only from the Ffairfach specimens in the shape of its shorter ventral muscle scar ($0{\cdot}02<p<0{\cdot}01$) and from the Llanelwedd sample in having a significantly wider brachial valve ($0{\cdot}05<p<0{\cdot}02$). Since the valves from Ffairfach and Llanelwedd are bigger than those from Newmead we have interpreted the greater length of the brachial valve and the ventral muscle scars in the former two samples as an acceleration in forward growth during later growth stages rather than as genotypic differences. Certainly observations of growth patterns in Scottish hesperorthids such as *H. australis exilis* Williams, *H. australis* Cooper and *H. craigensis* (Reed) (Williams 1962 : 107–9) reveal that the shape of the ventral muscle scar is quite variable. Yet when compared with the Welsh samples, the three Scottish taxa differ significantly. Differences in the density of costae in the Ffairfach and Newmead samples are directly related to size and, in the absence of sufficient specimens of comparable size from those two Welsh localities, the validity of a statistical comparison is in doubt.

Table 2 The distribution of various patterns of rib density for given range of size in samples of *Hesperorthis dynevorensis* Williams from the Llanvirn rocks of Newmead and, in brackets, Ffairfach.

	No. of ribs				
width mm	22–24	25–27	28–30	31–33	34–36
6—9	1 —	6 —	3 —	1 —	— —
10—13	— —	4 —	12 (1)	1 (3)	— —
14—17	— —	1 —	— (1)	1 (3)	— (1)
18—21	— —	— (1)	— (3)	— (3)	— (1)
22—25	— —	— —	— (1)	— (1)	— —
26—29	— —	— —	— (2)	— (1)	— —

Subfamily **GLYPTORTHINAE** Schuchert & Cooper, 1931

Genus ***GLYPTORTHIS*** Foerste, 1914

Glyptorthis cf. ***viriosa*** Williams
(Figs 86–88)

cf. 1974 *Glyptorthis viriosa* Williams : 64; pl. 10, figs 6, 8, 9, 11, 12, 14, 15; pl. 11, figs 1, 2, 4.

Diagnosis. Small biconvex *Glyptorthis* with slightly carinate pedicle valve 81% as long as wide and 34% as deep as long and a brachial valve 30% as deep as long, ventral muscle scar 82% as long as wide and 25% as long as valve.

Description. Small biconvex *Glyptorthis* with slightly obtuse cardinal angles; pedicle valve slightly carinate averaging 81% as long as wide (in 14 valves) and 34% as deep as long ($\bar{l}$ mm (var l) 3·01 (2·311), $\overline{th}$ (var th) 1·01 (0·308), r 0·971) in 7 specimens; brachial valve sulcate averaging 74% as long as wide ($\bar{l}$ mm (var l) 3·22 (0·724), $\bar{w}$ mm (var w) 4·33 (1·325), r 0·970 in 10 valves) and 30% as deep as long ($\bar{l}$ mm (var l) 3·32 (1·134), $\overline{th}$ (var th) 1·00 (0·104), r 0·901 in 6 valves); other features of the ventral and dorsal exterior are identical with those of the Ffairfach subspecies described below.

Ventral interior with small trigonal teeth supported by narrowly divergent dental plates extending forward for about 20% of valve length; ventral muscle scar with modified pentagonal to bilobed outline averaging 82% as long as wide ($\bar{l}$ mm (var l) 0·77 (0·126), $\bar{w}$ mm (var w) 0·94 (0·083), r 0·978 in 7 valves) and 25% as long ($\bar{l}$ mm (var l) 3·10 (2·04), $\overline{lsc}$ (var lsc) 0·77 (0·126), r 0·974 in 7 valves) and 21% as wide as pedicle valve; median adductor scars rectangular, about one-third as wide as muscle field and flanked by longitudinal divergent diductor scars.

Dorsal interior with simple blade-like cardinal process and blunt divergent brachiophores defining simple sockets with bases extending forward for 22% of valve length and occupying 31% of valve width (and just over half as long as wide, i.e. $\bar{l}$ mm (var l) 0·70 (0·050), $\bar{w}$ mm (var w) 1·33 (0·266), r 0·925 in 7 valves).

FIGURED MATERIAL		length	width
Internal mould of p.v.	BB 92319	5·0	6·0
„	BB 92320	4·5	5·3
Internal and external moulds of b.v.	BB 92321	4·4	6·0

HORIZON AND LOCALITY. BB 92319–22 from sandy ashes at the top of the Main Volcanic Series in the Howey Brook ('Main Feeder') section, 4 km east of Howey, outcrop on top of small hill on north side of brook (SO 0925 5915).

DISCUSSION. See below, p. 33.

Glyptorthis viriosa Williams *tumida* subsp. nov.

(Figs 81–85)

DIAGNOSIS. Biconvex *Glyptorthis* with slightly carinate pedicle valve 76% as long as wide and 28% as deep as long and a brachial valve 27% as deep as long; ventral muscle scar 98% as long as wide and 32% as long as valve.

NAME. 'Swollen'.

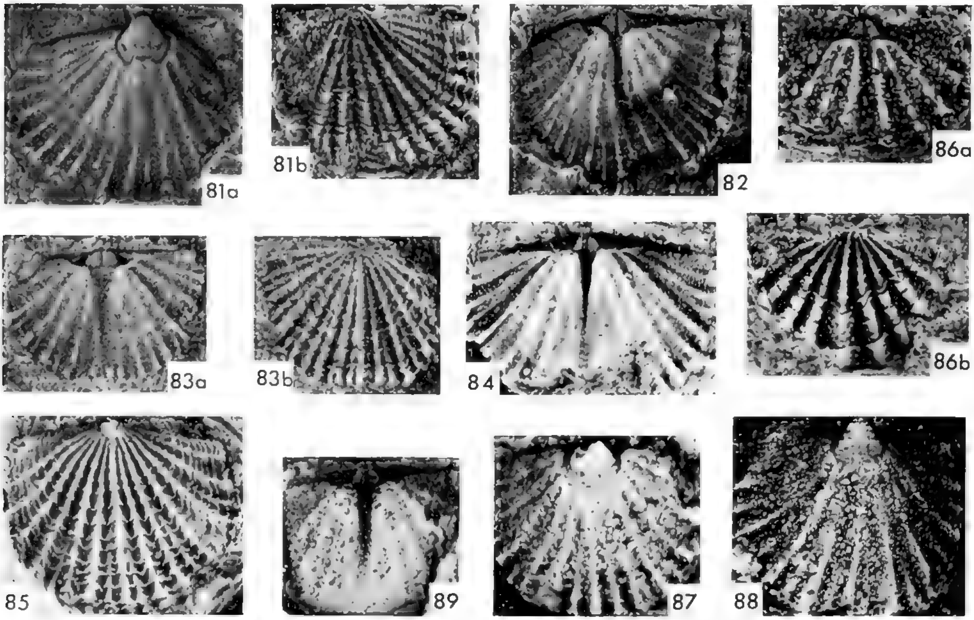
DESCRIPTION. Small biconvex *Glyptorthis* with slightly obtuse cardinal angles; pedicle valve slightly carinate, averaging 76% as long as wide and 28% as deep as long ($\bar{l}$ mm (var l) 4·26 (0·774), $\overline{th}$ (var th) 1·21 (0·009), r 0·631) in 12 specimens; brachial valve sulcate averaging 72% as long as wide ($\bar{l}$ mm (var l) 3·75 (1·349), $\bar{w}$ mm (var w) 5·21 (2·128), r 0·971 in 20 valves) and about 27% as deep as long ($\bar{l}$ mm (var l) 4·57 (0·472), $\overline{th}$ (var th) 1·23 (0·212), r 0·829 in 7 specimens); ventral interarea long, flat, apsacline, less than one-third as long as valve with narrow delthyrium bounded by subparallel to slightly divergent edges, pedicle callist usually conspicuous; dorsal interarea short anacline; radial ornamentation multicostellate with ribs branching internally in at least the first five sectors of brachial valves (e.g. $1\overline{a1}$, $1\bar{a}$, 1, $2\bar{a}$, 2, $3\bar{a}$, 3, $4\bar{a}$, 4, $5\bar{a}$, 5) and numbering 3–4 per mm at 2 mm anterior of the umbones in both valves. Concentric ornamentation consisting of strongly-developed lamellae numbering 3 per mm between 2 and 3 mm anteromedially of the umbones in both valves.

Ventral interior with small trigonal teeth supported by narrowly divergent dental plates extending forward for about 20% of valve length; ventral muscle scar with modified pentagonal to bilobed outline averaging 98% as long as wide ($\bar{l}$ mm (var l) 1·34 (0·125), $\bar{w}$ mm (var w) 1·36 (0·101), r 0·886 in 17 valves), 32% as long ($\bar{l}$ mm (var l) 4·36 (0·711), $\overline{lsc}$ (var lsc) 1·39 (0·104), r 0·884 in 17 valves) and 24% as wide as pedicle valve; median adductor scars subrectangular and about one-third as wide as muscle field, diductor scars longitudinally divergent.

Dorsal interior with simple, blade-like cardinal process and blunt divergent brachiophores defining simple sockets and with bases extending forward for 20% of length of valve and occupying 28% of valve width (i.e. 51% as long as wide: $\bar{l}$ mm (var l) 0·80 (0·080), $\bar{w}$ mm (var w) 1·57 (0·087), r 0·937 in 6 valves); the floor of notothyrial cavity with transverse muscle tracks is bounded anteriorly by poorly-defined notothyrial platform passing anteriorly into well-defined median ridge, adductor muscle scars obscure.

TYPE MATERIAL		length	width
Holotype, internal and external moulds of p.v.	BB 92315	5·0	7·0
Paratype, internal and external moulds of b.v.	BB 92316	4·9	6·4
,,	BB 92317	3·6	5·0
,,	BB 92318	4·5	6·0
Paratype, internal mould of b.v. . . .	BB 94245	4·8	6·0

HORIZON AND LOCALITY. BB 92315–8 and 94245 are from the argillaceous lower part of the Flags and Grits in the middle of the Ffairfach Group, Ffairfach railway cutting, Ffairfach, Llandeilo (SN 628211).



Figs 81–85 *Glyptorthis viriosa tumida* subsp. nov. Figs 81a, b, **holotype** BB 92315, internal and external moulds of a pedicle valve × 6; Fig. 82, paratype BB 92316, internal mould of a brachial valve × 6; Figs 83a, b, paratype BB 92317a, b, internal and external moulds of a brachial valve × 6; Fig. 84, paratype BB 92318, internal mould of a brachial valve × 6; Fig. 85, paratype BB 94245, latex cast of external mould of a pedicle valve × 6; all from the Flags and Grits, Ffairfach Group, type section.

Figs 86–88 *Glyptorthis* cf. *viriosa* Williams. Figs 86a, b, BB 92321, internal and external moulds of a brachial valve × 4; Figs 87–88, BB 92320 and 92319 respectively, internal moulds of two pedicle valves, both × 6; all from Llanvirn sandstones, Howey Brook, Llandrindod.

Fig. 89 *Glyptorthis* sp. BB 92295, internal mould of a brachial valve × 4, from Middle Llandeilo Limestone, Pontbren Araeth, Llandeilo. (See p. 33).

Discussion. The two penecontemporaneous populations described here are morphologically similar. Seven characters were tested and the only significant differences were in the relative length of the ventral muscle scar and the shape of the cardinalia ($0{\cdot}02 < p < 0{\cdot}01$ in both cases). Since both the ventral muscle scar and the dorsal cardinalia are known to have been affected by allometrical changes during growth, it is probable that these differences are related to the difference in mean size between the two populations. In the sample of smaller specimens both the ventral scar and the cardinalia are considerably wider than they are in the collection of larger shells. An examination of the ribbing in both populations reveals that they are virtually identical; in juvenile brachial valves up to 4 mm in width the primary costae and $1\bar{a}$ are the only ribs noted. Large brachial valves exhibit simple internal branching with $1\overline{a1}$ and $4\overline{a1}$ noted in the dorsal valves of both populations; $1\bar{b}$ occurs, only rarely, in Ffairfach dorsal valves.

Comparisons between the two samples described here and *G. viriosa* Williams (1974 : 64) from the Shelve Caradoc indicate the essential homogeneity of the Ordovician *Glyptorthis* from England and Wales, but there are differences. The ventral muscle scars of both Welsh forms are significantly different from that of the Shelve stock. If these differences are allometrically induced, variations in the relative depth of the brachial valves are more important. The average valve of the Ffairfach sample is not only deeper than its Shelve counterpart but it deepened at a signficantly faster rate during growth. This difference in growth also tends to set the Ffairfach sample apart from the Howey Brook *Glyptorthis*. The brachial valves of the latter appear deeper than those of the former but not significantly so, and their rate of deepening was actually much closer to that of the Shelve specimens.

These complex differences in growth and inherent shape characteristics suggest that in the Lower Ordovician the Anglo-Welsh *Glyptorthis* was subject to an unusually high rate of speciation. The evidence is admittedly based on small samples and needs further investigation. For the time being, however, it seems reasonable to erect a new subspecies based on the Ffairfach sample and to compare the Howey Brook specimens with *G. viriosa* s.s.

Recent studies of the Llandeilo Series in the type area have revealed the sporadic occurrence of *Glyptorthis* (sp. indet.) at horizons in the *Lloydolithus lloydi* Flags, the *Marrolithus maturus* Beds and the *Marrolithoides anomalis* Limestones of the Middle Llandeilo. A brachial valve (BB 92295) from the *M. anomalis* Limestones exposed in the old quarry beside the road in Pontbren Araeth Dingle SN 659237) is figured here (Fig. 89).

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

Subfamily **PLECTORTHINAE** Schuchert & Le Vene, 1929

Genus ***CORINEORTHIS*** Stubblefield, 1939

Corineorthis pustula Williams, emended
(Figs 90–101)

1851 *Orthis turgida* M'Coy *pars* : 399–400.
1852 *Orthis turgida* M'Coy; Sedgwick & M'Coy *pars* : 299; pl. 1H, figs 20, 22, 24, *non* figs 21, 23.
1949 *Corineorthis pustula* Williams : 230.
1961 *Corineorthis biconvexa* MacGregor : 180; pl. 19, figs 1–6.

Diagnosis. Dorsibiconvex, subcircular *Corineorthis* with brachial valve over one-quarter as deep as long and pedicle valve becoming slightly resupinate in late growth stages, multicostellate with hollow ribs numbering about 4 per mm; bilobed ventral muscle scar averaging 46% as long as valve and over three-fifths as wide as long.

Description. Dorsibiconvex, large *Corineorthis* with obtuse cardinal angles; pedicle valve with typically orthoid to subpentagonal outline and maximum depth posteromedially where a slight fold is developed, anterior part of valve flat with incipient resupination occurring sporadically in a few large valves, averaging 91% as long as wide ($\bar{l}$ mm (var 1) 14·75 (6·351),

$\bar{w}$ mm (var w) 16·20 (9·682), r 0·745 in 22 valves) and 21% as deep as long ($\bar{l}$ mm (var l) 15·07 (7·869), $\overline{th}$ (var th) 2·93 (0·746), r 0·801 in 7 valves); brachial valve sulcate, strongly convex with steep lateral and anterior slopes, averaging 82% as long as wide ($\bar{l}$ mm (var l) 13·61 (11·927), $\bar{w}$ mm (var w) 16·66 (18·231), r 0·896 in 35 valves) and 28% as deep as long ($\bar{l}$ mm (var l) 13·92 (10·091), $\overline{th}$ (var th) 3·84 (0·883), r 0·864 in 19 valves); ventral interarea curved apsacline with narrow open delthyrium subtending an acute angle of between 30° and 40°, dorsal interarea curved anacline with narrow open notothyrium; external ornament multicostellate with ribs numbering 2, 3 and 4 per mm at 5 mm anteromedially of the umbo in respectively 1, 5 and 1 dorsal valves, commonly between 7 and 9 primary ribs with dominantly internal branching in sectors I–III and both internal and external branching in sectors IV–VII; crests of costellae perforated by regularly-spaced exopunctae numbering 3 per mm at 5 mm anteromedially of the umbones of 3 ventral valves, finely developed concentric ridges between costellae number 7, 8, 9 and 10 per mm at the same growth stages in 2, 2, 1 and 1 pedicle valves.

Teeth short, stout, triangular with well-developed crural fossettes, supported by variably-developed dental plates averaging 20% as long as valve in 13 specimens (range 13 to 31%) and averaging 80% as long as wide in 15 specimens (range 56 to 123%); ventral muscle scar bilobed, consisting of a pair of diductor impressions averaging 46% as long as valve ($\bar{l}$ mm (var l) 14·53 (6·734), $\overline{lsc}$ (var lsc) 6·71 (1·346), r 0·875 in 17 valves) and 62% as wide as long ($\bar{l}$ mm (var l) 6·97 (1·644), $\bar{w}$ mm (var w) 4·36 (0·638), r 0·708 in 20 valves), and separated medially by a pair of elongated adductor impressions consisting of two closely adjacent parallel ridges arising along the median line at about one-quarter of the valve length from the umbo and extending to the anterior edge of the scar complex, where they pass into a single thicker ridge representing the *vascula media* which bifurcate just forward of the muscle field to enclose the posterior part of a subtriangular anteromedian depression; the posterolateral sectors of most pedicle valves are characterized by coarse pustules which are slightly elongated along radial lines.

Cardinal process simple, bladelike and variable in length averaging 22% as long as valve in 13 specimens (range 14 to 33%), nototyrial platform passing forward, beyond the anterior end of the brachiophore bases, into a median septum which extends towards the commissure for about half of valve length before subsiding rapidly to the valve floor (averaging 49% as long as valve in 6 specimens ($\bar{l}$ mm (var l) 13·05 (22·495), $\overline{ls}$ (var ls) 6·33 (3·567), r 0·971); brachiophores stout, up to about 20% as long as valve with variably developed platelike bases averaging 17% as long as valve ($\bar{l}$ mm (var l) 12·58 (13·546), $\overline{lc}$ (var lc) 2·15 (0·431), r 0·727 in 16 valves) and almost three-quarters as long as wide (average 72% for 17 valves; range 48 to 114%); simple deep sockets bounded anterodorsally by sporadically developed fulcral plates; quadripartite adductor scars only faintly impressed and sporadically developed, between two-thirds and half as long as valve in smaller and larger valves respectively and about three-quarters as long as wide with posterior pair of scars separated from anterior pair by transverse ridges; faint, anastamosing radial, pustular markings ornament the posterolateral sectors of a few of the larger valves.

FIGURED MATERIAL		length	width
Internal mould of b.v.	GSM 75266	18	22
,,	BB 94222	(10)	10
,,	BB 94075	4·8	5·0
,,	GSM TCC.360	15	16
Latex cast of b.v. internal mould	GSM 75262	18	22
Latex cast of b.v. external mould	GSM 75263a	17	19
,,	BB 94225	13	14
Internal mould of p.v.	BB 94077	16	17
,,	BB 94076	12	12·5
,,	BB 94218	12	14
,,	BB 94219	(12)	(14)
Latex cast of p.v. internal mould	GSM TCC.357	18	20

HORIZONS AND LOCALITIES. Lectotype SM A.16679 and syntypes SM A.44972–5 from Lower Llandeilo Beds near Llandeilo, exact horizon and locality unknown; SM A.34078–81, GSM 75262–6, BB 94075–7 and BB 94216–25 from late Lower Llandeilo, *Corineorthis* Flags, exposed 70 m SW of St Tyfei's Church, Dynevor Park, Llandeilo (SN 623222); GSM TCC.357 and 360 from late Lower Llandeilo calcareous flags exposed in bank 320 m NE of Cwrt-y-Gorphwys cottage, 1 km SW of Ffairfach (SN 620207).

DISCUSSION. The species *C. pustula* Williams was founded on the basis of 'syntypes' from the St Tyfei's Church locality in Dynevor Park. It is therefore unfortunate that the lectotype (SM A.16679) selected by Cocks (1978 : 53), although the basis for one of Sedgwick & M'Coy's original figures (1852 : pl. H, fig. 20), originates from an unknown locality. In the Llandeilo region the species is at present known from late Lower Llandeilo strata exposed at Pontbren Araeth (Wilcox 1979 : 46) and from the Cwrt-y-Gorphwys and Dynevor Park localities noted above. Since the latter best-known locality, which is the nearest to Llandeilo, yields material entirely similar to the lectotype in its calcareous, partially orange-weathered matrix, it is possible that the lectotype originates from this locality.

A sufficient number of external moulds were available to emend the ribbing data presented by Williams (1949 : 231). Ribs 1a̅1̅, 1a̅, 1b̅, 1, 2a̅1̅, 2a̅, 2b̅, 2, 3a̅1̅, 3a̅, 3b̅, 3, 3å, 4a̅, 4a1̊, 4, 4å, 5a̅, 5a̅1̊, 5, 5b̊, 5å, 5å1̊, 6, 6å, 7a̅ and 7 occurred in 3 out of 4 brachial valves between 10 and 14 mm in length, whilst 2å, 3b̊, 3å1̊, 4b̊, 4å1̊, 6a̅, 6b̊, 6å1̊ and 7å also occurred in 2 of these 4 valves.

M'Coy (1851 : 399–400) originally included various representatives of the genera *Salopia* and *Corineorthis* in his species *Orthis turgida* and Williams (1949) and MacGregor (1961) have attempted to distinguish between representatives of these genera occurring in the Ordovician rocks of north and south Wales. In so doing MacGregor (1961 : 180) erected a new species from a locality in the Berwyn Hills 5 km SW of Llanarmon. He discussed the differences between *C. pustula* and his *C. biconvexa,* concluding that the former species had a less convex pedicle valve and more massive brachiophores. The emended description of *C. pustula,* however, indicates that the Dyfed specimens can be moderately convex ventrally and possess variably developed brachiophores. We, therefore, consider *C. biconvexa* to be a junior synonym of *C. pustula.*

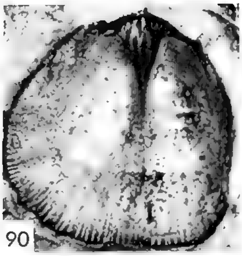
With respect to the remaining specimens originally described as *O. turgida* by M'Coy, the lectotype (SM A.11100) selected by Williams is a *Salopia* (see p. 53) whilst the material from near 'Conway Falls', Gwynedd, tentatively assigned by Williams (1949 : 233–234) to *Corineorthis globosa* has since been referred to *Salopia globosa* by MacGregor (1961 : 182), Diggens & Romano (1968 : 46) and Cocks (1978 : 82).

***Corineorthis* cf. *pustula* Williams**

(Figs 102–103)

DESCRIPTION. *Corineorthis* with convex brachial valve two-thirds to three-quarters as long as wide and about one-seventh as deep as long; interarea anacline; multicostellate ornament consisting of 1a̅, 1b̅, 1, 2a̅1̅, 2a̅, 2a̅1̊, 2b̊, 2, 2å, 3a̅, 3b̅, 3, 4̅a̅1̅, 4a̅, 4b̅, 4, 4å, 5a̅, 5, 5b̊, 5å, 6a̅, 6, 6b̊, 6å1̅, 6å, 7a̅, 7b̅, 7, etc., in the only known external mould; cardinal process simple, dividing notothyrial cavity and extending forward via notothyrial platform towards the median septum; brachiophores stout, up to one-quarter as long as valve and slightly more divergent than long, with bases converging anterodorsally to unite with notothyrial platform; sockets bounded anteriorly by fulcral plates; quadripartite adductor scar enclosed posterolaterally by radiating ridges; anterior pair of adductor scars triangular, separated from posterior pair by transverse ridges.

FIGURED MATERIAL		length	width
Internal mould of b.v.	SM A.104415	12	15
Internal and external moulds of b.v. . . .	SM A.104416	(7·8)	(11·5)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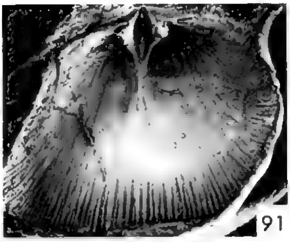
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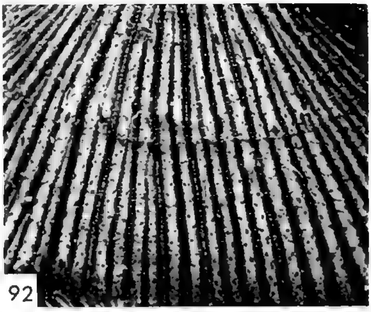
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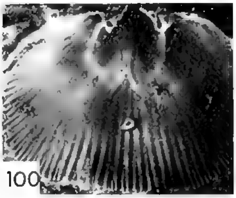
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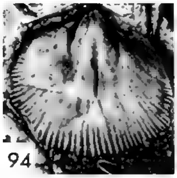
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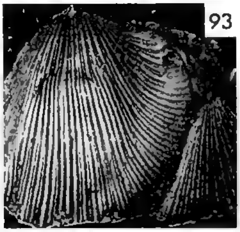
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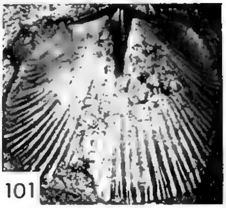
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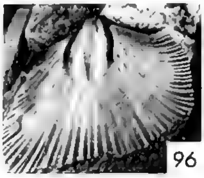
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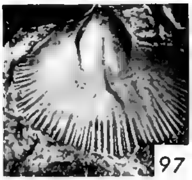
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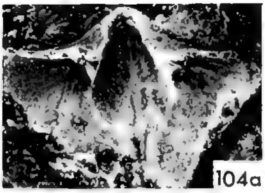
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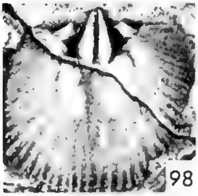
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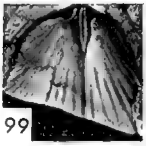
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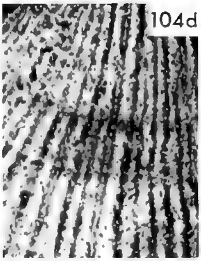
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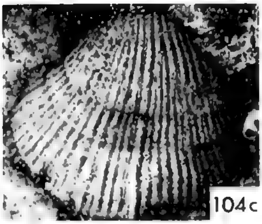
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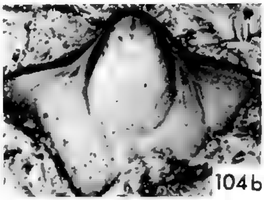
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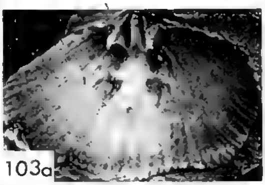

103a


103b

Figs 90–101 *Corineorthis pustula* Williams. Fig. 90, GSM 75266, internal mould of a brachial valve showing muscle scars × 2; Fig. 91, GSM 75262, latex cast of internal mould of a brachial valve × 2; Figs 92–93, BB 94225 and GSM 75263a respectively, latex casts of external moulds of brachial valves × 6 and × 3; Figs 94–97, BB 94076, 94077, 94219 and 94218 respectively, internal moulds of pedicle valves, all × 2; Figs 98–99, BB 94075 and 94222, internal moulds of brachial valves × 6 and × 2; all from Lower Llandeilo beds, St Tyfei's, Dynevor Park, Llandeilo. Fig. 100, GSM TCC.357, latex cast of internal mould of pedicle valve × 1·5; Fig. 101, GSM TCC. 360, internal mould of brachial valve × 2; both from Lower Llandeilo beds, Cwrt y Gorphwys, Llandeilo.

Horizon and locality. Both specimens from *Glyptograptus teretiusculus* to *Nemagraptus gracilis* shales exposed in the River Wye section (SW bank) at Penddol, 1·5 km north of Builth Wells (SO 031522).

Discussion. This is the first record of *Corineorthis* occurring in the Builth area.

Corineorthis sp.
(Figs 104a–d)

Internal and external moulds of two *Corineorthis* pedicle valves (BB 92296–7) from the lower, argillaceous part of the Flags and Grits Formation of the Ffairfach Group exposed in the type section (SN 628211) resemble *C. pustula* in style and distribution of costellae (3 to 4 per mm at the 5 mm growth stage) and exopunctae (about 3 per mm at 5 mm), and in the development of their ventral muscle scars, pedicle callist and *vascula media.* They differ from *C. pustula*, however, in being considerably more convex, with strongly-developed concentric growth lines at intervals of 1 to 2 mm. They also lack internal pustules although this is not necessarily a diagnostic feature.

The difference in profile of the pedicle valves from Ffairfach and those attributable to *C. pustula* s.s. may be because of the small size of the Ffairfach specimens, which are associated with an assemblage of relatively small individuals of other brachiopod species. In any event the Ffairfach specimens represent the earliest record of the genus yet reported.

Subfamily **ORTHOSTROPHIINAE** Schuchert & Cooper, 1931

Genus ***GELIDORTHIS*** Havlíček, 1968

Gelidorthis cennenensis sp. nov.
(Figs 105–111)

Diagnosis. Small, mucronate, ventribiconvex *Gelidorthis* with coarse radial costellae and strongly sulcate dorsal valve.

Name. From Cennen Brook, Dyfed, which flows through Ffairfach.

Description. Small, transversely subquadrate, ventribiconvex mucronate *Gelidorthis* with strongly acute cardinal angles becoming rounded and obtuse in large adults; pedicle valve carinate, averaging 75% as long as wide in 31 specimens and 25% as deep as long ($\bar{l}$ mm (var l) 3·62 (1·627), $\overline{th}$ (var th) 0·91 (0·086), r 0·671 in 13 valves), ventral interarea apsacline; brachial valve strongly sulcate averaging 66% as long as wide ($\bar{l}$ mm (var l) 2·24 (0·816), $\bar{w}$ mm (var w) 3·38 (1·386), r 0·934 in 41 valves) and 21% as deep as long ($\bar{l}$ mm (var l) 3·19 (0·796), $\overline{th}$ (var th) 0·67 (0·073), r 0·898 in 13 valves); dorsal interarea flat anacline with an open notothyrium defined by divergent boundaries; radial ornamentation consisting of relatively angular costellae numbering between 4 and 5 per mm at 2 mm anterior of the umbo in 6 brachial valves, branching dominantly internal in brachial valves (e.g. 1ā1, 1ā, 1, 2ā1, 2ā, 2, 2å, 3ā, 3, 3å, 4ā, 4, 5ā, 5 etc.); concentric growth lamellae sporadically developed towards anterior commissure with fine, regularly developed growth fila, numbering at least 20 per mm, observed in larger valves.

Ventral interior with short divergent dental plates extending forward for an average of 17% of valve length ($\bar{l}$ mm (var l) 2·81 (1·033), $\overline{dl}$ (var dl) 0·48 (0·049), r 0·869 in 14 valves) and a

Figs 102–103 *Corineorthis* cf. *pustula* Williams. Fig. 102, SM A.104415, internal mould of a brachial valve × 2; Figs 103a, b, SM A.104416a, b, latex casts of internal and external moulds of a brachial valve, both × 3; all from Llandeilo shales, Penddol, Builth.

Figs 104a–d *Corineorthis* sp. BB 92297. a, latex cast × 4 of b, internal mould of pedicle valve × 4, c, latex cast of external mould × 4 and d, detail of same × 6, from Flags and Grits, Ffairfach Group, type section.

length to maximum lateral extension (w) ratio of 52% ($\overline{dl}$ mm (var dl) 0·48 (0·049), $\overline{w}$ mm (var w) 0·92 (0·050), r 0·819 in 14 valves), muscle field indistinct and obscured by internal ribbing.

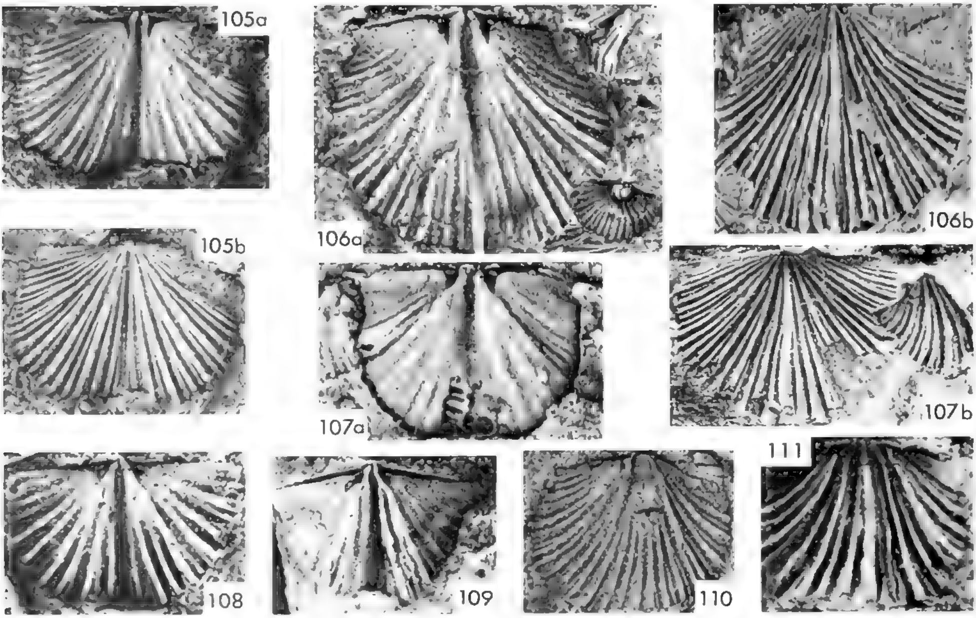
Dorsal interior with simple short brachiophores with bases extending forward for an average of 14% of valve length and averaging 47% as long as wide (l mm (var l) 0·35 (0·025), w mm (var w) 0·74 (0·030), r 0·281 in 18 valves); sockets simple, frequently poorly developed; notothyrial cavity divided by a simple ridge-like cardinal process which extends forward to commissure as a high angular median septum.

TYPE MATERIAL

		length	width
Holotype, internal and external moulds of b.v.	BB 92326	4·2	5·8
Paratype, internal mould of p.v.	BB 92323	6·0	8·0
,, internal and external moulds of b.v.	BB 92324	4·3	5·8
,, ,,	BB 92327	2·8	4·5
,, ,,	BB 92328	6·0	6·8
,, ,,	BB 92329	2·9	4·4
,, internal and external moulds of p.v.	BB 92325	3·5	4·5
,, ,,	BB 92330	2·0	2·6

HORIZON AND LOCALITY. All specimens from the argillaceous lower part of the Flags and Grits in the middle of the Ffairfach Group, railway cutting, Ffairfach, Llandeilo (SN 628211).

DISCUSSION. *Gelidorthis* has recently been recognized in the Ordovician of Britain by Williams (1974 : 74), who identified Upper Llandeilo specimens from Shropshire as *G.* cf.



Figs 105–111 *Gelidorthis cennenensis* sp. nov. Figs 105a, b. **holotype** BB 92326a, b, internal mould and latex cast of external mould of a brachial valve × 6; Figs 106a, b, 107a, b, paratypes BB 92328a, b and 92324a, b respectively, internal and external moulds of brachial valves, all × 6; Figs 108–109, paratypes BB 92329 and 92327 respectively, internal moulds of brachial valves, both × 6; Figs 110–111, paratypes BB 92323 and 92325 respectively, internal moulds of pedicle valves × 4 and × 6; all from the Flags and Grits, Ffairfach Group, type section.

partita (Barrande). The Shropshire stock is similar in size outline and ventral morphology to the present species but the former lacks 'a definite sulcus...' (*op. cit.* : 74) and is immediately distinguishable from the Ffairfach shells. Since the new species is represented by a large sample, it has been possible to present a more thoroughly quantitative description of it than is available for *G. partita* and indeed for the four Caradocian species from Bohemia (Havlíček 1977 : 79–84), all of which are considerably larger, and in many respects unlike the Ffairfach form.

Subfamily **PLATYSTROPHIINAE** Schuchert & Le Vene, 1929

Genus ***MCEWANELLA*** Foerste, 1920

Mcewanella berwynensis MacGregor
(Figs 112–122)

1961 *Mcewanella berwynensis* MacGregor : 183; pl. 19, figs 9–15.

Description. Biconvex, plicate *Mcewanella* with 4 pedicle valves averaging 86% as long as wide (range 75–95%) and about one-quarter as deep as long and 6 brachial valves averaging 78% as wide as long (range 67–94% : $\bar{l}$ mm (var l) 8·28 (3·56), $\bar{w}$ mm (var w) 10·67 (4·67), r 0·886) and about one-quarter as deep as long; ventral interarea flat apsacline, delthyrium open; dorsal interarea orthocline to slightly anacline, notothyrium open; exterior ornamented by angular costae numbering 8 and 10 in 1 and 4 brachial valves, with fine radial costellae on and between costae; dorsal fold, bearing two median costae, developed in larger valves.

Ventral interior with short, stout dental lamellae supporting simple teeth; muscle field simple diamond-shaped, over one-third as long as valve and about as wide as long.

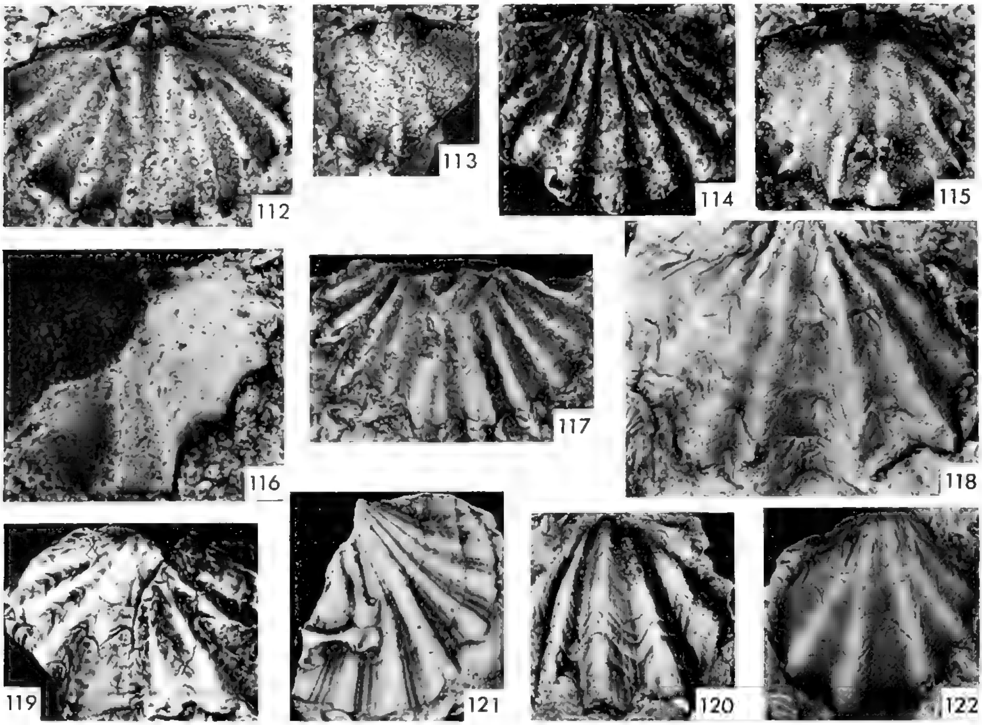
Dorsal interior with simple blade-like cardinal process extending forward for about one-fifth of valve length and becoming thickened towards the anterior edge of the notothyrial platform, whence the median septum extends towards the commissure, subsiding to valve floor in anterior half of valve; brachiophores short, thick with bases extending forward for an average of 21% of length of 4 valves and an average of 50% of their maximum lateral extension in four specimens; sockets simple with obscure fulcral plates.

Figured material		length	width
Internal mould of b.v.	BB 92331	(10)	12
,, ...	BB 94069	8·2	11
,, ...	BB 94070	7·5	(8)
Exterior of p.v.	BB 94068	5·8	7
Internal part of exfoliated p.v.	BB 94067	8·2	11
Internal mould of p.v.	BB 94072	5·5	5·8

Horizon and locality. BB 92331 and BB 94066–72 from tuffaceous sandstones exposed at the top of the small hill just north of Howey Brook, 4 km east of Howey (SO 0925 5915).

Discussion. The six brachial, four pedicle and two fragmentary *Mcewanella* valves recovered from the *Didymograptus murchisoni* sandstones of Howey Brook resemble *M. berwynensis* MacGregor (1961 : 183) in all morphological features. They constitute a larger and better-preserved sample than those from the type locality and provide some information on the variability of the species. The Builth material also represents the earliest known record of the genus anywhere.

The internal and external parts of an exfoliated *Mcewanella* pedicle valve (BB 92279a, b), the external mould of a brachial valve (BB 94073) and exfoliated exteriors of two brachial valves (BB 92280 and BB 94074a, b) from the Lower Llandeilo *Sowerbyella* Beds exposed beside the old track in the Deer Park (SN 609223) also resemble *M. berwynensis* in all observed features (Figs 118–120). Moreover Addison (1974 : 42) reported *Mcewanella* from the Upper Llandeilo Bryn Glas Limestones exposed at Llan Mill, west of Lampeter Velfrey. A specimen (GSM 11965) from this locality (Fig. 121) substantiates this record while GSM specimens Pr. 652–3, the internal and external parts of an exfoliated *Mcewanella* brachial valve (Fig. 122), have been collected from 'Llandeilo' beds exposed at Clog-y-fran Farm, west of St Clears, Dyfed (SN 161238 approx.). These identifications testify to the widespread, though rare, occurrence of *Mcewanella* in the Lower to Middle Ordovician rocks of Wales.



Figs 112–122 *Mcewanella berwynensis* MacGregor. Fig. 112, BB 94069, internal mould of a brachial valve × 4; Fig. 113, BB 94072, internal mould of a pedicle valve × 4; Fig. 114, BB 94068, latex cast of the external mould of a pedicle valve × 5; Figs 115–116, BB 94070 and 92331 respectively, internal moulds of brachial valves both × 4; Fig. 117, BB 94067, partially exfoliated pedicle valve × 4; all from Llanvirn sandstones, Howey Brook, Llandrindod. Figs 118–119, BB 92279 and 94074 respectively, partially exfoliated brachial valves × 4 and × 2; Fig. 120, BB 94073, latex cast of external mould of a pedicle valve × 2·5; all from Lower Llandeilo Limestones, Dynevor Park, Llandeilo. Fig. 121, GSM 11965, latex cast of external mould of a brachial valve × 3, from Llandeilo Beds, Llan Mill, Lampeter Velfrey, Dyfed. Fig. 122, GSM Pr.652–3, partially exfoliated brachial valve × 2, from Llandeilo Beds, Clog y fran, St Clears, Dyfed.

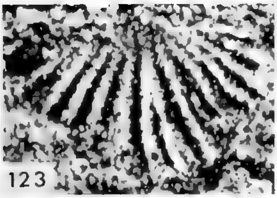
Family **SKENIDIIDAE** Kozlowski, 1929

Genus ***SKENIDIOIDES*** Schuchert & Cooper, 1931

Skenidioides sp.

(Fig. 123)

Two small external moulds of transverse dorsal valves (BB 92332 and a smaller incomplete specimen) from the upper part of the Flags and Grits in the Ffairfach Group, Ffairfach, Llandeilo (SN 628211) are provisionally assigned to *Skenidioides*. The valves are planar to slightly convex and between half to two-thirds as long as wide with acute cardinal angles;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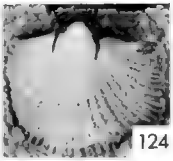
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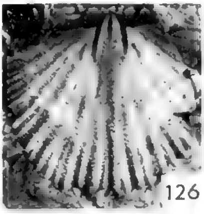
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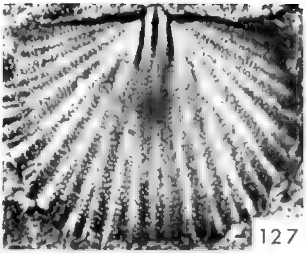
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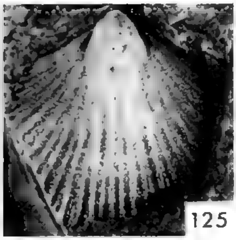
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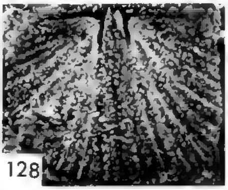
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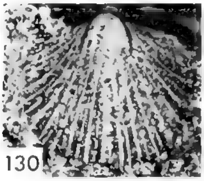
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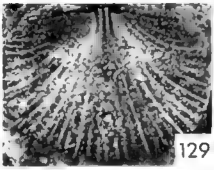

129

Fig. 123 *Skenidioides* sp. BB 92332, external mould of a brachial valve × 12, from the Flags and Grits, Ffairfach Group, type section.

Figs 124–130 *Dalmanella parva* Williams. Figs 124–125, BB 92336 and 92333 respectively, internal moulds of pedicle valves × 6 and × 8; Figs 126–127, BB 92334 and 92335 respectively, internal moulds of brachial valves × 6 and × 12; all from the Flags and Grits, Ffairfach Group, type section. Figs 128–129, BB 92337 and 92339 respectively, internal moulds of brachial valves both × 6; Fig. 130, BB 92340, internal mould of a pedicle valve × 6; all from Llanvirn sandstones, Howey Brook, Llandrindod.

ornamentation consists of at least 10 dorsal costae with occasional costellae branching internally in the first two sectors; pedicle valve and internal features unknown.

Superfamily **ENTELETACEA** Waagen, 1884

Family **DALMANELLIDAE** Schuchert, 1913

Genus ***DALMANELLA*** Hall & Clarke, 1892

Dalmanella parva Williams
(Figs 124–130)

1949 *Dalmanella parva* Williams : 169; pl. 8, figs 11–14.
1974 *Dalmanella parva* Williams; Williams : 89; pl. 15, figs 1–4, 7.

DESCRIPTION. Small, ventribiconvex *Dalmanella* with obtuse cardinal angles; pedicle valve carinate, 80 to 85% as wide as long and 29 to 27% as deep as long (e.g. 45 valves from Ffairfach : $\bar{l}$ mm (var l) 2·69 (0·862), $\bar{th}$ (var th) 0·77 (0·084), r 0·912); brachial valve sulcate, 75 to 77% as wide as long (e.g. 111 valves from Ffairfach : $\bar{l}$ mm (var l) 2·43 (0·362), $\bar{w}$ mm (var w) 3·22 (0·472), r 0·932) and 20 to 21% as deep as long (e.g. 27 valves from Ffairfach : $\bar{l}$ mm (var l) 2·79 (0·184), $\bar{th}$ (var th) 0·59 (0·011), r 0·649); ventral interarea curved apsacline longer than anacline dorsal interarea, delthyrium and notothyrium open, pedicle callist usually conspicuous; radial ornamentation costellate with 5 or 6 ribs per mm, 2 mm anteromedially of the dorsal umbones of 20 specimens; branching simple and almost invariably internal in the brachial valve, e.g. 1, 2ā, 2, 3ā, 3, 4ā, 4, 5ā, 5, 6ā and 6 were always present in 30 brachial valves but with 4å, 5å and 6å present on the surfaces of 10, 8 and 1 valves.

Ventral interior with small teeth supported by dental plates extending anteriorly for 23 to 27% of pedicle valve length (e.g. 20 valves from Howey Brook : $\bar{l}$ mm (var l) 3·53 (0·642), $\bar{dl}$

(var dl) 0·97 (0·124), r 0·859) and diverging at 71 to 96% of their length (e.g. 21 valves from Howey Brook: $\bar{l}$ mm (var l) 1·02 (0·047), $\bar{w}$ mm (var w) 0·98 (0·126), r 0·817); ventral muscle field bilobed, variably developed with diductor scars extending anteriorly for 33% the length of 6 valves.

Dorsal interior with cardinal process consisting of linear shaft and small rounded myophore; brachiophores short divergent, with long subparallel bases extending anteriorly for 24 to 28% of valve length (e.g. 65 valves from Ffairfach: $\bar{l}$ mm (var l) 2·52 (0·288), $\overline{lc}$ (var lc) 0·70 (0·034), r 0·781) and separated from each other by 65 to 69% of their length (e.g. 64 valves from Ffairfach: $\bar{l}$ mm (var l) 0·70 (0·05), $\bar{w}$ mm (var w) 0·48 (0·009), r 0·525); adductor scars poorly differentiated extending for just over half of valve length and about 60% as wide as long.

FIGURED MATERIAL		length	width
Internal and external mould of p.v.	BB 92333	4·2	4·2
,, . . .	BB 92336	3·5	4·0
Internal and external mould of b.v.	BB 92334	3·4	4·0
,, . . .	BB 92335	3·0	4·0
,,	BB 92337	4·0	5·4
,,	BB 92339	4·0	5·2
Internal mould of p.v.	BB 92340	3·9	4·3

HORIZON AND LOCALITIES. BB 92333–6 from the argillaceous lower part of the Flags and Grits in the Ffairfach Group, Ffairfach railway cutting, Ffairfach, Llandeilo (SN 628211); BB 92337–41 from the Sandy Ashes at the top of the Main Volcanic Series in the Howey Brook ('Main Feeder') section, 4 km east of Howey, outcrop on top of small hill north of brook (SO 0925 5915).

DISCUSSION. Comparisons of the material from Ffairfach and Howey indicate a close morphological similarity between the two samples with no significant difference observed for eight characters tested except for the greater relative length of the brachiophore bases in the Howey brachial valves ($0{\cdot}02 < p < 0{\cdot}01$). In the sample of smaller-sized valves from Ffairfach the greater mean relative length of the brachiophore bases apparently corresponds to the relative difference in size between the two populations. Since allometric effects are observed in all relevant growth vectors the differences are probably explained by a slowing down in the forward growth of the bases in late stages of development. Comparisons of dorsal ribbing patterns in the two samples, which reveal that external secondary costellae arise only in sectors IV, V and VI, further substantiate our view that both samples should be included in the same species.

The species *D. parva* was first described by Williams in 1949 and later amended by him (1974: 89–90) on the basis of a sample of topotypes from the Pantau quarry (SN 644224). The Ffairfach specimens are identical with those from Pantau in 5 of the 6 morphological characters tested. They differ significantly ($0{\cdot}001 < p$) only in the divergence of the dental lamellae, a character already shown to be particularly variable and controlled by allometry. The age of the strata in the Pantau quarry has recently been reconsidered by Wilcox (1979) who concludes, on newly-obtained faunal evidence, that these beds may be late Upper Llanvirn (Ffairfach Group) rather than Lower Llandeilo in age.

Family **HARKNESSELLIDAE** Bancroft, 1928

Genus ***HORDERLEYELLA*** Bancroft, 1928

Horderleyella convexa Williams, emended

(Figs 131–138)

1949 *Horderleyella convexa* Williams: 171; pl. 8, figs 15–17.
1949 *Horderleyella lata* Williams: 172; pl. 8, figs 18, 19.

DIAGNOSIS. Ventribiconvex *Horderleyella* with obtuse cardinal angles, a normally carinate pedicle valve 87% as long as wide and a strongly sulcate brachial valve, fascicostellae numbering 3 per mm at the 5 mm growth stage.

DESCRIPTION. Medium-sized, ventribiconvex *Horderleyella* with slightly obtuse cardinal angles, slightly to strongly carinate pedicle valve and strongly sulcate brachial valve; pedicle valve subhexagonal to transversely rectangular in outline averaging 87% as long as wide (in 30 valves) and 28% as deep as long ($\bar{l}$ mm (var l) 10·54 (9·383), $\overline{th}$ (var th) 2·99 (0·700), r 0·903 in 27 valves); ventral interarea long, slightly curved, apascline with open delthyrium and subtending an angle about 40°, pedicle callist usually conspicuous; brachial valve transversely rectangular in outline averaging 76% as long as wide ($\bar{l}$ mm (var l) 8·54 (8·625), $\bar{w}$ mm (var w) 11·18 (10·879), r 0·927 in 41 valves) and 24% as deep as long ($\bar{l}$ mm (var l) 8·97 (8·439), $\overline{th}$ (var th) 2·11 (0·421), r 0·852 in 32 valves), with short flat anacline interarea and open notothyrium subtending an angle of about 60°; external ornament fascicostellate with costellae numbering 3 per mm, 5 mm anteromedially of the umbones of 8 brachial valves; ribbing arrangement typically with $1\bar{a}$, $1\bar{b}$, 1, $2\overline{a1}$, $2\bar{a}$, $2\bar{b}$, 2, $2\mathring{a}$, $3\overline{a1}$, $3\bar{a}$, 3, $3\mathring{b}$, $3\mathring{a}$, $3\mathring{a}\mathring{1}$, $4\overline{a1}$, $4\bar{a}$, $4\bar{b}$, 4, $4\mathring{b}$, $4\mathring{a}$, $4\mathring{a}\mathring{1}$, $5\bar{a}$, 5, $5\mathring{a}$, $6\bar{a}$, 6, $6\mathring{a}$, $7\bar{a}$, 7, $7\mathring{a}$ and with sectors III and IV exhibiting a more compound, less differentiated parvicostellate type of pattern; inconspicuous irregularly-spaced growth lines are developed towards the commissure.

Ventral interior with deep delthyrium bounded by dental plates which support short teeth and extend anteriorly for an average of 24% of valve length ($\bar{l}$ mm (var l) 12·04 (10·075), $\overline{dl}$ (var dl) 2·86 (0·849), r 0·717 in 27 valves) enclosing the posterior part of the muscle field which is 79% as wide as long ($\bar{l}$ mm (var l) 4·57 (1·496), $\bar{w}$ mm (var w) 3·59 (0·433), r 0·829 in 19 valves) and extends anteriorly for an average of 38% of valve length ($\bar{l}$ mm (var l) 11·94 (8·830), $\overline{lsc}$ (var lsc) 4·54 (1·496), r 0·875 in 19 valves); muscle field subcordate, consisting of narrow, elongate, centrally disposed median adductor scars flanking median groove and, laterally to them, wider, elongately triangular to lobate diductor scars.

Dorsal interior with deep notothyrial cavity divided by a simple blade-like cardinal process attaining maximum height posteriorly and passing anteriorly into the notothyrial platform, from which a broad median septum extends almost to the commissure where it widens and subsides to valve floor; cavity bounded laterally by medially-facing ridges ('dorsal brachiophore ridges') which extend anteriorly beyond brachiophore bases to form dorsal component of brachiophores; ventral components of brachiophores shorter, arising directly from slightly acute 'ventral brachiophore ridges' corresponding to the boundary between notothyrium and interarea; brachiophore bases 73% as long as wide ($\bar{l}$ mm (var l) 2·22 (0·401), $\bar{w}$ mm (var w) 3·03 (6·676), r 0·897 in 31 valves), 26% as long as valve and 70% to 80% as long as brachiophores, sockets angular, diverging and widening anterolaterally and supported by fulcral plates overlying well-developed crural pits; adductor muscle scars about 62% as long as valve and 89% as wide as long, poorly defined anteriorly but deeply impressed posteriorly where adductor pits underlie brachiophores.

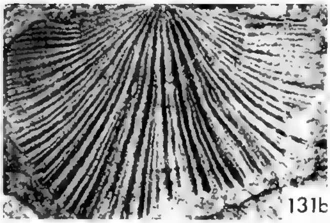
FIGURED MATERIAL

		length	width
Internal and external moulds of p.v.	BB 92342	13·0	16·0
Internal mould of p.v.	BB 92343	13·0	14·0
External mould of p.v.	GSM 75247	7·0	8·5
Internal and external moulds of b.v.	BB 92344	12·0	15·5
,, . . .	BB 92345	8·0	11·0
,, . . .	BB 92346	8·0	12·0
Internal mould of b.v.	SM A.33345	8·0	10·0
External mould of b.v.	GSM 75246	6·0	9·0

HORIZONS AND LOCALITIES. BB 92342–7 from arenaceous middle beds of the Flags and Grits in the middle of the Ffairfach Group, Ffairfach railway cutting, Ffairfach, Llandeilo (SN 628211); GSM 75240–4 from Upper Llanvirn Grits, quarry 210 m north of the Lodge, 2 km SSW of Llangadog (SN 693259); GSM 75245–7 and SM A.33345–6 from Upper Llanvirn ashes exposed 200 m NW of Bryntowy Farm 3 km SSW of Llangadog (SN 695262).

DISCUSSION. See below, p. 45.


131a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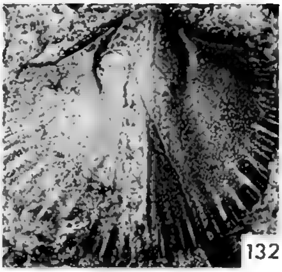
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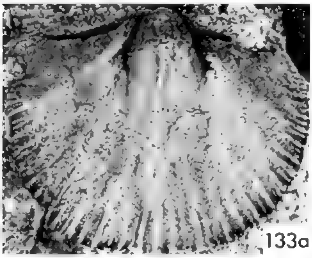
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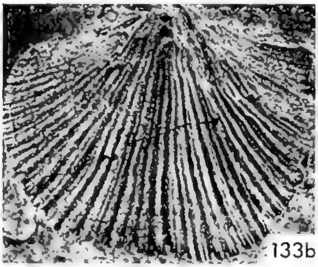
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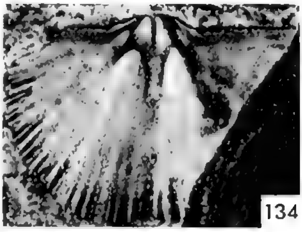
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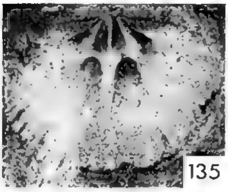
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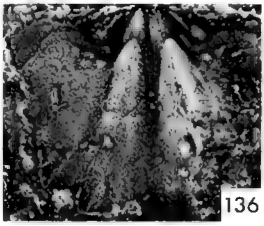
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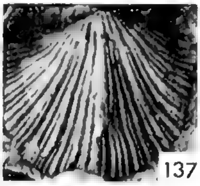
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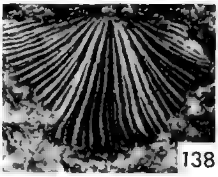
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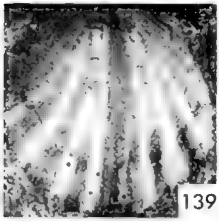
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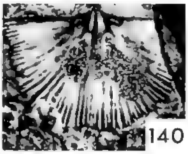
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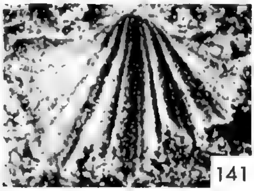
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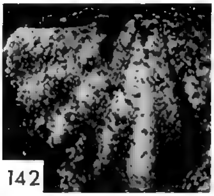
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Figs 131–138 *Horderleyella convexa* Williams. Figs 131a, b, BB 92344a, b, internal and external moulds of a brachial valve, both × 3; Fig. 132, BB 92343, internal mould of a pedicle valve × 3; Figs 133a, b, BB 92342a, b, internal and external moulds of a pedicle valve, both × 3; Fig. 134, BB 92346, internal mould of a brachial valve × 4; Fig. 135, BB 92345, latex cast of brachial valve × 3; all from Flags and Grits, Ffairfach Group, type section. Fig. 136, SM A.33345, internal mould of a brachial valve × 4; Figs 137–138, GSM 75247 and 75246 respectively, latex casts of the external moulds of a pedicle and a brachial valve, both × 4; all from Llanvirn Ashes, Bryntowy, Bethlehem.

Figs 139–142 *Horderleyella* sp. Fig. 139, BB 92477, a brachial valve exterior × 4, from Llanvirn beds, Coed Duon, Llanadog (p. 46). Fig. 140, GSM TCC. 362, internal mould of a brachial valve × 2, from Lower Llandeilo beds, Cwrt-y-Gorphwys, Ffairfach (p. 46). Figs 141–142, BB 92348 and 92355 respectively, internal and external moulds of pedicle valves, both × 5, from the Pebbly Sands, Ffairfach Group, type section.

Horderleyella sp.
(Figs 141–142)

DIAGNOSIS. Small transverse mucronate *Horderleyella* with pedicle valve about 70% as long as wide and simple fascicostellate ornament developing from juvenile costate condition.

DESCRIPTION. Small ventribiconvex mucronate *Horderleyella* with carinate pedicle valve, sulcate brachial valve and strongly angular fascicostellate bundles. Pedicle valve transverse subtriangular in outline, about 70% as long as wide ($\bar{l}$ mm (var l) 6·23 (0·934), $\bar{w}$ mm (var w) 8·85 (1·305), r 0·770 in 11 valves) and about 32% as deep as long in 6 specimens, ventral interarea apsacline; brachial valve wider than long and about 15% as deep as long with anacline interarea; external ornament essentially consisting of up to 8 coarse angular costae but exhibiting the following fasciocostellae in a few pedicle valves: 1b̊, 1å1å, 1, 2ă2å, 3å and 3å; ribbing patterns on brachial valves poorly known; concentric growth lines fine, regularly spaced throughout.

Ventral interior with dental plates and muscle scar respectively extending anteriorly for about one-quarter and two-fifths of valve length.

Dorsal interior with open notothyrial cavity divided by simple cardinal process consisting of slightly differentiated myophore and shaft, notothyrial platform extending forward into broad median septum; brachiophores relatively short, blade-like, supported by bases which are almost as long as wide, sockets supported by fulcral plates with underlying crural pits; adductor scars deeply impressed posteriorly in region of adductor pit but poorly known anteriorly.

		length	width
FIGURED MATERIAL			
External mould of p.v.	BB 92348	(6·0)	8·0
Internal and external moulds of p.v. . . .	BB 92355	5·6	9·2
OTHER MATERIAL			
Internal and external moulds of b.v. . . .	BB 92349	5·0	(6·0)
,, . . .	BB 92352	7·9	10·0
Internal and external moulds of p.v. . . .	BB 92350	8·0	10·0
,, . . .	BB 92351	(6·0)	8·0
External mould of p.v.	BB 92353	7·3	11·0
,, ...	BB 92354	5·0	8·0

HORIZON AND LOCALITY. BB 92348–55 from the upper part of the Pebbly Sands in the lower part of the Ffairfach Group, Ffairfach railway cutting, Ffairfach, Llandeilo (SN 628211).

DISCUSSION. Attempts to collect taxonomically useful samples of both *H. convexa* and *H. lata* from their respective type localities in Long Wood near Bethlehem (SN 693259 and 695262) have proved unsuccessful. However, a large sample of *H. convexa* from the middle part of the Ffairfach Group, which compares with the type material in every respect, has allowed us to assess the variability of this species.

Although we have examined the lectotype (GSM 75245), the paralectotypes (GSM 75246–7) and topotypes (SM A.33345–6) of *H. lata*, insufficient material is available to assess the variability of this 'species' thoroughly. Our observations suggest that, apart from differences in size, these two *Horderleyella* 'species' do not differ substantially in any fundamental morphological respect. Such differences as the differentiation of the ventral muscle scar and the prominence of internal ribbing noted by Williams (1949 : 171–173) are most readily attributable to changes in size. We therefore conclude that *H. lata* should be regarded as a synonym of *H. convexa*.

The small sample of *Horderleyella* from the Pebbly Sands is particularly distinctive in that the specimens appear to be persistently coarsely costate; similar forms from the Lower Llandeilo (e.g. BB 94058) are associated with strongly fascicostellate individuals (e.g. BB 94059, see below) of the same size. Although unweathered and partially exfoliated shells, e.g. BB 92476 and 92477 (Fig. 139), appear more strongly costate than any external moulds of comparable size, such differences are not entirely preservational as *Horderleyella* moulds from the Pebbly Sands (i.e. BB 92348–55) are undoubtedly more coarsely costate than similar-sized moulds of *H. convexa* such as GSM 75246–7 and BB 94059.

Detailed collecting throughout most of the key Upper Llanvirn and Lower to Middle Llandeilo sections of the Llandeilo area revealed the sporadic occurrence of *Horderleyella* in a variety of facies including: BB 92476–7 from loose calcareous blocks from the Flags and Grits Formation of the Ffairfach Group exposed at Coed Duon, 3 km south of Llangadog (SN 709256); BB 94058–9 from the Lower Llandeilo *Sowerbyella* Limestones exposed to the east of the Old Castle in Dynevor Park, Llandeilo (SN 612217); and GSM TCC.362 (Fig. 140) from the Late Lower Llandeilo calcareous Flags exposed 320 m NE of Cwrt-y-Gorphwys Cottage SW of Ffairfach (SN 520207). In addition *H. convexa* occurs abundantly in sandstones and tuffaceous sandstones at various horizons in the Ffairfach Group. In this respect therefore there are no indications that specific *Horderleyella* stocks are exclusively confined to particular stratigraphical horizons, although the forms assigned here to *Horderleyella* sp. cannot at present be shown to be conspecific with *H. convexa*.

Numerous harknessellid species are known from the Ordovician rocks of the Welsh Borderland (Bancroft 1945, Williams 1974), north Wales (MacGregor 1961, Williams 1963) and west Wales (Addison 1974). Until a thorough revision of the family is undertaken, however, we consider it premature to discuss the affinities of *H. convexa*.

Family **HETERORTHIDAE** Schuchert & Cooper, 1932

Genus ***TISSINTIA*** Havlíček, 1970

A study of the various *Tissintia* samples recovered during the present investigation has shown that there are three distinct forms of this genus within the Llanvirn and Llandeilo successions of south and central Wales. All three were first identified by Williams in 1949. Two of them, *T. prototypa* and *T. immatura*, have already been revised (Williams 1974 : 108–114) and only the form originally designated '*Resserella immatura* var. *plana*' (Williams 1949 : 167) has to be formally emended.

Tissintia prototypa (Williams)

(Figs 143–151)

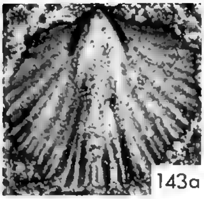
1949 *Dalmanella prototypa* Williams : 168; pl. 8, figs 7–10.
1974 *Tissintia prototypa* (Williams) Williams : 108; pl. 17, figs 15–19; pl. 18, figs 1–9, 11.

A large sample of *T. prototypa* specimens (including BB 92369, BB 94062–4 and BB 94237–40) from a bivalve-dominated coquina in the *Didymograptus bifidus* Beds exposed in the upper reaches of Camnant Brook, 8 km NE of Builth (SO 088576), resembles the samples described by Williams (1974 : 107–114) from contemporaneous horizons in the Shelve and Llandeilo areas.

Comparisons between the Builth and the Llandeilo samples reveal no significant differences although in the former sample the costellae are slightly coarser, numbering 4 and 5 per mm, 5 mm forward of the umbones in 8 and 2 brachial valves. Although the Shelve specimens also have a higher density of costellae than those from Builth, the two samples differ significantly ($0{\cdot}01 < p < 0{\cdot}001$) only in respect of the relative length of their dental plates, which average 20% as long as the valve in the latter sample ($\bar{l}$ mm (var l) 6·90 (3·478), $\overline{dl}$ (var dl) 1·37 (0·101), r 0·821 in 30 valves; cf. 14% for the Shelve sample *in* Williams 1974 : 108; 112, table 81).

The low density of costellae in the Builth specimens is related to the strongly developed fascicostellate style of ornament; the sample also well illustrates the sulcate nature of the brachial valve (cf. Havlíček 1977 : 114) and the variability of the cardinal process.

Numerous small specimens (e.g. BB 92556) of this species have also been recovered from the top of the Upper *Didymograptus bifidus* Beds beneath the Red Agglomerate and Ashes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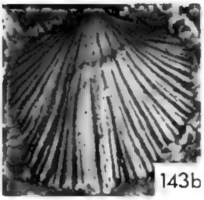
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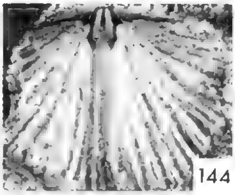
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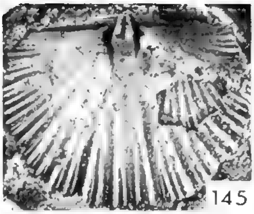
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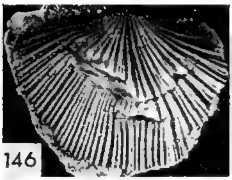
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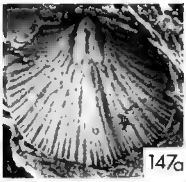
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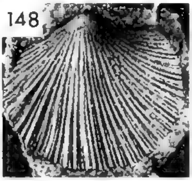
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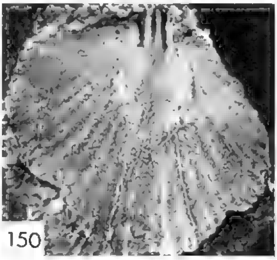
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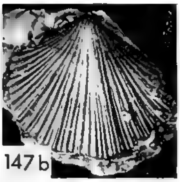
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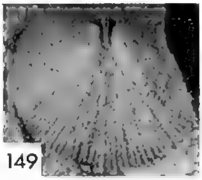
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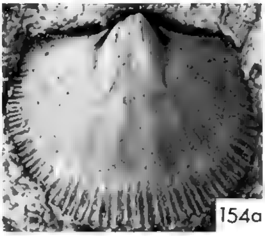
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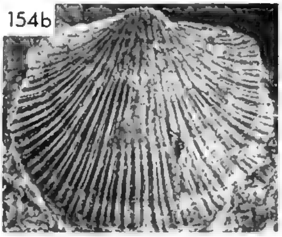
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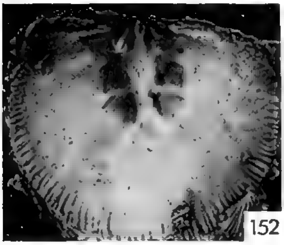
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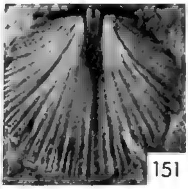
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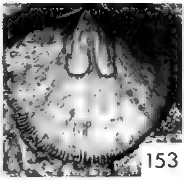
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Figs 143–151 *Tissintia prototypa* (Williams). Figs 143a, b, BB 94062, internal mould and latex cast of external mould of a pedicle valve × 4; Figs 144–145, BB 94063 and 94064 respectively, internal moulds of brachial valves, both × 4; Fig. 146, BB 92369, latex cast of external mould of a brachial valve × 3; Figs 147a, b, BB 94237, internal mould and latex cast of the external mould of a pedicle valve × 2; Fig. 148, BB 94238, latex cast of the external mould of a pedicle valve × 3; all from Lower Llanvirn shales, Camnant Brook, Builth. Fig. 149, BB 92358, internal mould of a brachial valve × 3, from the Llanvirn Bwlch y Cefn tuffs, Llandrindod. Fig. 150, BB 92359, internal mould of a brachial valve × 4, from the Llanvirn, Llandegley tuffs, Llandrindod. Fig. 151, BB 92356, internal mould of a brachial valve × 4, from Llanvirn shales at Howey Brook, Llandrindod.

Figs 152–154 *Tissintia immatura* (Williams). Fig. 152, BB 92362, latex cast of internal mould of a brachial valve × 3; Fig. 153, BB 94241, internal mould of a pedicle valve × 1·5; Figs 154a, b, BB 92363a, b, internal and external moulds of a pedicle valve, both × 3; all from Flags and Grits, Ffairfach Group, type section.

(Rhyolitic Tuffs) of Howey Brook, 4 km east of Howey (SO 089592). The dorsal ribbing pattern with $1\overline{al}$)$1\overline{b}$, $1\overline{b}$) 1å, $2\overline{b}$) 2å, $2\overline{al} = 2\overline{b}$, $3\overline{ala}$)3å, $3\overline{c}$)3å, $3\overline{ala}$) 2å, 4b) $4\overline{b}$, and all other observed morphological features compare in every aspect with the emended description given by Williams (1974 : 108–9). Similarly, larger specimens from penecontemporaneous horizons in the Bwlch-y-cefn Tuffs (BB 92357–8) and the Llandegley Tuffs (BB 92359) (SO 120609 and 128614 respectively) can also be assigned to this species. These observations confirm the reports of Williams (1969 : 121) of *D. prototypa* at this horizon in the Builth area.

Tissintia prototypa (BB 92360–1) has also been recovered from the Ffairfach Grit at Ffairfach (SN 630212). Although known from the underlying Lower Llanvirn *D. bifidus* shales (Williams 1949 : 169; 1974 : 109) this represents the first record of the species in the Ffairfach Group.

Tissintia immatura (Williams)
(Figs 152–155)

1949 *Resserella immatura* Williams : 165; pl. 8, figs 1–4.
1974 *Tissintia immatura* (Williams) Williams : 109; pl. 18, figs 10, 12–15; pl. 19, figs 1–5.

Well-preserved specimens (BB 92362–3, 94241–2 and 94247) from the argillaceous lower part of the Flags and Grits in the middle of the Ffairfach Group at its type locality (SN 628211) represent the first record of this form in the Upper Llanvirn of this area. The well-preserved specimen BB 92362 (Figs 152, 155) clearly illustrates the presence of mantle canals arising from the anterior and lateral margins of the dorsal adductor scar and radiating to the commissure. Williams (1949 : 166) noted the presence of anteromedian 'pallial sinuses' in Middle Llandeilo representatives of this species but was unable to deduce from that material the extent of the lemniscate mantle canal system evident in this upper Llanvirn representative. Similarly the mainly internally branching multicostellate pattern seen in the specimen, with $1a\bar{l} = 1b\bar{l}$, $1\bar{b}$)1å, $2\bar{b}$) 2å, $2\bar{c}$) 2å, $2\overline{al}$)$2\bar{b}$, $3\overline{a}la$) 3å, $3\bar{c}$) 3å, $4\bar{b}$) 4b, $4\bar{a}\mathring{l}$)$4\overline{bl}$, is considered a more accurate reflection of the typical configuration than the example given by Williams (1949 : 166) and compares with the ribbing facies of the Shelve sample (Williams 1974 : 113).

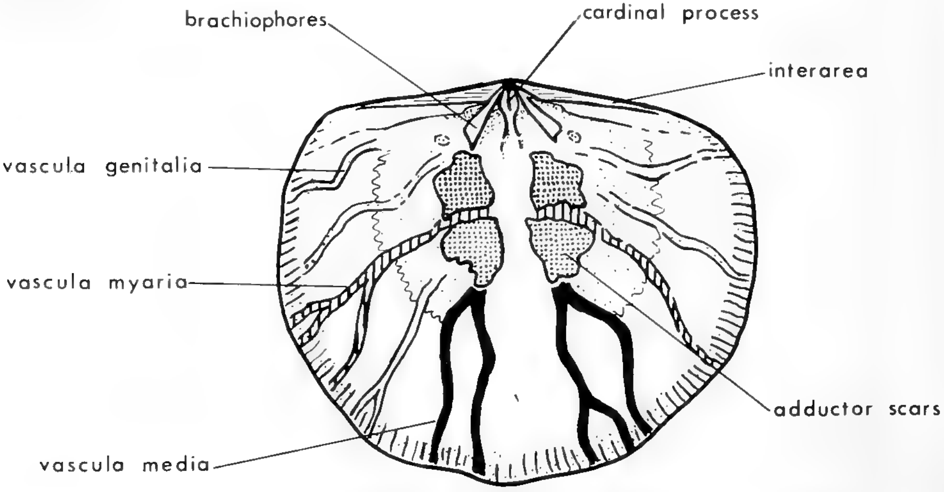


Fig. 155 Diagrammatic view of the dorsal interior of *Tissintia immatura* (Williams), based on specimen BB 92362.

Tissintia plana (Williams)
(Figs 156–162)

1848 *Orthis Testudinaria* Dalman *in* Phillips & Salter : 373.
1869 *Orthis testudinaria* Dalman; Davidson : 226 *pars*; pl. 28, fig. 14 only.
1949 *Resserella immatura* var. *plana* Williams : 167; pl. 8, figs 5, 6.

DIAGNOSIS. Large ventriconvex *Tissintia* with posteriorly reflexed, partially hollow multicostellae and elongate, subflabellate ventral muscle field averaging almost half as long as valve.

DESCRIPTION. Large planoconvex to ventribiconvex, subcircular *Tissintia* with pedicle valve between 69 and 91% as long as wide in 8 specimens and 15 to 21% as deep as long in 5 specimens; brachial valve 72 to 94% as long as wide in 6 specimens and 10 to 11% as deep as long in 2 specimens; ventral interarea slightly curved, apsacline about 10% as long as valve with transverse striations parallel to hinge line and an open delthyrium subtending an angle of about 70°, dorsal interarea short, flat anacline; external ornament consisting of hollow multicostellae reflexed posteriorly along the hinge line and numbering respectively 3 and 2 per mm, 5 and 10 mm anterior of the umbo and branching mainly internally with $1\overline{a1}$ ($1\bar{b}$, $\overline{1b}$)$1\mathring{a}$, $2\bar{b}$) $2\mathring{a}$, $2\bar{c}$)$2\mathring{a}$, $2\overline{a1} = 2\bar{b}$, $3\overline{a1a}$)$3\mathring{a}$, $3\bar{c}$)$3\mathring{a}$, $3\overline{a1a}$) $2\mathring{a}$, $4\bar{b}$)$4\mathring{b}$, $4\overline{a\mathring{1}}$) $4\overline{b1}$.

Delthyrial cavity deep, bounded laterally by short, thick divergent dental plates extending forward for 16 to 19% of the length of 3 valves and supporting short, stout, divergent teeth with crural fossettes, denticular cavity continuous with pronounced hinge line groove; muscle field extending forward for 44 to 58% of the length of 4 valves (mean 47%) as impressed diductor scars enclosing raised adductor platform divided by fine median ridge up to one-third as wide as muscle field posteriorly but tapering anteriorly to about one-tenth of the field width; diductor scars subflabellate with component lobes separated anteromedially by strongly developed longitudinal ridges.

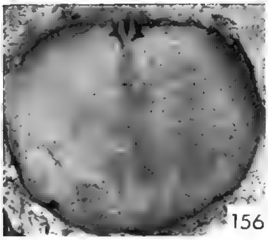
Cardinal process bilobed, stout, undifferentiated; notothyrial platform passing into short median septum extending forward for about one-third of valve length; sockets simple, enclosed by hinge and short divergent brachiophores with bases 57 to 64% as long as wide and 10 to 16% as long as two measured valves; dorsal muscle field obscure except for impressed posterior adductor pits.

FIGURED MATERIAL		length	width
Internal and external moulds of p.v.	BB 92364	23·5	27·0
Internal and external moulds of b.v.	BB 92368	17·0	18·0
Internal mould of p.v.	BB 36164	19·5	24
Internal mould of b.v.	BB 36165	18	23
,, ...	GSM 10341	22	26
External mould of b.v.	BB 36172	20	25
External mould of p.v.	GSM 10341	22	24
OTHER MATERIAL			
Internal and external moulds of p.v.	BB 92365	19·5	22·0
,, . . .	BB 92366	16·0	18·0
Internal and external moulds of b.v.	BB 92367	17·0	22·0

HORIZONS AND LOCALITIES. BB 92364–7 and BB 92368 respectively from the upper part of the Flags and Grits Formation and from the Rhyolitic Conglomerates Formation of the upper part of the Ffairfach railway cutting, Ffairfach, Llandeilo (SN 627210); BB 36164–72 from the calciferous Lower Caradoc Bryn Banc Limestone exposed in old quarry 800 m SSW of Henllan Lodge, Llanddewi Velfrey, Dyfed (SN 131160). GSM 10341–3 from Llandeilo Flags, Pant-dwfn 1·5 km SSE of St Clears, Dyfed (SN 289151 approx.); lectotype (selected Cocks 1978 : 74) GSM 75237 from Lower Llandeilo beds exposed in quarry 100 m NE of Pant-y-ffynon, Llandeilo, Dyfed (SN 652228).

DISCUSSION. *T. plana* is regarded here as a distinct species since its partially hollow ribs and large size immediately distinguish it from *T. prototypa* and *T. immatura.* Being also characterized by its larger subflabellate ventral muscle scar, it is elevated from a subspecies to a species. Specimens collected from Llanddewi Velfrey by Addison (1974), including BB 36172, also exhibit hollow ribs.

The present studies have shown that the widespread Lower Llanvirn form *T. prototypa* persisted into early Upper Llanvirn (Ffairfach Grit) times, when it was succeeded after a short stratigraphical interval by *T. immatura* and then, in the succeeding formation, by *T. plana*. Thus all three species occur within a 37 m portion of the Ffairfach Group although only the latter two are known with certainty from the Llandeilo Series of the type area.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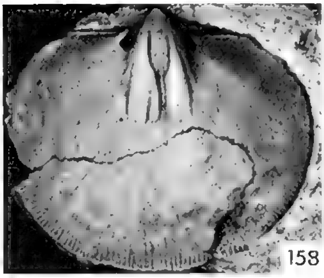
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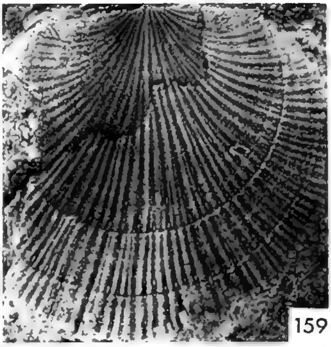
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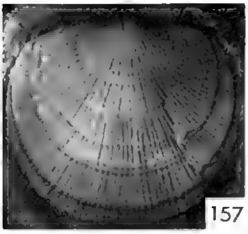
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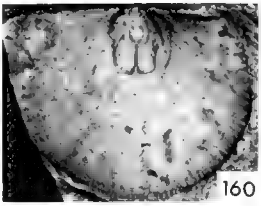
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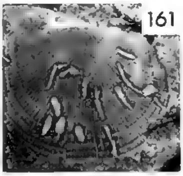
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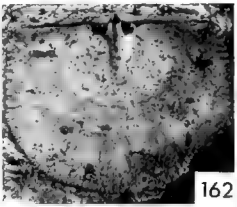
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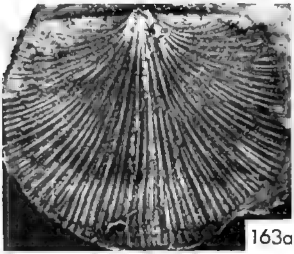
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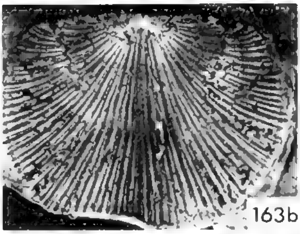
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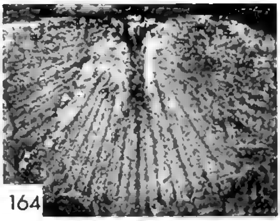
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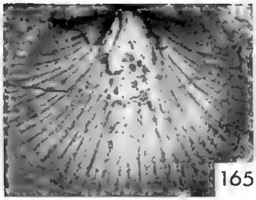
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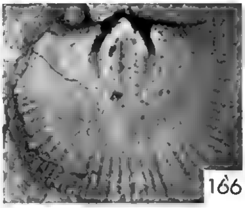
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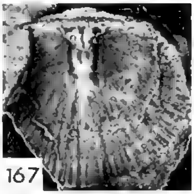
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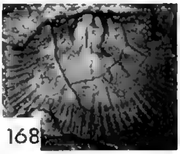
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Figs 156–162 *Tissintia plana* (Williams). Figs 156–157, GSM 10341, internal mould of a brachial valve and latex cast of the exterior of a pedicle valve, both × 1·5, from Llandeilo Flags, Pant-dwfn, St Clears, Dyfed. Fig. 158, BB 92364, internal mould of a pedicle valve × 1·5, from the Flags and Grits, Ffairfach Group, type section. Fig. 159, BB 92368, external mould of a brachial valve showing moulds of hollow ribs × 3, from the Rhyolitic Conglomerates, Ffairfach Group, type section. Fig. 160, BB 36164, internal mould of a pedicle valve × 1·5; Fig. 161, BB 36172, external mould of a brachial valve × 1; Fig. 162, BB 36165, internal mould of a brachial valve × 1·5; all from Lower Caradoc limestones, Llanddewi Velfrey, Dyfed.

Figs 163–168 *Tissintia* sp. Figs 163a, b, SM A.46528, latex casts of the external moulds of respectively the pedicle and brachial valves of an articulated specimen, both × 4; Fig. 164, BB 94234, internal mould of a brachial valve × 4; Figs 165–166, SM A.46527 and BB 94233 respectively, internal moulds of pedicle valves, both × 4; Fig. 167, SM A.46525, latex cast of the internal mould of a brachial valve × 3; Fig. 168, SM A.46526, internal mould of a pedicle valve × 2; all from Llandeilo shales, Llanfawr quarry, Llandrindod.

Tissintia sp.
(Figs 163–168)

Description. Subcircular, ventribiconvex to planoconvex *Tissintia* with obtuse cardinal angles; pedicle valve averaging 12% as deep as long ($\bar{l}$ mm (var l) 5·90 (2·735), $\overline{th}$ (var th) 0·72 (0·047), r 0·600 in 5 valves) and 80% as wide as long ($\bar{l}$ mm (var l) 6·72 (2·972), $\bar{w}$ mm (var w) 8·58 (4·236), r 0·962 in 12 valves) with slightly carinate median zone; brachial valve averaging 78% as long as wide; ventral interarea planar, apsacline, longer than anacline dorsal interarea; radial ornamentation multicostellate to fascicostellate with 5 and 6 ribs per mm, at 5 mm anteromedially of the umbones of 2 and 3 brachial valves; branching mainly internal in first 5 sectors of brachial valve with posterolateral costellae reflexed towards the hinge line.

Ventral interior with small teeth supported by dental plates which extend forward for between 12 and 25% of valve length in 3 specimens (mean 16%) and laterally for between 50 and 85% of their length in 3 specimens (mean 63%), and enclosing the posterior sector of an elongate bilobed muscle field which is between two-thirds and three-quarters as wide as long and between one-third and two-fifths as long as the valve in two specimens.

Cardinalia unknown, situated behind low median ridge which extends forward for about half of valve length; adductor scars elongate, about half as wide as long and half as long as valve.

Figured material		length	width
External mould of articulated valves . .	SM A.46528	8·8	11
Internal mould of b.v.	SM A.46525	8·5	10
,, ...	BB 94234	7·5	10
Internal mould of p.v.	SM A.46527	7·5	9
,, ...	BB 94233	7·3	8·5

Horizon and locality. SM A.46525–8, BB 94233–6 and Llandrindod Wells Museum specimen No. 0357/56 from *Nemagraptus gracilis* Shales exposed in Llanfawr Quarry, 0·5 km east of Llandrindod Wells (SO 066617); UCW (Aberystwyth) specimens 23101–5 also from this locality.

Discussion. Although the material described here exhibits the reflexed posterolateral costellae and ribbing facies typical of the genus *Tissintia*, insufficient is known of the internal morphology of this form to determine its specific affinities. Until more material is available its relationships to older and to contemporary stocks, i.e. *T. prototypa* and *T. immatura*, remain unknown.

Family **LINOPORELLIDAE** Schuchert & Cooper, 1931

Genus ***SALOPIA*** Williams, 1955

Salopia turgida (M'Coy), emended
(Figs 169–178)

1851 *Orthis turgida* M'Coy : 339 *pars*.
1852 *Orthis turgida* M'Coy; M'Coy *in* Sedgwick & M'Coy : 229 *pars*; pl. 1H, fig. 21, *non* figs 20, 22–24.
1949 *Paurorthis turgida* (M'Coy) Williams : 228; pl. 11, figs 9–11.

Diagnosis. Strongly biconvex, subspherical *Salopia* with multicostellate ornament consisting of 5–6 ribs per mm at 2 mm anteriomedially of umbones; pedicle valve with elongately oval muscle scar about 43% as long as valve; brachial valve with well-developed brachiophores up to 41% as long as valve and a strong median septum extending forward for about three-quarters of the valve length.

Description. Strongly biconvex, subspherical, rectimarginate *Salopia* with adult pedicle valve averaging 99% as long as wide and 27% as deep as long ($\bar{l}$ mm (var l) 14·94 (5·277), $\overline{th}$ (var th) 4·00 (0·474), r 0·772 in 25 valves from Ffairfach) with rounded obtuse cardinal angles; adult brachial valve 88% as long as wide ($\bar{l}$ mm (var l) 11·99 (8·329), $\bar{w}$ mm (var w) 13·62 (10·071), r 0·946 in 40 valves) and 25% as deep as long ($\bar{l}$ mm (var l) 11·82 (10·349), $\overline{th}$ (var th) 2·92 (0·727), r 0·880 in 23 valves); ventral interarea curved apsacline with wide open delthyrium subtending an angle of 20°–40°, dorsal interarea slightly curved anacline with open notothyrium subtending an angle of 30°–40°, external ornament generally poorly preserved but finely multicostellate with concentric growth lines.

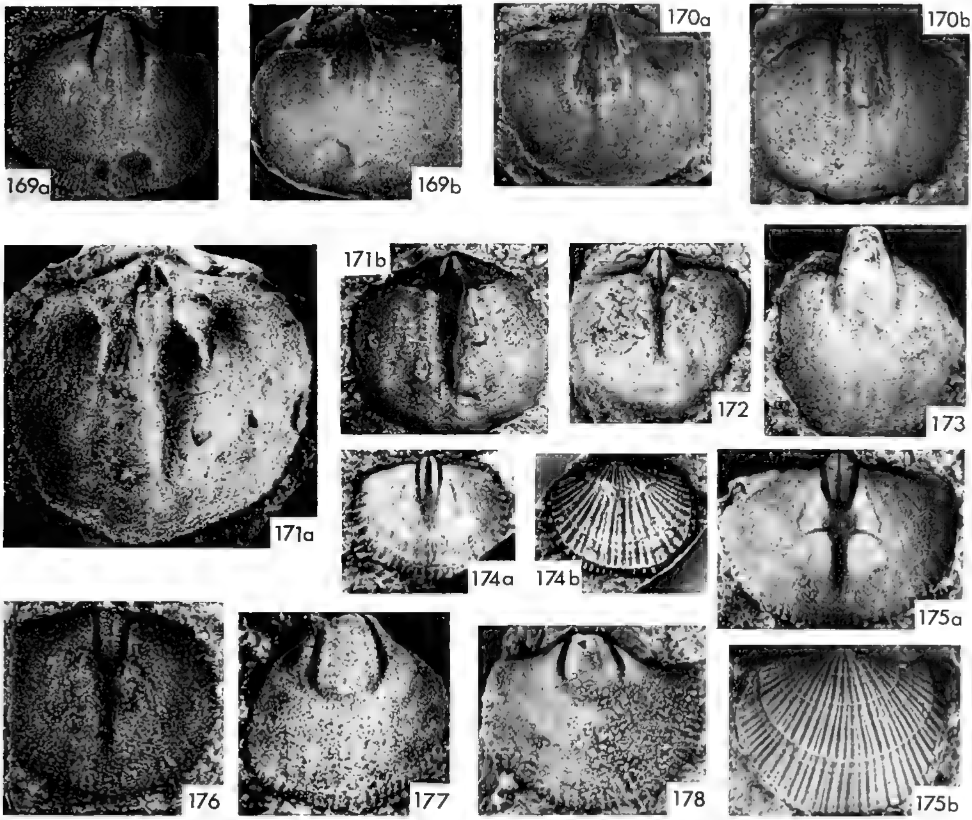
Ventral interior with well-developed teeth and accessory sockets, crural fossettes oblique with thick fossette ridges; dental plates short, passing anteriorly into ridges forming lateral boundaries of longitudinally rectangular muscle scar averaging 65% as wide as long ($\bar{l}$ mm (var l) 6·59 (1·679), $\bar{w}$ mm (var w) 4·27 (0·502), r 0·652 in 24 valves) and extending forward for 43% of valve length ($\bar{l}$ mm (var l) 15·04 (5·237), $\overline{lsc}$ (var lsc) 6·59 (1·679), r 0·680 in 24 valves); three fine, medially situated longitudinal ridges extend for most of length of muscle field and bound two parallel grooves representing adductor scars which separate diductor scars on either side; faint mantle canal markings resemble a saccate arrangement.

Dorsal interior with notothyrial cavity well developed, divided by blade-like cardinal process and bounded anteriorly by a bulbous bilobed notothyrial platform which extends forward into a broad, high, anteriorly tapering median septum persisting for an average of 73% of valve length ($\bar{l}$ mm (var l) 12·23 (6·335), $\overline{ls}$ (var ls) 9·41 (4·069), r 0·910 in 36 valves); notothyrial platform bounded laterally by two grooves which separate it from the laterally located brachiophore processes; shallow sockets with poorly defined socket plates supported by and ankylosed to posterior, thicker part of well-developed blade-like brachiophores which extend anteriorly, subparallel to median line, for up to 41% of valve length; narrowly quadripartite dorsal muscle scar pattern generally poorly defined, but seen in some specimens to extend forward for up to 70% of the valve length.

FIGURED MATERIAL		length	width
Internal and external moulds of p.v.	BB 92370	15·5	17·0
,, ...	BB 92371	16·0	18·0
,, ...	BB 92372	18·0	15·0
,, ...	BB 92378	6·6	8·5
,, ...	BB 92379	7·0	8·0
Internal and external moulds of b.v.	BB 92373	15·0	16·0
,, ...	BB 92374	14·0	15·0
,, ...	BB 92375	4·5	5·5
,, ...	BB 92376	3·2	4·0
,, ...	BB 82377	7·8	8·4

HORIZONS AND LOCALITIES. BB 92370–3 from the upper part of the Pebbly Sands of the Ffairfach Group, Ffairfach railway cutting, Llandeilo (SN 628211); BB 92375–6 are from the argillaceous base of the Flags and Grits immediately above the Pebbly Sands at the same locality; BB 92377–9 from sandy ashes at top of Main Volcanic Series in Howey Brook ('Main Feeder') 4 km east of Howey, outcrop on top of small hill north of brook (SO 0925 5915).

DISCUSSION. Although numerous topotypes from good samples of adult specimens were available for study, the sandy matrix in which they are preserved militates against the preservation of the external ornament, which in any case may have suffered some abrasion. However, two brachial valves (BB 92375–6) were entombed in an argillaceous matrix and the moulds are so well preserved that it is possible to provide supplementary descriptions. The ornament is multicostellate with 5 to 6 ribs per mm, 2 mm anteromedially of the umbones of these two valves, with the first three sectors narrow exhibiting simple internal branching (i.e. 1$\bar{a}$, 1, 2$\bar{a}$, 2, 3$\bar{a}\bar{1}$, 3$\bar{a}$, 3). The interiors of both brachial valves also reveal the nature of the musculature; the adductor scar is a well-developed quadripartite field occupying 56–70% of valve length and 35–40% of valve width in the smaller and larger valves respectively. The floor of the notothyrial cavity is characterized by a series of fine transverse furrows representing diductor muscle tracks.



Figs 169–178 *Salopia turgida* (M'Coy). Figs 169a, b, BB 92370, internal mould and latex cast of a pedicle valve, both × 2; Figs 170a, b, BB 92371, latex cast and internal mould of a pedicle valve, both × 2; Figs 171a, b, BB 92373, latex cast × 3 and internal mould × 2 of a brachial valve; Fig. 172, BB 92374, internal mould of a brachial valve × 2; Fig. 173, BB 92372, internal mould of a pedicle valve × 2; all from Pebbly Sands, Ffairfach Group, type section. Figs 174a, b, BB 92376a, b, internal mould and latex cast of the external mould of a brachial valve, both × 6; Figs 175a, b, BB 92375a, b, internal mould and latex cast of the external mould of a brachial valve, both × 6, both from Flags and Grits, Ffairfach Group, type section. Fig. 176, BB 92377, internal mould of a brachial valve × 4; Figs 177–178, BB 92379 and 92378 respectively, internal moulds of pedicle valves, both × 4; all from Llanvirn sandstones, Howey Brook, Llandrindod.

When one of us (Williams 1949 : 228) emended the original description of *O. turgida* M'Coy on the basis of a sample from the type Ffairfach section, the species was placed in the genus *Paurorthis*. Examination of the sample described here, from the same horizon and locality, clearly indicates that the species is representative of the genus *Salopia*, which is particularly characterized by well-developed, anteriorly extending brachiophores and a cardinal process which is continuous anteriorly with the median septum; the pedicle valve lacks the prominent anteromedian ridge typical of *Paurorthis*. The two genera also differ in style of ornament and configuration of muscle scars.

Penecontemporaneous *Salopia* from the Builth area are apparently conspecific with *S. turgida* (M'Coy) and represent the first record of the genus in this area.

Although it would be desirable to investigate the relationship of *S. turgida* (M'Coy) to penecontemporaneous species from north Wales and Shropshire (i.e. *S. globosa* (Williams), *S. salteri* (Davidson), *S. salteri gracilis* (Williams) and *S. triangularis* (Sowerby); see Cocks (1978 : 82) for details), we have been unable to obtain sufficient comparative material to warrant undertaking a thorough revision of *Salopia* from the Anglo-Welsh province.

Suborder **CLITAMBONITIDINA** Öpik, 1934

Superfamily **GONAMBONITACEA** Schuchert & Cooper, 1931

Family **KULLERVOIDAE** Öpik, 1932

Genus ***KULLERVO*** Öpik, 1932

Kullervo sp.

(Figs 179–181)

Description. Biconvex clitambonitacean with pyramidal pedicle valve and conspicuous lateral extensions of the hinge-line imparting a diamond-shaped outline to shell in ventral view; pedicle valve averaging 55% as long as wide ($\bar{l}$ mm (var l) 3·40 (0·668), $\bar{w}$ mm (var w) 6·23 (1·783), r 0·964 in 6 valves) and almost two-thirds as deep as long with a faintly developed anteromedian sulcus; long, slightly curved, apsacline ventral interarea extending anteriorly for about half the length of valve and characterized by fine growth ridges parallel to the hinge; brachial valve 55% as long as wide in only known specimen, interarea unknown, remainder of valve essentially planar.

External ornament consisting of at least 14 well-developed primary costae, numbering about 3 per mm, 2 mm anteromedially of umbo with occasional secondary costellae; radial component of ornament intersected by equally well developed concentric lamellae (numbering 4–5 per mm between 2 and 3 mm anterior of the umbo) giving surface a reticulate appearance; posterolateral flanks of valves characterized by virtual absence of radial component of ornament.

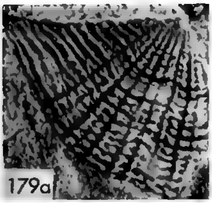
Ventral interior with spondylium with hemisyrinx supported by well-developed median septum extending anteriorly for over half of valve length.

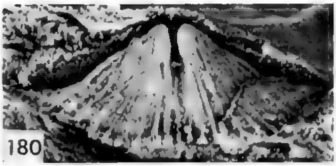
Dorsal interior poorly known but exhibiting median septum and widely divergent socket ridges effectively forming anteroventral extensions of the interarea.

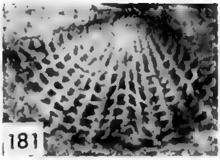
Figured material		length	width
Internal and external moulds of p.v.	BB 92380	4·7	8·0
,, ...	BB 92381	4·0	7·8
,, ...	BB 92400	2·6	5·2

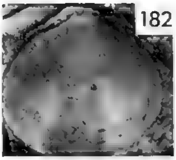
Horizon and locality. BB 92380–2 and BB 92400 from Flags and Grits in middle part of Ffairfach Group, SW side of main quarry, Ffairfach railway cutting, Llandeilo (SN 628211); BB 92383 from arenaceous upper part of Pebbly Grits on west side of same quarry.

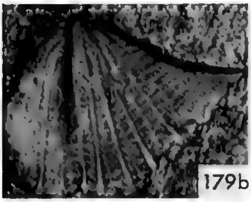
Discussion. Two forms of post-Llanvirn *Kullervo* from Wales and the Borderlands have hitherto been assigned to, or compared with, *K. panderi* (Öpik) by Williams (*in* Whittington & Williams 1955 : 413; Williams 1974 : 116). But although the Upper Llanvirn form described here is similar in internal morphology, it apparently differs in the external characters of shell outline and in its posterolateral ornamentation. Indeed this latter feature is closely reminiscent of the pattern observed by Wright (1964 : 241–2) for *K. complectens* (Wiman) *albida* (Reed). Other features, however, such as the **B**-shaped outline of the Ashgill species, do not compare so closely with the Welsh material. In view of the small number of complete specimens available for study and the variation in pedicle valve outline and ribbing pattern known to be characteristic of this genus, it is considered inappropriate to identify the Ffairfach specimens specifically until more material is available.

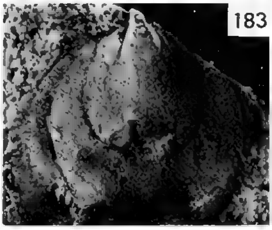


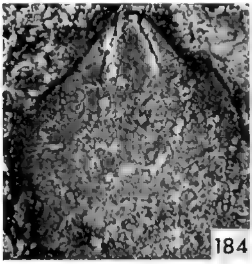


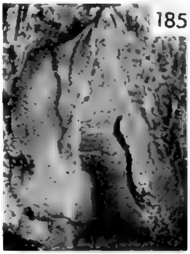












Figs 179–181 *Kullervo* sp. Figs 179a, b, BB 92380, external and internal moulds of a pedicle valve, both × 6; Fig. 180, BB 92381, internal mould of a pedicle valve × 6; Fig. 181, BB 92400, latex cast of external mould of a pedicle valve × 6; all from the Flags and Grits, Ffairfach Group, type section.

Figs 182–185 *Triplesia edgelliana* (Davidson). Fig. 182, BB 92386, exterior of a pedicle valve × 4; Fig. 183, BB 92385, internal mould of a pedicle valve × 5; Fig. 184, BB 92399, internal mould of a juvenile pedicle valve × 12; Fig. 185, BB 92395, internal mould of a pedicle valve × 4; all from Flags and Grits, Ffairfach Group, type section. See also Figs 186–191.

Suborder **TRIPLESIIDINA** Moore, 1952

Superfamily **TRIPLECIACEA** Schuchert, 1913

Family **TRIPLECIIDAE** Schuchert, 1913

Genus ***TRIPLESIA*** Hall, 1859

Triplesia edgelliana (Davidson)
(Figs 182–191)

1869 *Rhynchonella* ? *Edgelliana* Davidson : 190; pl. 24, figs 27, 28.
1978 *Camerella edgelliana* (Davidson) Cocks : 137.

Diagnosis. Globular, equally biconvex, plicate *Triplesia* with pedicle and brachial valves respectively 91% and 88% as long as wide and 27% and 29% as deep as long.

Description. Globular, biconvex, plicate *Triplesia* with well-rounded obtuse cardinal angles; adult pedicle valve about 90% as long as wide and about 27% as deep as long ($\bar{l}$ mm (var l) 5·38 (1·45), $\overline{th}$ (var th) 1·45 (0·477), r 0·761 in 8 valves); ventral umbo slightly acute with short curved apsacline interarea with pseudodeltidium; broad, gently rounded ventral sulcus originating at about the 4 mm growth stage, with boundaries diverging at about 15° so that anteriorly sulcus and corresponding dorsal fold are about one-third as wide as valve in average-sized specimens; brachial valve about 88% as wide as long ($\bar{l}$ mm (var l) 5·26 (6·529), $\bar{w}$ mm (var w) 5·97 (9·127), r 0·977 in 21 valves) and about 33% as deep as long ($\bar{l}$ mm (var l) 4·87 (5·569), $\overline{th}$ (var th) 1·60 (1·120), r 9·27 in 16 valves) with rounded incurved umbo obscuring very small interarea; external surface smooth except for fine growth lamellae numbering at least 12 per mm anteromedially and most conspicuous towards commissure.

Ventral interior with short, low, divergent dental plates about 23% as long as valve ($\bar{l}$ mm (var l) 4·20 (1·773), $\overline{dl}$ (var dl) 0·96 (0·060), r 0·386 in 9 valves) and about as divergent as long ($\overline{l}$ mm (var l) 0·96 (0·060), $\overline{w}$ mm (var w) 0·97 (0·128), r 0·780 in 9 valves) and supporting widely divergent, low transverse teeth; pedicle passage and muscle scars obscure.

Dorsal interior characterized by typical forked cardinal process and widely divergent brachiophores subparallel to hinge to which they are fused except at lateral extremities; a fine, variably developed median ridge extends forward from bulbous anterior base of cardinal process for up to one-quarter of valve length; muscle scars obscure.

TYPE MATERIAL		length	width
Lectotype, internal mould of p.v.	GSM 10354	11	13
Paralectotype, internal mould of b.v.	GSM 10356	(7·5)	(9)
OTHER FIGURED MATERIAL			
Internal and external moulds of p.v.	BB 92384	8·0	10·0
,,	BB 92385	6·0	7·5
,,	BB 92386	5·9	6·2
,,	BB 92395	10·0	—
,,	BB 92399	3·7	3·0
Internal and external mould of b.v.	BB 92387	5·5	6·5
Internal mould of b.v.	BB 92393	7·5	8·5
Articulated specimen (p.v. dimensions given)	BB 92394	6·2	7·4

HORIZONS AND LOCALITY. All material from the Ffairfach Group, Ffairfach railway cutting, Ffairfach, Llandeilo (SN 628211); BB 92384–5, 92389–90, 92392–3, 92395, 92399 and probably GSM 10354–7 from the argillaceous lower part of the Flags and Grits and BB 92386, 92388 and 92394 from the calcareous upper part of the same formation; BB 92387 and 92391 from argillaceous beds in the lower part of the Rhyolitic Ashes and Lavas Formation.

DISCUSSION. This species, variously classified by Davidson (1869 : 190) and Cocks (1978 : 137), is a triplesiid and is more properly assigned to the genus *Triplesia* because of its distinctive cardinal process and gross morphology.

Several specimens have a crumpled or collapsed appearance suggesting that this typical triplesiid was thin-shelled. Observations on its ontogeny indicate that juveniles prior to the development of plication are typically elongately lobate, averaging 114% as long as wide in 5 observed pedicle valves less than 4 mm in width.

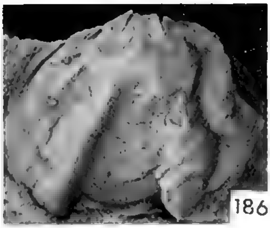
T. edgelliana (Davidson) is the oldest triplesiid species known from the Ordovician rocks of Wales; it resembles *T. maccoyana* Davidson from the Lower Bala Group, north Wales except for its significantly shallower dorsal valve (Lockley 1980) and may also ultimately prove to be closely related to the Soudleyan *Triplesia* from Shropshire (Williams 1974 : 116). Although little is known of the internal characteristics of the Anglo-Welsh *Triplesia*, it is apparent that, despite its sporadic occurrence, the stock retained morphological homogeneity throughout much of the Ordovician.

Genus ***OXOPLECIA*** Wilson, 1913

Oxoplecia cf. ***nantensis*** MacGregor
(Figs 192–195)

cf. 1961 *Oxoplecia nantensis* MacGregor : 196; pl. 20, figs 15–19.

Three brachial valve specimens, BB 92396–8, from the uppermost Rhyolitic Conglomerates Formation of the Ffairfach Group, Ffairfach railway cutting, Ffairfach, Llandeilo (SN 627210) closely resemble *O. nantensis* MacGregor. They are about 84% as long as wide and 28% as deep as long with obtuse cardinal angles and a well-developed dorsal fold. The ornament is costellate with bifurcating ribs and internal and external secondary branches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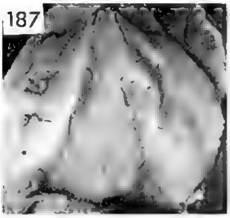
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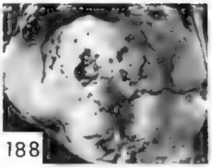
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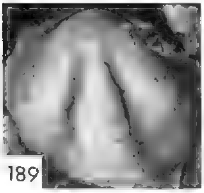
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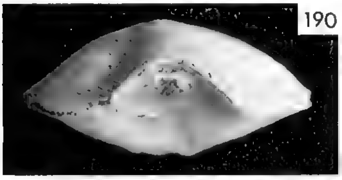
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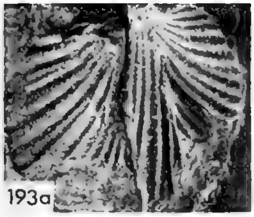
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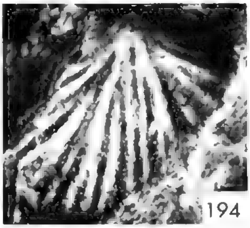
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Figs 186–191 *Triplesia edgelliania* (Davidson). Fig. 186, BB 92383, internal mould of a pedicle valve × 4; Fig. 187, lectotype GSM 10354, internal mould of a pedicle valve × 3; Fig. 188, paralectotype GSM 10356, internal mould of a brachial valve × 3; Fig. 190, BB 92394, anterior view of articulated valves × 6; Fig. 191, BB 92393, latex cast of cardinal area of brachial valve × 16; all from Flags and Grits, Ffairfach Group, type section. Fig. 189, BB 92387, exterior of a brachial valve × 4, from overlying member in same section. See also Figs 182–185.

Figs 192–195 *Oxoplecia* cf. *nantensis* MacGregor. Fig. 192, SM A.44948 internal mould of a brachial valve × 2, from Lower Llandeilo shales, Tre Gib, Llandeilo. Figs 193a, b, BB 92398a, b, external and internal moulds of a brachial valve × 3; Fig. 194, BB 92397, exterior of a brachial valve × 8; Fig. 195, BB 92396, internal mould of a brachial valve × 4; all from the Rhyolitic Conglomerates, Ffairfach Group, type section.

numbering 2–3 per mm, 5 mm anteromedially, with at least 12 costae on each lateral flank and 5 to 8 on the median fold. Concentric ornamentation consists of delicate lamellae numbering 10 and 12 per mm, between 5 and 6 mm anteriorly of the dorsal umbo, in 2 specimens. The internal moulds show only traces of ribs.

FIGURED MATERIAL		length	width
Internal and external moulds of b.v.	BB 92396	10·5	12·0
,, ...	BB 92398	9·5	12·0
Exterior of b.v.	BB 92397	4·0	4.5

DISCUSSION. Williams (1974 : 125) has discussed the differences between *O. nantensis* from the Berwyns and from the Shelve area. It is clear from evidence given above that the Ffairfach specimens resemble those from the Shelve more closely, being virtually identical in dorsal shape, depth and radial ornamentation and differing only in the relative coarseness of the concentric lamellae of the Shelve form. Wilcox (1979) reports *Oxoplecia* (i.e. *Cliftonia* sp. of Williams 1953 : 191 etc.) occurring sporadically throughout the Lower Llandeilo and occasionally in the Middle Llandeilo; SM A.34086–7 are recorded from lower Lower Llandeilo strata exposed at Careg-y-foel-gam farm 3 km SSE of Llangadog (SN 706249 approx.) and SM A.44948 (Fig. 192) originates from Lower Llandeilo exposures at Tregîb farm 1 km SSE of Llandeilo (SN 636212). However, BB 92396–8 represent the first record of this form in the pre-Llandeilo rocks of Wales.

Order **STROPHOMENIDA** Öpik, 1934

Suborder **STROPHOMENIDINA** Öpik, 1934

Superfamily **PLECTAMBONITACEA** Jones, 1928

Family **SOWERBYELLIDAE** Öpik, 1930

Subfamily **SOWERBYELLINAE** Öpik, 1930

Genus ***SOWERBYELLA*** Jones, 1928

Sowerbyella antiqua Jones

(Figs 196–212)

1928 *Sowerbyella antiqua* Jones : 419; pl. 21, figs 7–11.
1949 *Sowerbyella antiqua* Jones, var. *llandeiloensis* Williams : 234; pl. 11, figs 12–14.
1961 *Sowerbyella antiqua* Jones; MacGregor : 201; pl. 23, figs 11–15.
1974 *Sowerbyella antiqua* Jones; Williams : 130; pl. 22, figs 4, 7–14; pl. 23, figs 1, 3, 4.

DISCUSSION. The taxonomic distinction between the widely distributed Welsh *S. antiqua* Jones and the 'variety' *S. antiqua* Jones *llandeiloensis* Williams (1949 : 234) is ambiguous. Spjeldnaes (1957 : 84) considered the two forms to be specifically distinct, while MacGregor (1961 : 203) regarded the latter taxon as a junior synonym of the former. To ascertain the morphological relationship, specimens of *S. antiqua* from Maes y fallen, the source of Jones' paratypes, and topotypes of *llandeiloensis* from both Dynevor Park localities cited by Williams (1949 : 235), were compared with two collections of *Sowerbyella* from the type Ffairfach succession and with another sample from Coed Duon previously taken to be representative of *S. antiqua* s.s. (Williams 1974 : tables 98, 100–104). All six samples were compared with one from the Builth area and the results are summarized in Tables 3 and 4, which illustrate the extent of statistically useful data.

The syntypes from the coarse Lower Llandeilo sandstones exposed at Maes y fallen are much less well preserved than the remaining samples. There is even some deformation of the rock fabric of the locally inverted succession which has resulted in a slight, yet perceptible,

Table 3 *Sowerbyella antiqua* (Jones). Percent ratios of pedicle valve length/width (a), length/depth (b), length of muscle scar/valve length (c), length/width of muscle scar (d), brachial valve length/width (e), length of socket ridges/valve length (f), length/width of socket ridges (g), length of septa/valve length (h), length/width of septa (i), and ribbing counts (j) at 2 mm anteromedially of the dorsal umbo, in samples from the Lower Llandeilo at Maes y Fallen (A), Dynevor Park, Old Castle (B) and Dynevor Park boat house (C); also from the Ffairfach Group in the type section (D) and (E), at Coed Duon (F) and from Upper Llanvirn tuffaceous sandstones near Builth Wells (G).

	a	b	c	d	e	f	g	h	i	j, ribs per mm			
										9	10	11	12
A	57	—	—	—	56	—	—	—	—	—	—	—	—
B	52	19	33	70	50	10	33	61	91	1	7	10	1
C	52	18	—	—	49	—	—	—	—	2	13	9	5
D	53	24	—	—	50	—	—	—	—	0	8	6	3
E	51	—	36	74	48	10	31	66	96	1	12	11	5
F	—	—	32	74	51	12	36	56	—	6	30	19	9
G	52	21	35	69	50	12	31	66	83	—	—	—	—

asymmetry in some of the examined specimens. However, sufficient undeformed and well-preserved material was obtained to examine the internal morphology of both valves and show that, although the valves are relatively less transverse than in other samples, the differences in outline are not statistically significant.

Material from the *Sowerbyella* Limestones at the two Dynevor Park localities, cited by Williams (1949 : 235) as the type localities for the *llandeiloensis* variety, are shown to be identical in all respects to the *S. antiqua* sample from the Upper Llanvirn Ffairfach Group exposed at Coed Duon and described by Williams (1974 : 130); see Table 4. Since all three samples are also similar to samples from the Ffairfach Group Flags and Grits at the type section and from Builth Wells (Table 4), it is concluded that the subjectively derived opinion of MacGregor (1961 : 204) that the two forms . . . 'should be united as a single species' is valid.

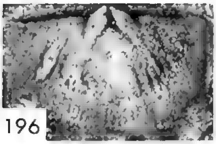
Table 4 Distribution of significant differences between morphological characters (a to j, Table 3) in samples A to G of *Sowerbyella antiqua* (Jones).

	A	B	C	D	E	F
B	—					
C	—	—				
D	—	—	—			
E	—	g	e	e		
F	—	—	—	—	e,g,h	
G	—	—	—	—	f	—

Unlike the samples discussed above, which were collected from single horizons, the sample from the Rhyolitic Conglomerates Formation of the standard section of the Ffairfach Group was derived from four equally-spaced horizons between 8 and 5 m below the top of the formation. This pooled sample differs significantly from eastern Dynevor Park, Ffairfach Flags and Grits and Coed Duon samples in possessing a relatively more transverse brachial valve ($0{\cdot}01<p<0{\cdot}001$, $0{\cdot}02<p<0{\cdot}01$ and $0{\cdot}05<p<0{\cdot}02$ respectively); it differs significantly from the western Dynevor Park and Coed Duon samples in exhibiting relatively divergent socket ridges ($0{\cdot}05<p<0{\cdot}02$ and $0{\cdot}01<p<0{\cdot}001$ respectively); and from the Builth Wells sample in having significantly shorter socket ridges relative to valve length ($0{\cdot}05<p<0{\cdot}02$). When compared with the Coed Duon population the relative length of the dorsal septa is significantly greater than in the pooled Ffairfach sample ($0{\cdot}001>p$).

These differences in the dorsal morphology of *Sowerbyella* recovered from the Rhyolitic Conglomerates seem to be of limited taxonomic significance. They have been demonstrated for a pooled sample of four collections of predominantly adult valves. The absence of young and immature valves from the shell residues preserved in the Rhyolitic Conglomerates could well account for the statistically identifiable difference in outline because large shells in all samples tend to be more mucronate than young ones. Moreover, the interiors of brachial valves undergo considerable changes during growth. In particular, secondary shell accretion on the socket ridges and septa supporting the adductor muscle bases changes the morphology of such apophyses. The ridges tend to become more stumpy and the septa become ankylosed to form a cleft platform (e.g. Figs 197–198).

The diagnosis and description of *S. antiqua* have recently been amended (Williams 1974 : 130). The revision was based on a study of well-preserved moulds of *Sowerbyella* from Coed Duon which are here shown to be indistinguishable from basal Llandeilo *Sowerbyella* from Maes y fallen where the syntypes of the species were collected. In these circumstances, no further amendment is called for and the formal diagnosis for the species and its 'variety' remains that cited above.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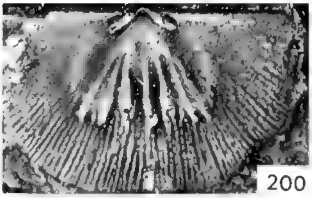
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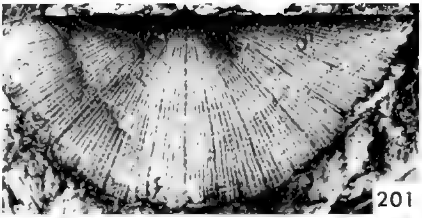
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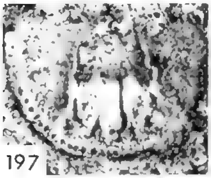
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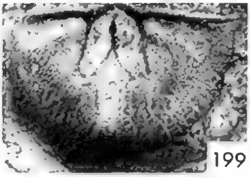
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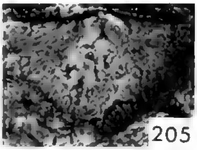
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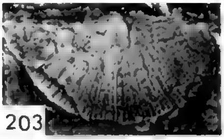
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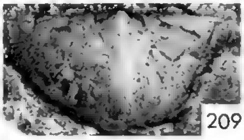
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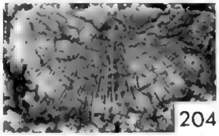
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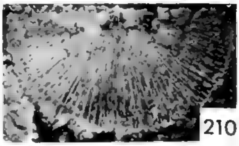
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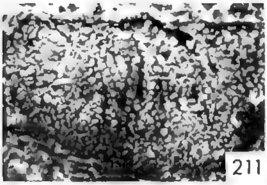
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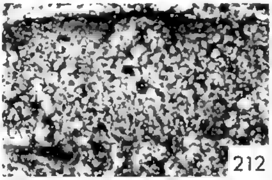
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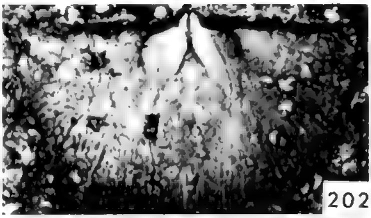
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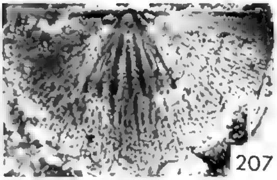
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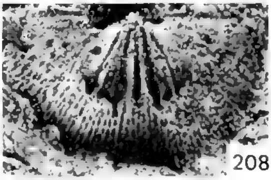
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Figs 196–212 *Sowerbyella antiqua* Jones. Fig. 196, BB 94060, internal mould of a pedicle valve × 2·5; Fig. 197, BB 92499, latex cast of internal mould of a brachial valve, showing marginal follicular embayments, × 3; Fig. 198, BB 92495, latex cast of internal mould of a brachial valve × 3; Fig. 199, BB 92496, internal mould of a pedicle valve × 3; all from Lower Llandeilo sandstones, Maes y fallen, Llandeilo. Fig. 200, BB 92401, latex cast of internal mould of a pedicle valve × 6; Fig. 201, BB 92403, external mould of a brachial valve × 6; Fig. 202, BB 92404, internal mould of a pedicle valve × 6; all from the Rhyolitic Conglomerates, Ffairfach Group, type section. Figs 203–204, BB 92408 and 92407 respectively, exteriors of a pedicle and of a brachial valve, both × 3, both from the Flags and Grits, Ffairfach Group, type section. Figs 205–206, BB 94039 and 94037 respectively, internal moulds of pedicle valves, both × 6; Figs 207–208, BB 94038 and 94036 respectively, internal moulds of brachial valves, both × 6; all from Lower Llandeilo Limestones, Old Castle, south Dynevor Park, Llandeilo. Figs 209–210, BB 94041 and 94040 respectively, exteriors of a pedicle and of a brachial valve, both × 3, from Lower Llandeilo Limestones, west Dynevor Park, Llandeilo. Figs 211–212, NMW 68.376.153–3, internal moulds of a brachial and of a pedicle valve, both × 6, from Llanvirn sandstones at Tan y Graig, Builth.

HORIZONS AND LOCALITIES. GSM 10292 (holotype of *S. antiqua* by original designation) and SM A.11314–5 from unknown horizons and localities in the Llandeilo Limestone of Llandeilo, possibly the Lower Llandeilo *Sowerbyella* limestones of Dynevor Park. Paratypes, GSM 37533–4 from the Llandeilo Limestone in the old quarry 275 m SW of Ffynonddewi near Nantgaredig (SN 4785 2075) and GSM 32152a, 32152b[2] from Lower Llandeilo Basal Sandstones 275 m SW of Maes y fallen (SN 649210); SM A.34101–5, BB 942495–9 and BB 94060 also from the same Maes y fallen locality; GSM 75268[3] and 75270 (syntypes of the *llandeiloensis* variety, Williams 1949 : 234) and BB 94040–3 from Lower Llandeilo *Sowerbyella* Limestones in old quarry 70 m west of Boat House, western Dynevor Park (SN 609223); SM A.34094–5, GSM 75267 and GSM 75269 (also *llandeiloensis* syntypes, Williams 1949 : 235) from Lower Llandeilo *Sowerbyella* Limestones 5 m north of Old Dynevor Castle, southern Dynevor Park (SN 6115 2176); BB 94036–9 from the same horizon 50 m east of the Old Castle (SN 6123 2172); BB 92407–8 from limestones in the upper part of the Flags and Grits Formation of the Ffairfach Group in the type section (SN 628211); BB 92401–6 from the uppermost Ffairfach Rhyolitic Conglomerates Formation at the same locality; BB 35524–34 from the Flags and Grits Formation of the Ffairfach Group exposed on the western side of Coed Duon near Llangadog (SN 709256); NMW 68.376.G.150–161 from quarry east of Tan y Graig 1 km north of Llanelwedd near Builth Wells (SO 048528).

Superfamily **STROPHOMENACEA** King, 1846

Family **STROPHOMENIDAE** King, 1846

Subfamily **FURCITELLINAE** Williams, 1965

Genus ***MURINELLA*** Cooper, 1956

Murinella sp.

(Figs 213–215)

DESCRIPTION. Plano- to slightly biconvex *Murinella* with slightly obtuse cardinal angles and semi-elliptical outline; pedicle valve about 90% as long as wide and 14% as deep as long with apsacline interarea characterized by a narrow pseudodeltidium with a median fold: brachial valve at least 60% as long as wide and about 10% as deep as wide with anacline interarea characterized by a low, broad, medially indented chilidium extending laterally for 15–20% of hinge width; exterior of both valves ornamented by fine parvicostellae numbering 6 per mm at 5 mm anteromedially of the umbo, crossed by fine regularly developed fila (numbering about 25 per mm) and sporadically-occurring growth lines.

Ventral interior exhibiting ill-defined muscle field medially divided by indistinct low, narrow ridge marked by very fine longitudinal median striations within muscle field; muscle scar about 77% as long as wide extending anteriorly for about 32% of valve length and bounded posterolaterally by short, widely divergent dental plates extending anteriorly for about 18% of valve length and supporting simple teeth; diductor component of scar characteristically elongate and occupying the lateral sectors of the muscle field.

Dorsal interior with a bilobed cardinal process with a small undifferentiated median process flanked by well-developed subsidiary ridges acting as diductor bases, and socket ridges extending laterally, parallel to the hinge line, for about 45% of valve width; median septum broad and low extending anteriorly from the low, broad notothyrial platform for about 40% of valve length with a fine narrow median ridge continuing to commissure and dividing well-impressed, semicircular dorsal adductor scars which are further divided by a few variably developed fine, radiating ridges and grooves.

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[2] Spjeldnaes (1957 : 84) chose this as the lectotype of *antiqua*, a choice which was also recognized by MacGregor (1961 : 201). However, since the holotype had already been designated by Jones (1928 : 419; pl. 21), this was superfluous.

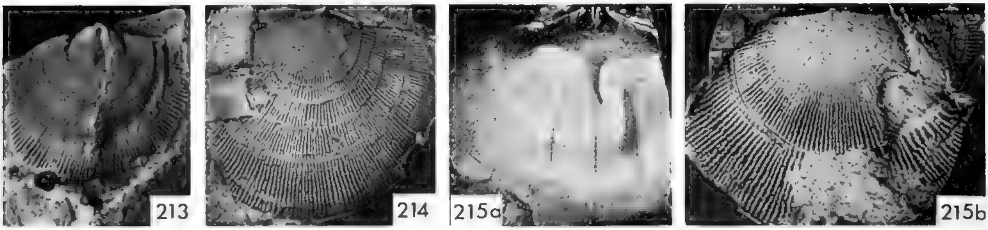
[3] Cocks (1978 : 97) chose this as the lectotype of *llandeiloensis*.

FIGURED MATERIAL		length	width
Internal and external moulds of b.v. . . .	BB 92461	(12)	20
Internal and external moulds of p.v. . . .	BB 92462	8·5	9·5
External mould of p.v.	GSM 10889	16·5	18·0

HORIZON AND LOCALITY. BB 92461–3 from the Flags and Grits in the middle of the Ffairfach Group, Ffairfach railway cutting, Llandeilo (SN 628211); GSM 10889 probably from the same horizon and locality.

DISCUSSION. The brachial valve BB 92461 exhibits pronounced growth distortions on both anterolateral flanks; each side of the valve initially grew radially but then irregularly towards the anteromedian and anterolateral sectors of the shell.

A single pedicle valve of *Murinella* is known from the Lower Llandeilo Meadowtown Beds of the Shelve area (Williams 1974 : 141) and compares with the Ffairfach valve in the arrangement of the muscle field. In the absence of further material, however, it is not possible to do more than conclude that these penecontemporaneous forms may be closely related.



Figs 213–215 *Murinella* sp. Fig. 213, BB 92462, internal mould of a pedicle valve × 3; Fig. 214, GSM 10889, latex cast of the external mould of a pedicle valve, × 2; Figs 215a, b, BB 92461a, b, internal mould and latex cast of the external mould of a brachial valve, both × 2·5; all from the Flags and Grits, Ffairfach Group, type section.

Subfamily **OEPIKINAE** Sokolskaya, 1960

Genus ***MACROCOELIA*** Cooper, 1956

Macrocoelia llandeiloensis (Davidson)
(Figs 216–226)

1871 *Strophomena compressa* (J. de C. Sowerby) var. *Llandeiloensis* Davidson : 316; pl. 46, figs 11–14.
1959 *Rafinesquina ? llandeiloensis* (Davidson) Spjeldnaes : 16; pl. 1. figs 1–7.
1961 *Macrocoelia llandeiloensis* (Davidson) MacGregor : 206; pl. 23, figs 1–10.

DIAGNOSIS. Planoconvex *Macrocoelia*, becoming slightly geniculate in late adult stages of growth with subperipheral rim; finely ornamented with about 8 parvicostellae per mm, 10 mm anterior of umbo, and with a flabellate ventral muscle scar over one-third as long as the adult pedicle valve.

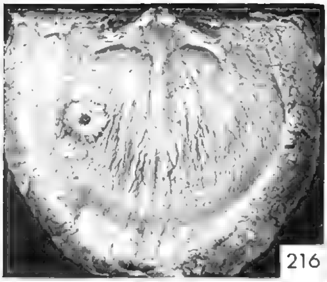
DESCRIPTION. Planoconvex semicircular to semi-elliptical *Macrocoelia* with slightly obtuse rounded cardinal angles and maximum width at, or more commonly just anterior to, the hinge line, variably but evenly convex in transverse profile and unevenly convex in longitudinal profile with incipient geniculation developed in adult specimens; pedicle valve averaging 73% and 78% as long as wide in two samples from Ffairfach and Coed Duon respectively, with smaller and larger mean size (N = 35 and N = 7), and averaging 14% as deep as long (range 8 to 22%, e.g. 20 valves from Ffairfach: $\bar{l}$ mm (var l) 10·88 (5·383), th (var th) 1·56 (0·585), r 0·641); brachial valve averaging 72 to 77% as long as wide in the same two samples (e.g. 20 valves from Ffairfach: $\bar{l}$ mm (var l) 8·87 (8·165), $\bar{w}$ mm (var w) 12·35 (16·792), r 0·974); ventral interarea long apsacline with transverse growth lines parallel to hinge and a well-developed pseudodeltidium and low chilidium, dorsal interarea short anacline; radial ornamentation unequally parvicostellate with 5, 6, 7, 8 and 9 ribs per mm at 10 mm anteromedially of the umbones of 1, 4, 5, 8 and 2 brachial valves respectively.

Ventral interior with widely divergent dental plates supporting simple teeth and extending anteriorly for an average of 14 to 21% of valve length (e.g. 20 valves from Ffairfach: $\bar{l}$ mm (var l) 9·64 (9·343), $\overline{dl}$ (var dl) 1·40 (0·304), r 0·770) and for an average of 45 to 49% of their maximum lateral extension in the same two samples (e.g. 23 valves from Ffairfach: $\bar{l}$ mm (var l) 1·37 (0·302), $\bar{w}$ mm (var w) 3·05 (2·010), r 0892); muscle field poorly developed, equidimensional in small specimens with rare incipient flabellate patterns at lateral margins but with strongly-developed, flabellate paired diductor scars (in larger specimens) averaging 85% as long as wide and 38% as long as valve and enclosing narrow longitudinal adductor scars medially; pedicle tube short and narrow in small specimens but vestigial or absent in larger individuals with tendency for closure to begin anteriorly.

Dorsal interior with stout bifid cardinal process characterized by flattened anterior attachment platforms disposed roughly parallel to the interarea and extending anteriorly for up to 8% of valve length (in larger specimens, e.g. 13 valves from Ffairfach: $\bar{l}$ mm (var l) 8·88 (9·048), $\overline{lc}$ (var lc) 0·52 (0·031), r 0·886) and for 63 to 73% of their maximum lateral extension in respective samples (e.g. 13 valves from Ffairfach: $\bar{l}$ mm (var l) 0·52 (0·031), $\bar{w}$ mm (var w) 0·83 (0·073), r 0·903); processes tapering posteriorly towards umbo and ankylosed anterodorsally to widely divergent socket ridges which extend anteriorly for 10 to 14% of valve length (e.g. 12 valves from Ffairfach : $\bar{l}$ mm (var l) 8·88 (8·778), $\overline{lsr}$ (var lsr) 0·89 (0·055), r 0·872) and for 31 to 39% of their maximum lateral extension in respective samples (e.g. 12 valves from Ffairfach: $\bar{l}$ mm (var l) 0·89 (0·055), $\bar{w}$ mm (var w) 2·86 (0·737), r 0·862); genital markings, consisting of rounded raised pustules, are confined to socket region between socket ridges and hinge line and developed sporadically; notothyrial platform low, obscure, passing anteriorly into a low, broad median septum dividing muscle field; musculature only well-defined in adult individuals where adductor scars average 38% as long as valve (e.g. 10 valves from Coed Duon; $\bar{l}$ mm (var l) 19·45 (8·914), $\overline{lsc}$ (var lsc) 7·75 (2·014), r 0·875) and 77% as wide as long (e.g. 11 valves from Coed Duon: $\bar{l}$ mm (var l) 7·52 (2·404), $\bar{w}$ mm (var w) 9·71 (4·081), r 0·931); radial ridges at an angle of about 30° to median line and dividing the adductor scars into anteromedian and posterolateral sectors.

The greater parts of the posteromedian sectors of both valves are characterized by fine pustules which are strongly elongated along radial lines and tend to become thickened and amalgamated into irregular, slightly anastomosing radial ridges in some larger individuals; these markings are absent towards the periphery which in large forms invariably exhibits a pronounced subperipheral rim which is fluted, particularly dorsally, by radial mantle canals of a lemniscate system.

FIGURED MATERIAL		length	width
Internal mould of b.v.	BB 92421	22	25
,, ...	BB 92445	21	28
Internal and external moulds of b.v.	BB 92432	11	15
,, . . .	BB 92431	10·5	15
Internal mould of p.v.	B 13618	16·5	19
,, ...	BB 92433	14·5	23
,, ...	BB 69520	22·5	27
,, ...	BB 92442	—	23
,, ...	NMW 68.376.G.176.3	12	16
Internal and external moulds of p.v.	BB 92443	17	22
Internal and external parts of exfoliated p.v. exterior	BB 92444	11	14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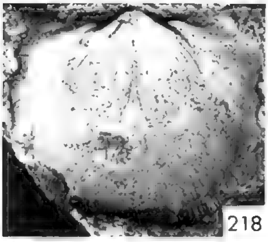
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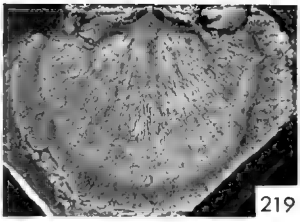
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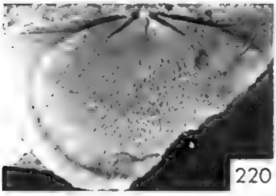
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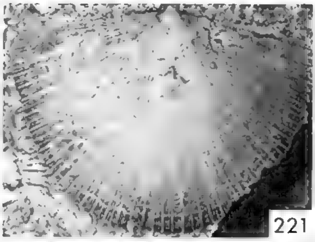
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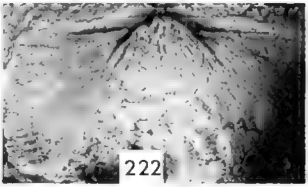
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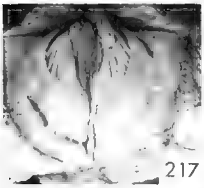
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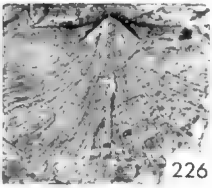
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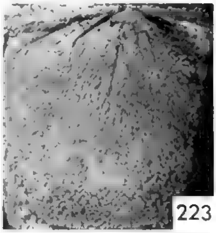
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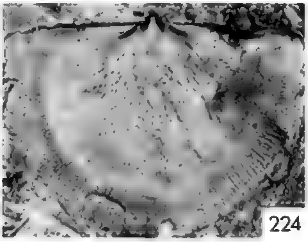
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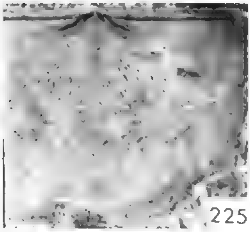
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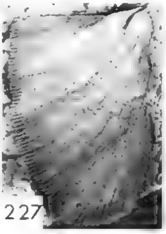
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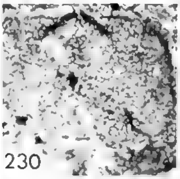
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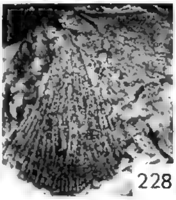
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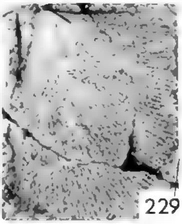
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Figs 216–226 *Macrocoelia llandeiloensis* (Davidson). Fig. 216, BB 92421, latex cast of the internal mould of a brachial valve × 2; Fig. 217, BB 69520, internal mould of a medially split pedicle valve × 1; both from Llanvirn shales, Coed Duon, Llangadog. Fig. 218, B 13618, internal mould of a pedicle valve × 2, from the Ffairfach Group, type section. Fig. 219, BB 92445, internal mould of a brachial valve × 1·5, from the Ashes and Lavas, Ffairfach Group type section. Fig. 220, BB 92433, internal mould of a pedicle valve × 2; Fig. 221, BB 92444, internal part of an exfoliated pedicle valve × 3; Figs 222–223, BB 92442 and 92443 respectively, internal moulds of pedicle valves, both × 2; Figs 224–225, BB 92432 and 92431 respectively, internal moulds of brachial valves, both × 3; all from the Flags and Grits, Ffairfach Group, type section. Fig. 226, NMW 68.376.G.176.3, internal mould of a pedicle valve × 2, from Llanvirn shales at Tanlan, Builth.

Figs 227–230 *Macrocoelia llandeiloensis elongata* subsp. nov. Fig. 227, **holotype** BB 92409, internal mould of a pedicle valve × 2; Fig. 228, BB 92410, internal mould of a pedicle valve × 2; Fig. 229, BB 92411, internal mould of a pedicle valve × 3; Fig. 230, BB 92418, internal mould of a brachial valve × 4; all from Llanvirn sandstones, Howey Brook, Llandrindod.

HORIZONS AND LOCALITIES. BB 92421–8 and BB 69520–5 from argillaceous shell beds in the Flags and Grits Formation on the west side of Coed Duon ridge, 3 km south of Llangadog (SN 709256); BB 92429–39 from argillaceous lower part of the Flags and Grits in the Ffairfach Railway Cutting, Ffairfach (SN 628211); BB 92441 from the uppermost part of the underlying Pebbly Sands Formation at the same locality and BB 92442–4 from the limestones in the upper part of the Flags and Grits Formation exposed immediately to the south in the railway embankment; BB 92445 from the lower ashy part of the overlying Ashes and Lavas Formation at the same locality; BB 92440 from the sandy beds of the Ffairfach Grit Formation exposed in the field beside the Longwood road 300 m NW of Beili-dyffryn Farm (SN 693257); B 13618 from an unknown horizon and locality at Ffairfach (probably from the same locality as BB 92441); NMW 68.376.G.176.2–3 from Upper Llanvirn sandstones exposed 40 m from gate on hill road from Tanlan, 4 km NNE of Builth Wells (SO 057547); SM A.34098–100 from Lower Llandeilo sandstones exposed 275 m SW of Maes y fallen, Llandeilo (SN 649210); SM A.34096–7 from Lower Llandeilo beds exposed at Dynevor Park Old Castle, Llandeilo (SN 6115 2176).

DISCUSSION. Comparison between the two samples described here indicate that the smaller-sized Ffairfach individuals are significantly more transverse in ventral outline than the larger individuals from Coed Duon ($0·02<p<0·01$). Similarly the dorsal socket ridges are significantly longer relative to valve length and significantly more divergent than long in the Coed Duon sample ($0·01<p<0·001$ and $0·05<p<0·02$ respectively). Allometric effects, causing the relative increase in length of the pedicle valve during growth, are particularly significant in the development of the dorsal socket ridges which, whilst becoming relatively more divergent during growth, also show a marked acceleration in their forward growth relative to valve length. Since the two samples not only fail to differ significantly in any of the nine other comparative tests conducted, but also show progressive trends in the development of pustules and atrophy of the pedicle tube during growth, we conclude that no taxonomic significance should be attached to the size-related morphological differences which have been observed.

A small sample, consisting mainly of pedicle valves, from penecontemporaneous rocks in the Builth area compares closely with *M. llandeiloensis* s.s. from the Llandeilo district. Although they are significantly less transverse in ventral outline than the Ffairfach specimens, they exhibit a characteristic pedicle tube and do not differ significantly from the Ffairfach or the Coed Duon samples in any other observed respect. The relevant statistics are: for the pedicle valve outline ($n=10$) $\bar{l}$ mm (var l) 8·29 (5·388), $\bar{w}$ mm (var w) 10·04 (7·118), $r=0·937$, $\bar{a}$ (var a) 1·1494 (0·0202); for the relative length of the dental lamellae (dl) ($n=5$) $\bar{l}$ mm (var l) 8·60 (6·925), $\overline{dl}$ (var dl) 1·42 (0·127), $r=0·784$; and for the length and width of the dental lamellae ($n=6$) $\bar{l}$ mm (var l) 1·38 (0·114), $\bar{w}$ mm (var w) 2·83 (0·355), $r=0·820$.

Macrocoelia llandeiloensis (Davidson) ***elongata*** subsp. nov.

(Figs 227–230)

DIAGNOSIS. Elongately semi-elliptical, planoconvex *Macrocoelia* becoming slightly geniculate in late adult stages of growth with subperipheral rim; ornamented with about 5 parvicostellae per mm, 10 mm anterior of the umbo.

DESCRIPTION. Planoconvex elongately semi-elliptical *Macrocoelia* with slightly rounded, normally orthogonal cardinal angles and maximum width at or near hinge line; pedicle valve averaging 80% as long as wide in 13 valves ($\bar{l}$ mm (var l) 8·67 (17·847), $\bar{w}$ mm (var w) 10·83 (22·711), r 0·961; range 63 to 100%) and 15% as deep as long ($\bar{l}$ mm (var l) 8·67 (17·847), $\overline{th}$ (var th) 1·27 (0·471), r 0·955 in 13 valves) with smaller valves generally transverse but larger valves almost or equally as long as wide and sporadically exhibiting incipient geniculation; brachial valve flat averaging 81% as long as wide in 3 juvenile valves (range 76 to 86%); ventral interarea apsacline with supra-apical foramen, dorsal interarea short anacline, pseudodeltidium and chilidium unknown; radial ornamentation unequally parvicostellate with 5 ribs per mm, 10 mm anteromedially of the umbones of 3 pedicle valves.

Ventral interior with short, divergent dental plates extending anteriorly for an average of 12% of valve length ($\bar{l}$ mm (var l) 8·67 (17·847), $\overline{dl}$ (var dl) 1·05 (0·148), r 0·895 in 13 valves) and for an average of 44% of their maximum lateral extension ($\bar{l}$ mm (var l) 1·05 (0·148), $\bar{w}$ mm (var w) 2·38 (1·116), r 0·879 in 13 valves) and partially enclosing an obscure equidimensional muscle field with subflabellate diductors about one-quarter as long as valve developed in the largest known specimen.

Dorsal cardinal process lobes delicate, extending anteriorly for about 10% of valve length and 72% of their width with bases ankylosed to widely divergent, thin socket ridges extending anteriorly for 16% of the length of the valve and for 40% of their lateral extension ($\bar{l}$ mm (var l) 1·08 (0·254), $\bar{w}$ mm (var w) 2·72 (1·222), r 0·834 in 6 valves), dorsal muscle scar pattern obscure.

TYPE MATERIAL		length	width
Holotype, internal and external moulds of p.v.	BB 92409	18	22
Paratype, internal and external moulds of p.v.	BB 92410	14	14
,, ,,	BB 92411	11·2	12
,, internal mould of b.v.	BB 92418	(6)	7

HORIZON AND LOCALITY. BB 92409–20 from sandy ashes at the top of the Main Volcanic Series in the Howey Brook ('Main feeder') section 4 km east of Howey, outcrop on top of small hill on north side of brook (SO 0925 5915).

DISCUSSION. Although *M. llandeiloensis elongata* subsp. nov. only differs from the penecontemporaneous *M. llandeiloensis* from Tan-lan in its lack of a pedicle tube, it differs from both Llandeilo samples in having a coarser ornament. It also differs significantly from the Ffairfach sample, of virtually identical mean size, in its significantly more elongate pedicle valve ($0·01 < p < 0·001$), its more elongate brachial valve ($0·05 < p < 0·02$), its deeper pedicle valve ($0·05 < p < 0·02$) and its relatively shorter dental lamellae ($0·05 < p < 0·02$). It thus differs from the related Ffairfach specimens in the majority of compared features. Like the Builth Strophomenida generally, *Macrocoelia* from this area is relatively poorly represented, but the Howey Brook sample is sufficiently distinct to warrant systematic recognition at the subspecific level. Indeed additional material from loose tuffaceous blocks at the Howey Brook locality (including BB 94243–4) resemble the subspecies in the characteristic elongate outline.

Family **CHRISTIANIIDAE** Williams, 1953

Genus ***CHRISTIANIA*** Hall & Clarke, 1892

Christiania elusa sp. nov.

(Figs 231–240)

DIAGNOSIS. Small plano- to concavoconvex, transverse *Christiania* with valves averaging about two-thirds as long as wide; ventral anterior with median and lateral pair of dental lamellae.

NAME. 'Mocked, deceived'.

DESCRIPTION. Small plano- to concavoconvex, transverse, slightly plicate *Christiania* with pedicle valve averaging 69% as long as wide in 16 valves ($\bar{l}$ mm (var l) 4·34 (0·655), $\bar{w}$ mm (var w) 6·30 (1·475), r 0·926; range 63 to 80%) and 25% as deep as long ($\bar{l}$ mm (var l) 4·34 (0·655), $\overline{th}$ (var th) 1·09 (0·116), r 0·770 in 16 valves) with flat apsacline interarea; brachial valve averaging 64% as wide as long in 5 valves ($\bar{l}$ mm (var l) 3·94 (0·573), $\bar{w}$ mm (var w) 6·22 (0·602), r 0·849; range 56 to 71%) with a very short anacline interarea; exterior of both valves poorly known but exhibiting obscure concentric growth lines towards anterior commissure.

Ventral interior with short, thick pedicle tube in centre of posteriorly thickened median septum which extends anteriorly for about 33% of valve length; diductor muscle field bounded posterolaterally by well-developed ridges (dental plates) arising beneath the hinge teeth and extending for about 33% of valve length ($\bar{l}$ mm (var l) 4·87 (0·387), $\overline{dl}$ (var dl) 1·60 (0·148), r 0·811 in 6 valves) towards the anterolateral commissure; fine, slightly convergent or anteriorly extending ridges also arise beneath the triangular hinge teeth and extend forward subparallel to median septum for about 20% of valve length, presumably intervening between adductor and diductor muscle attachment areas.

Dorsal interior with simple, bilobed cardinal process and fine, sporadically developed median septum arising anterior to the hinge line and extending almost to the commissure; well-developed double pair of high, sharp, slightly curved septa extending from posteromedian part of valve to near commissure, enclosing slightly raised sector unequally bisected by diagonal septa; submedian septa diverging from median septum at about 15° initially but curving away from median line towards anteromedian margins; posterolateral septa also diverging from hinge line at about 15° to curve away towards posterolateral margins; septa, presumed to enclose adductor muscle fields, confined anteriorly by a curved row of low tubercles, aligned with commissure.

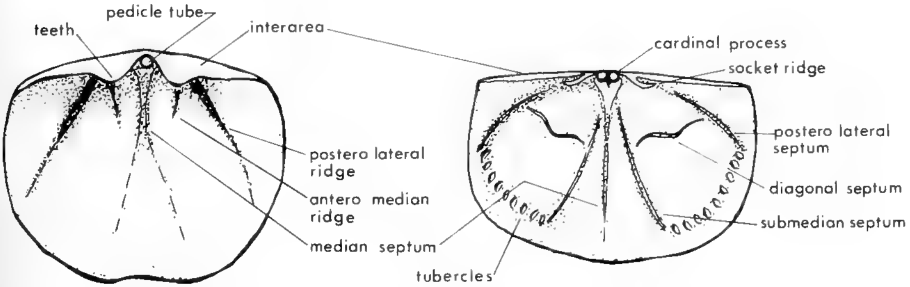
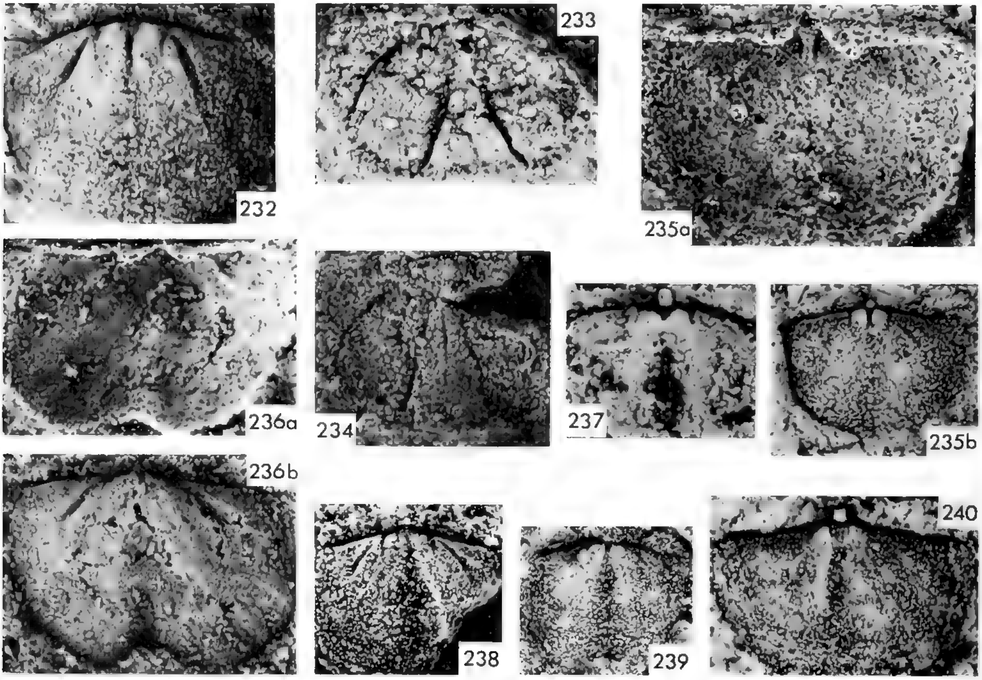


Fig. 231 Diagrammatic views of the interiors of a pedicle (left) and a brachial (right) valve of *Christiania elusa* sp. nov.

TYPE MATERIAL		length	width
Holotype, internal and external moulds of p.v. . .	BB 92451	5·9	7·4
Paratype, internal and external moulds of p.v. . .	BB 92446	5·1	8·0
,, ,, ...	BB 92447	4·1	6·1
,, ,, ...	BB 92448	4·4	6·1
,, ,, ...	BB 92449	5·0	7·5
,, ,, ...	BB 92450	4·2	6·1
,, ,, ...	BB 92452	4·5	6·0
,, internal mould of p.v.	BB 92453	3·0	4·8
,, ,, ...	BB 92454	4·6	7·0
,, ,, ...	BB 92455	4·5	6·5
,, Internal and external moulds of b.v. . .	BB 92456	4·4	7·0
,, ,, . .	BB 92457	3·7	5·4
,, ,, . .	BB 92458	5·0	7·0
,, ,, . .	BB 92459	3·5	6·2
,, Internal mould of p.v.	BB 94246	3·5	5·0

HORIZON AND LOCALITY. BB 94246 and BB 92446–60 are from the sandy ashes at the top of the Main Volcanic Series in Howey Brook ('Main Feeder') section, 4 km east of Howey, outcrop on top of small hill on north side of brook (SO 0925 5915).

DISCUSSION. Although *Christiania* is well known in the Ordovician successions of Scotland, Ireland and North America (Hall & Clarke 1892, Cooper 1956, Williams 1962, Mitchell 1977) and parts of Europe (Spjeldnaes 1957, Havlíček 1967), until recently (Cocks 1978: 123, 203; Hurst 1979) the genus was unknown from Caradoc and older rocks in the Anglo-Welsh region.



Figs 232–240 *Christiania elusa* sp. nov. Fig. 232, **holotype** BB 92451, internal mould of a pedicle valve × 6; Fig. 233, BB 92456, internal mould of a brachial valve × 6; Fig. 234, BB 92457, internal mould of a brachial valve × 6; Figs 235a, b, BB 92449, latex cast × 8 and internal mould × 4 of a pedicle valve; Figs, 236a, b, BB 92447, latex cast and internal mould of a pedicle valve, both × 8; Figs 237–240, BB 94246, 92446, 92455 and 92452 respectively, internal moulds of pedicle valves × 6, × 4, × 4 and × 6 respectively; all from Llanvirn sandstones, Howey Brook, Llandrindod. Figs 233–240 are all paratypes.

The specimens described here are representative of a distinctive specific stock within the genus and constitute the first record of *Christiania* in the pre-Ashgill successions of Wales. *C. elusa* sp. nov. differs from the penecontemporaneous *C. oblonga* Pander from Norway and Russia (Spjeldnaes 1957: 113–127) in having neither a continuous 'branchial loop' nor diagonal septa arising forward of the cardinal process (1957 : fig. 27a). Indeed the new species is more reminiscent of the younger *C. holtedahli* Spjeldnaes with its 'branchial loop' which is discontinuous near the anterolateral commissure and its transversely disposed, curved diagonal septa and fine median septum. Similarly *C. elusa* differs from known Scoto-Irish species, e.g. *C. bilobata* Reed, *C. perrugata* (Reed), *C. portlocki* Mitchell, *C. sulcata* Williams and *C. tenuicincta* (M'Coy), in numerous respects particularly its transverse outline and fine dorsal septa.

Order **PENTAMERIDA** Schuchert & Cooper, 1931

Suborder **SYNTROPHIIDINA** Ulrich & Cooper, 1936

Superfamily **PORAMBONITACEA** Davidson, 1853

Family **PORAMBONITIDAE** Davidson, 1853

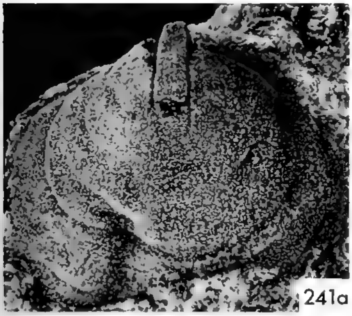
Genus ***PORAMBONITES*** Pander, 1850

Porambonites sp.
(Figs 241–242)

Description. *Porambonites* with large plicate pedicle valve with subpentagonal outline, 84% as long as wide and 25% as deep as long with ventral sulcus beginning in anterior third of valve; exterior ornament poorly preserved but multicostellate with costellae numbering 3–4 per mm on the anterolateral part of the valve; strong, irregularly spaced concentric growth lines also characterize the anterior parts of the valve; interarea unknown; subparallel dental plates supporting very small teeth arise directly from valve floor and extend anteriorly for about one-third of valve length; brachial valve unknown.

Dimensions. Internal and external moulds of p.v. BB 92464, length 16 mm, width 19 mm.

Horizon and locality. BB 92464–5 are from the sandy ashes at top of Main Volcanic Series in Howey Brook ('Main Feeder') section, 4 km east of Howey, outcrop on top of small hill on north side of brook (SO 0925 5915).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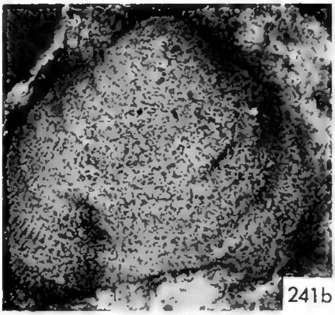
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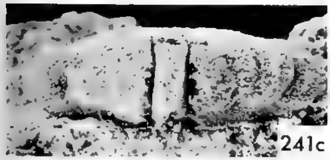
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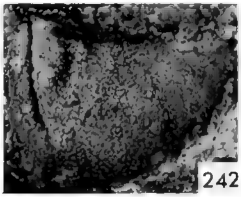
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Figs 241–242 *Porambonites* sp. Figs 241a–c, BB 92464, a, ventral view of internal mould, b, latex cast of external mould and c, posterior view of a pedicle valve, all × 2·5; Fig. 242, BB 92465, internal mould of posterolateral fragment of a pedicle valve × 4; both from Llanvirn sandstones at Howey Brook, Llandrindod.

Figs 243–244 *Parastrophinella parva* MacGregor. Fig. 243, BB 92282, internal mould of a pedicle valve × 8, from Lower Llandeilo beds, Ffairfach. Fig. 244, BB 92466, internal mould of a pedicle valve × 6, from Llanvirn sandstones, Howey Brook, Llandrindod.

Fig. 245 *Parastrophinella* cf. *musculosa* Williams. GSM 10291, internal mould of a brachial valve × 8, from Llandeilo Beds, Llandeilo.

DISCUSSION. This is the first record of *Porambonites* in the Ordovician of the Anglo-Welsh region. Until more material is available to assess its variability, the taxonomic relationships of this form to known species from Scotland, Ireland and Scandinavia cannot be determined. The material also represents the earliest recorded occurrence of the genus in the Ordovician of Britain.

Family **PARASTROPHINIDAE** Ulrich & Cooper, 1938

Genus ***PARASTROPHINELLA*** Schuchert & Cooper, 1951

Parastrophinella parva MacGregor

(Figs 243–244)

1961 *Parastrophinella parva* MacGregor : 197; pl. 22, figs 5–10.

DESCRIPTION. Small, biconvex, subtriangular *Parastrophinella* with pedicle valve 83% as wide as long and 25% as deep as long, characterized by multiplicate anterior commissure composed of a median and two lateral rounded plications arising in the anterior half of the valve; valve surface almost smooth except for coarse concentric growth lines close to anterior commissure; interior dominated by spondylium extending forward for about one-quarter of valve length and supported anteriorly by a median septum; ventral interarea unknown; brachial valve unknown.

DIMENSIONS. Internal and external moulds of p.v. BB 92466, length 6·5 mm, width 5·4 mm.

HORIZONS AND LOCALITIES. BB 92466 from sandy ashes at top of Main Volcanic Series in the Howey Brook ('Main Feeder') section, 4 km east of Howey, outcrop on top of small hill on north side of brook (SO 0925 5915). BB 92282 from Lower Llandeilo Flags exposed in small quarry on north side (embankment) of Ffairfach railway cutting, Ffairfach, Llandeilo (SN 6376 2105).

DISCUSSION. Moulds of the pedicle valves of *Parastrophinella* have been collected from two different horizons in the Builth and Llandeilo successions. Both compare closely with *P. parva* MacGregor in all preserved morphological features. *P. parva* is fundamentally different from the three larger Anglo-Welsh *Parastrophinella* species hitherto known, *P. costata* MacGregor, *P. musculosa* Williams and *P. brenchleyi* Lockley (1980), which all bear an average of at least twelve costae. We therefore consider that ultimately *P. parva* MacGregor may be better accommodated in a separate genus.

Parastrophinella cf. ***musculosa*** Williams

(Fig. 245)

cf. 1974 *Parastrophinella* musculosa Williams : 151; pl. 28, figs 9–13, 17.

A single internal mould of a brachial valve (GSM 10291), labelled as *Camerella* (?) sp. from the 'Lower ? Llandeilo' of an unknown locality in the Llandeilo region, closely resembles *P. musculosa* Williams. The specimen is 4 mm long, 5 mm wide and about 1·4 mm deep with an incipient fold, a convex transverse profile characterized by steep lateral slopes and a convex longitudinal profile becoming anteriorly geniculate; the ornament consists of 14 slightly rounded delayed costae. The umbonal region bears the faint impression of a pair of medially situated, elongate, septalial outer plates which extend forward for at least one-quarter of valve length. *P. musculosa* itself was originally described from the Spy Wood Grit (Costonian) of Shropshire (Williams 1974).

Order **RHYNCHONELLIDA** Kuhn, 1949

Superfamily **RHYNCHONELLACEA** Gray, 1849

Family **TRIGONIRHYNCHIIDAE** McLaren, 1965

Genus ***ROSTRICELLULA*** Ulrich & Cooper, 1942

Rostricellula triangularis Williams, emended
(Figs 245–263)

1949 *Rostricellula triangularis* Williams : 235; pl. 11, figs 15–18.

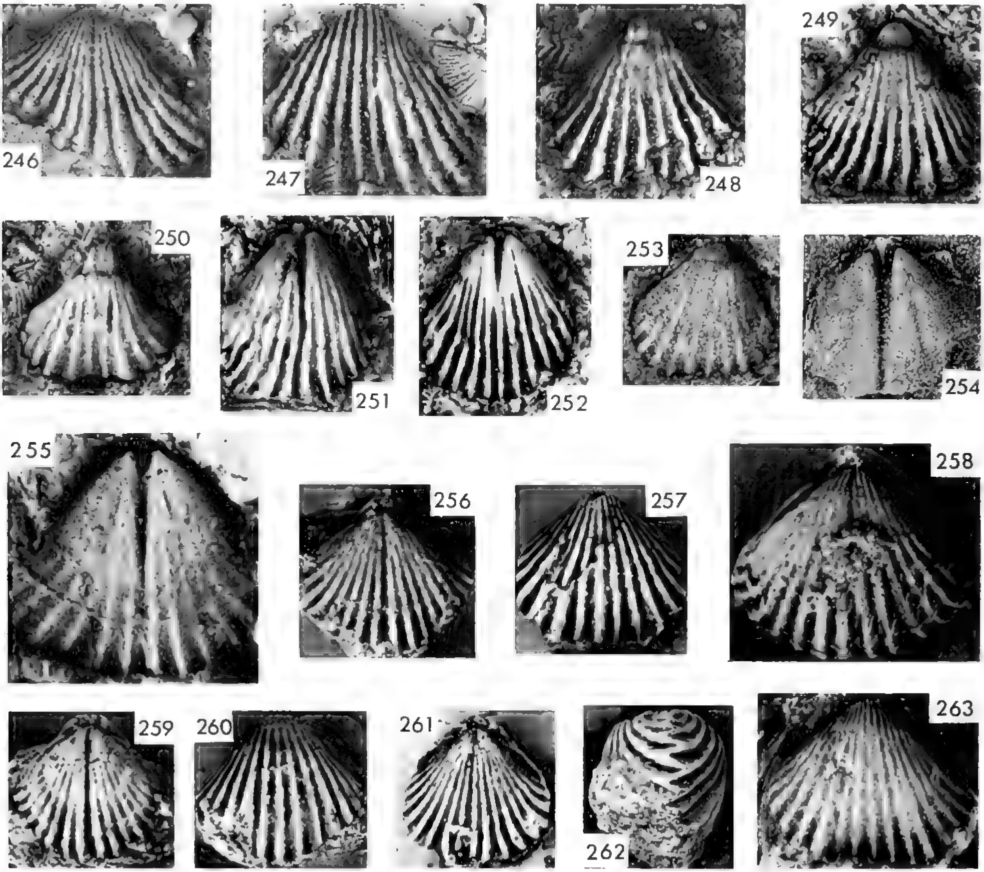
DIAGNOSIS. Biconvex, plicate, costate *Rostricellula* with triangular outline and pedicle valve averaging 89% as long as wide; dental plates averaging 25% as long as valve and enclosing compound ventral muscle scar; wavelength of costae averaging about 0·6 mm at 5 mm anteromedially of the dorsal umbo.

DESCRIPTION. Biconvex to dorsibiconvex, uniplicate, globular *Rostricellula* with triangular outline and maximum width in anterior half of valve; broad ventral sulcus complemented by dorsal fold; pedicle valve averaging 89% as long as wide (e.g. 13 valves from Coed Duon: $\bar{l}$ mm (var l) 5·30 (1·037), $\overline{w}$ mm (var w) 5·97 (1·436), r 0·909) and 32% as deep as long (e.g. 10 valves from Coed Duon : $\bar{l}$ mm (var l) 5·60 (0·467), $\overline{th}$ (var th) 1·81 (0·148), r 0·652), with brachial valve 82% as long as wide (e.g. 10 valves from Coed Duon : $\bar{l}$ mm (var l) 4·91 (0·605), $\overline{w}$ mm (var w) 5·98 (0·877), r 0·784) and 37% as deep as long (e.g. 10 valves from Coed Duon : $\bar{l}$ mm (var l) 4·91 (0·605), $\overline{th}$ (var th) 1·81 (·329), r 0·853); slightly rostrate with apical angle of about 90° and a slightly elongated pedicle foramen, palintropes very depressed; exterior ornamented by an even number of dorsal primary costae, numbering 16 and 18 respectively in 6 and 5 brachial valves between 4 and 7 mm in length, complementary ventral costae uneven in number; ventral sulcus broad, containing 3 costae corresponding to 4 on the dorsal fold, which are divided medially by a relatively wide spacing between the two inner costae, averaging 0·7 mm at 5 mm anteromedially of the umbo in 7 valves compared with an average spacing of 0·6 mm for other anteromedian costae.

Ventral interior with small teeth supported by slightly divergent dental plates extending anteriorly for an average of 25% of the length of the valve (e.g. 25 valves from Bryntowy : $\bar{l}$ mm (var l) 5·62 (0·893), $\overline{dl}$ (var dl) 1·40 (0·111), r 0·471) and 82% of their maximum lateral extension (e.g. same 25 valves: $\bar{l}$ mm (var l) 1·40 (0·111), $\overline{w}$ mm (var w) 1·70 (0·144), r 0·665) to enclose a compound posteriorly-situated muscle field which is sporadically differentiated to show a median adductor impression, between one-third and half as wide as field, flanked by narrower elongate diductor scars; whole scar complex extends forward for an average of 23% of valve length (e.g. 16 valves from Bryntowy : $\bar{l}$ mm (var l) 5·66 (0·916), $\overline{lsc}$ (var lsc) 1·33 (0·155), r 0·648) and for 86% of its maximum width (e.g. same 16 valves: $\bar{l}$ mm (var l) 1·33 (0·155), $\overline{w}$ mm (var w) 1·54 (0·141), r 0·815), which occurs at the transverse ridge marking the anterior edge of the scar; faint transverse muscle tracks sporadically developed.

Hinge plate of dorsal interior small, divided by septalium which is buttressed by median ridge extending forward for at least half of valve length and often continuing to commissure by passing anteriorly into median internal costa corresponding to conspicuous external median groove between submedian costae; crural bases short, averaging 14% as long as valve (e.g. 16 valves from Bryntowy : $\bar{l}$ mm (var l) 4·13 (1·804), $\overline{lc}$ (var lc) 0·59 (0·018), r 0·749) and 55% as long as their maximum width; muscle scars faint, sporadically developed as elongate posteriorly-tapering impressions extending, on either side of the median ridge, from the posterior adductor pits towards the anterior half of the valve.

HORIZONS AND LOCALITIES. BB 94226–32 (topotypes) from Upper Llanvirn ashes exposed in stream 200 m NW of Bryntowy Farm, 2 km SSW of Llangadog, Dyfed (SN 695262); BB 92478–89 from loose calcareous blocks from the Flags and Grits Formation of the Ffairfach Group exposed at Coed Duon, 3 km south of Llangadog (SN 709256); BB 92490 from underlying Rhyolitic Grits and Conglomerates at the same locality; BB 92491 from the calcareous upper part of the Flags and Grits Formation of the Ffairfach Group in the type section (SN 628211); BB 92467–9 from the Rhyolitic Conglomerate Member of the Ffairfach Group at the type section (SN 628211); BB 92281 from probable Upper Llanvirn sandstones exposed in the Old Pantau quarry, 1·5 km east of Llandeilo (SN 644224).



Figs 246–263 *Rostricellula triangularis* Williams. Figs 246, 247, paralectotypes GSM 75232b, a, latex casts of the external moulds of brachial valve and of a pedicle valve, both × 4; Figs 248–250, topotypes BB 94227, 94226 and 94229 respectively, internal moulds of pedicle valves, all × 4; Figs 251–252, topotypes BB 94231 and 94228 respectively, internal moulds of brachial valves, both × 4; all from Llanvirn ashes, Bryntowy, Bethlehem. Fig. 253, BB 92491, internal mould of a pedicle valve × 6; Fig. 254, BB 92468, internal mould of the posterior part of a brachial valve × 6; Fig. 255, BB 92467, internal mould of a brachial valve × 8; all from the Rhyolitic Conglomerates, Ffairfach Group, type section. Fig. 256, BB 92489, dorsal view of a complete specimen × 4; Fig. 257, BB 92486, ventral view of a complete specimen × 4; Figs 258–259, BB 92483 and 92485 respectively, dorsal views of complete specimens × 6 and × 4; Fig. 260, BB 92487, ventral view of a complete specimen × 4; Fig. 261, BB 92480, dorsal view of a complete specimen × 4; Fig. 262, BB 92481, anterolateral view of a complete specimen × 4; Fig. 263, BB 92478, exterior of a pedicle valve × 4; all from calcareous Llanvirn beds, Coed Duon, Llangadog.

FIGURED MATERIAL		length	width
External mould of p.v.	GSM 75232a	(8·0)	(10·0)
External mould of b.v.	GSM 75232b	(6·0)	(8·0)
Exterior of p.v.	BB 92478	6·0	7·5
Complete specimen	BB 92481	6·0	7·0
,,	BB 92483	5·5	6·5
,,	BB 92480	5·4	5·4
,,	BB 92485	5·5	5·5
,,	BB 92486	5·5	6·8
,,	BB 92487	5·2	6·2
,,	BB 92489	4·6	5·2
Internal mould of p.v.	BB 92491	3·4	3·8
,,	BB 94227	(6·6)	(6·5)
,,	BB 94229	5·4	6·0
,,	BB 94226	6·5	6·3
Internal mould of b.v.	BB 92467	4·5	5·0
,,	BB 94231	6·5	6·0
,,	BB 94228	6·3	5·9

DISCUSSION. A comparison between the Bryntowy topotypes, preserved exclusively as internal and external moulds, and the smaller number of complete shells from Coed Duon suggests that the latter sample consists of less elongate individuals. However, a large proportion of the topotypes are broken or slightly distorted. The parameters of external shape derived from the smaller Coed Duon sample therefore better define the proportions of *R. triangularis,* while the topotypes provide information on the variability of the internal morphology.

Since *R. triangularis* was first described, the species has been recorded in Upper Llandeilo rocks of the Berwyn Hills (McGregor 1961 : 201) and the related species *R. sparsa* Williams has been described (Williams 1963 : 467; 1974 : 153) from Caradoc rocks of the Bala and Shelve areas. It is evident, from the description given by MacGregor and a re-examination of his material, that the Berwyn specimens resemble *R. sparsa* both in outline and density of costae. We therefore doubt whether *R. triangularis* occurs outside the Llandeilo area.

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The fossil alga *Girvanella* Nicholson & Etheridge

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Contents

Synopsis

This group of microfossils is reviewed and compared with its modern counterpart, the Cyanophyta. *Girvanella* consists of carbonate tubes, believed to have formed in and around the sheaths of filamentous blue-green algae. The characteristics of the genus are discussed in terms of those of the living forms, and an emended generic diagnosis is offered to take account of modern knowledge. The ultrastructure of the fossil consists of equidimensional and prismatic grains in the micrite to fine spar range, with the prisms arranged perpendicularly to the tube axis. This is similar to *Rothpletzella* Wood, from preliminary studies. Specific subdivision of *Girvanella* is considered briefly, and a list of the species is provided with full references. Suggestions for an approach to revision of the specific systematics are made, with emphasis on sampling along single horizons to allow clinal variation to be studied.

Introduction

The genus *Girvanella* was defined by Nicholson & Etheridge (1878 : 23) as containing certain calcareous tubular fossils. It was first described from the Stinchar Limestone of south Scotland, which is of Caradocian (Middle Ordovician) age. The biological source of the fossil was the subject of some debate during the latter part of the nineteenth century (*cf.* Green 1959 : 41). It was first described as a foraminifer, but was then transferred to the Cyanophyta *sensu* Smith 1938. Attempts have been made to move it to the Chlorophyta *sensu* Smith 1938, for example by J. H. Johnson (1961 : 194), and recently some related forms have been described as members of the Rhodophyta *sensu* Smith 1938 by Korde (1973 : 212).

The Porostromata of Pia (1927 : 37), the group to which most workers believe *Girvanella* belongs, is itself poorly understood. Pia's definition is brief, and no general study of the organisms contained in it has been published. The group was erected to hold fossils of tubular construction, which resemble modern calcified filamentous cyanophytes. Unfortunately, little is known about these plants either, except that they do not seem to occur in the marine environments to which most *Girvanella* species are confined.

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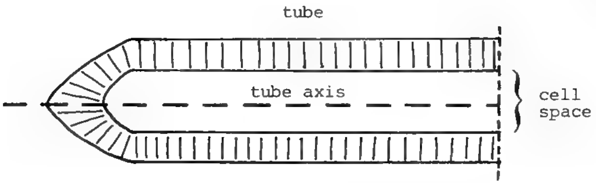
(a) Longitudinal section.



(b) Cross and oblique sections.

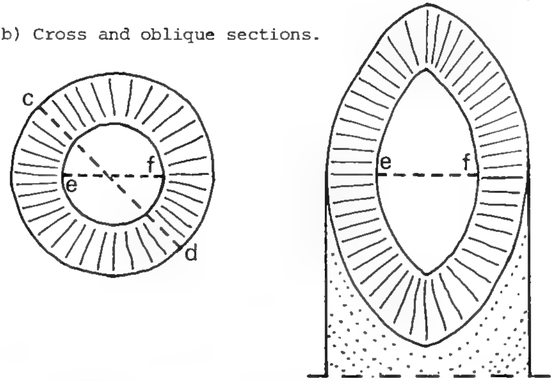


Fig. 1 Generalized diagrams of *Girvanella*, with terminology. ef – true internal diameter. cd – external diameter.

Girvanellids appear to be simple fossils, with few features suitable for use in systematic subdivision. This has led to the introduction of a great number of species, with overlapping and subjectively-defined characteristics. The classification has become unwieldy and confusing, and does not seem in any real way to reflect the biology of the original organisms.

The intention of this paper is to review the generic concept *Girvanella*, to present an analysis of a sample of the fossil taken from the Stinchar Limestone, and to attempt a more representative generic diagnosis and description. The relationship of the genus to modern cyanophytes will be considered, and its specific subdivision discussed. Morphological terms used are as follows. Filament: the tube and cell space. Growth: a group of filaments which seem to have formed an original nodule, cluster or sheet. Density: percentage volume of filaments in a growth. Others are illustrated in Fig. 1.

The systematic criteria of Pia (1927) are used for the higher taxa of fossil algae, and Tilden (1910) has been used as a source for the Recent taxa.

The term 'carbonate tube' is employed for the fossil structures themselves. It has no biological implications, and is therefore preferable to the often-used 'wall' or 'sheath'. The former could be confused with 'cell wall', which has little relation to the carbonate tube, while a cyanophyte sheath is a mucilaginous, extracellular part of the cell envelope and is rarely preserved.

Sources of material and methods of study

The Stinchar Limestone rests unconformably on the Ballantrae ophiolite sequence, with a zone of serpentinite débris at the contact (Table 1). Most of the Limestone formation is exposed at Aldons Quarry (nat. grid ref. NX 197896), south of Girvan, Ayrshire (*cf.* Williams 1962). *Girvanella* was first described from samples collected at another quarry about 6 km NE of Aldons, Tormitchell (NX 235944) (Nicholson & Etheridge 1978). Aldons Quarry was preferred to Tormitchell because the limestone sequence is relatively undisturbed, and because it is not at present (1980) being quarried.

Samples were collected at intervals of a maximum of 0·30 m or less from the top of the ophiolites, through the entire limestone sequence. A total of 34 thin sections were cut from these samples, as shown on Table 1, and all were studied for mineralogy and general palaeontology. Five samples were selected for detailed study of *Girvanella* with a binocular

Table 1 The Stinchar Limestone at Aldons Quarry.

Field characteristics	level (cm) of base	level (cm) of thin sections	% *Girvanella*
Benan Conglomerate (above thrust)	variable	–	–
0 to 10 cm mylonite		–	–
micrite with crystal elongation lineation, some spar lenses	2000	–	–
no nodules, some neomorphic spar		–	–
		1658	low
nodular zone at base	1620		
fewer nodules	1510	–	–
friable micrite with many nodules		–	–
	960		
		931	–
		833*	low
slumped, with poor and very undulose bedding; nodular with micritic matrix.		750	high
	490		
grey micrite with poor bedding	450	461, 470*	high
banding of fine and coarse layers, laminated, fine serpentinite debris in micrite		439, 434, 417	low
		400, 388	low
	300	338	
conglomeratic, serpentinite pebbles in micritic matrix; 1 m-thick bedding.		230, 221, 195*	
		180*, 165*, 155*	
	155		appears
(1 m gap)	57	–	
soft green silts	0	(5 thin sections)	none
Ballantrae Ophiolites			

*section used in population study.

Table 2 A list of the species of *Girvanella*.

Species	Key to Fig. 7	Original generic assignment	Author	Approximate age
involuntans		(*Nicholsonia*)	Korde 1973	Upper Proterozoic
antiqua			Dawson 1896	Lower Cambrian
antiqua	1		Maslov 1937	Lower Cambrian
bayankolica		(*Batinevia*)	Korde 1973	Lower Cambrian
composita		(*Nicholsonia*)	Korde 1973	Lower Cambrian
decipiens		(*Fistulella*)	Korde 1973	Lower Cambrian
glomerata		(*Nicholsonia*)	Korde 1973	Lower Cambrian
grandis		(*Nicholsonia*)	Korde 1973	Lower Cambrian
lineata		(*Botominella*)	Reitlinger 1959	Lower Cambrian
manchurica	2		Yabe & Osaki 1930	Lower Cambrian
ornata		(*Kenella*)	Korde 1973	Lower Cambrian
ramosa		(*Batinevia*)	Korde 1966	Lower Cambrian
sanashtykgolica		(*Fistulella*)	Korde 1973	Lower Cambrian
sibirica	3		Maslov 1956	Lower Cambrian
mexicana	4		J. H. Johnson 1952	Lower Cambrian
incrustans	50	(*Siphonema*)	Bornemann 1886	Cambrian
		(range extends from Cambrian to Silurian, and Jurassic).		
grandis	5		Banks & Johnson 1957	Llanvirn to Llandeilo
atratus		(*Strephochetus*)	Seely 1902	Llanvirn to Llandeilo
brainierdi		(*Strephochetus*)	Seely 1902	Llanvirn to Llandeilo
prunus		(*Strephochetus*)	Seely 1902	Llanvirn to Llandeilo
ocellatus		(*Strephochetus*)	Seely 1885	Llanvirn to Llandeilo
richmondense		(*Stromatocerium*)	Miller 1882	Llanvirn to Llandeilo
tasmaniensis	6		Banks & Johnson 1957	Llanvirn to Llandeilo
ambigua	7		Luchinina, *in* Nikitin *et al.* 1974	Middle Ordovician
convoluta	8		Luchinina, *in* Nikitin *et al.* 1974	Middle Ordovician
problematica	9		Nicholson & Etheridge 1878	Caradocian
problematica	10		(Nich. & Eth.) Wood 1957	Caradocian
problematica lumbricalis	11		Høeg 1932	Caradocian
problematica moniliformis	12		Høeg 1932	Caradocian
(*problematica spiralis*	13: this form has been rejected)		Lewis 1942	Caradocian

problematica typica	14		Høeg 1932	Caradocian
incrustans	50	(*Sphaerocodium*)	Bornemann 1886	Ordovician
siluriana	15		Parks 1933	Up. Llandoverian to Wenlockian
bornemanni		(*Sphaerocodium*)	(Roth.) Dricot & Tsien 1977	Wenlockian
conferta	16		Chapman 1907	Wenlockian
effusa	17		H. M. Johnson 1966	Wenlockian
fragila	18		H. M. Johnson 1966	Wenlockian
media	19		H. M. Johnson 1966	Wenlockian
prolixa	20		H. M. Johnson 1966	Wenlockian
pusilla	21		H. M. Johnson 1966	Wenlockian
ramosa	22		H. M. Johnson 1966	Wenlockian
sarmenta	23		H. M. Johnson 1966	Wenlockian
wetheredii	24		Chapman 1907	Wenlockian
incompta	25		H. M. Johnson 1966	Wenlockian to Lower Ludlovian
incrustans	50	(*Siphonema*)	Bornemann 1886	Silurian
maslovi			Shuĭskii 1973	Lower Devonian
ducii chuvashovi	26		Bilan & Golonka 1973	Famenian
		(range extends from Devonian to Permian)		
amplefurcata	27		Pia 1932	Upper Devonian
zimmermanni		(*Sphaerocodium*)	(Roth.) Dricot & Tsien 1977	Upper Devonian
ottonosia			(Pia) Wood 1963	Lower Tournaisian
ottonosia	28		Pia 1937	Tournaisian
stamenia			Garwood 1931	Upper Tournaisian
stamenia	29		(Garwood) Wood 1963	Upper Tournaisian
nicholsoni	30		(Weth.) Wood 1941	Tournaisian to Lower Visean
densa	31		Conil & Lys 1964	Lower to Middle Visean
distans	32		Conil & Lys 1964	Lower to Middle Visean
ducii	33		Wethered 1890	Upper Visean
ducii			(Weth.) Wood 1963	Upper Visean
incrustans			Wethered 1890	Upper Visean
wetheredii			(Chapman) Wood 1963	Upper Visean
ducii kasakiensis	34		Maslov 1949	Lower Carboniferous
liebusi	35		Paul 1937	Lower Carboniferous

Table 2, continued

Species	Key to Fig. 7	Original generic assignment	Author	Approximate age
silesiaca	36		Paul 1937	Lower Carboniferous
maplewoodensis	37		J. H. Johnson 1946*a*	Namurian to Westphalian
moorei	38		J. H. Johnson 1946*b*	Westphalian
magna	39		J. H. Johnson 1946*b*	Upper Westphalian
ducii chuvashovi	26		Bilan & Golonka 1973	Upper Carboniferous
sinensis	40		Yabe 1912	Upper Carboniferous
johnsoni	41		Kulik 1973	Carboniferous
ducii chuvashovi	26		Bilan & Golonka 1973	Lower Permian
grabaui	42		Paul 1938	Lower Permian
subparallela			Flügel & Flügel-Kahler 1980	Lower Permian
catenoides	43		Homan 1972	Lower to Middle Permian
permica	44		Pia 1937	Middle Permian
texana	45		J. H. Johnson 1950	Permian
incrustans lucii	46		Wethered 1890	Bathonian
pisolitica	47		Wethered 1889	Bathonian
minuta	48		Wethered 1890	Bathonian
intermedia	49		Wethered 1890	Bathonian
incrustans	50	(*Siphonema*)	Bornemann 1886	Jurassic
jurassica		(*Symploca jurassica* Frém. & Dan.; *G. minuta* Weth.)	Dragastan 1975	Jurassic
tosaensis	51		Yabe & Toyama 1928	Lower Mesozoic
minima	52		Romanes 1916	Albian
palustris	53		Colin & Vachard 1977	Middle Cretaceous

Güvenç (1965) describes the following species as part of a Ph.D. thesis: *G. magna goksuensis*, Upper Visean. *G. magna yatani*, Upper Carboniferous. *G. kordei*, Upper Carboniferous to Lower Permian. *G. embergeri*, Lower Permian.

Gollesstaneh has found several species dating from the Cambrian, in Iranian deposits (personal communication), but the descriptions are not published as yet. *G. shirazica* (Liassic to Oxfordian) is mentioned by Gollesstaneh (1974), but it has not been possible to obtain a diagnosis of the species.

microscope. Acetate peels were also tried, but were found unsuitable because of the fine grain-size of the limestone, and because of certain artefacts inherent in their use. Registered numbers given with the halftone illustrations (Figs 2, 3, 5) are those of the British Museum (Natural History), Dept. of Palaeontology.

Measurements were made with an eyepiece graticule. This method gives results to about the same degree of accuracy as Wood's (1957 : 24) technique of measuring from photographic prints. The correction of errors introduced by photographic processes is cancelled by the small scale of the graticule.

The number of tubes present in growths varied a great deal, as did the degree of preservation. Frequently the boundaries of a tube were obscured by neomorphism or by contact with other tubes. It was necessary to measure both diameters for each tube since comparisons of the two diameters were needed. For this reason, only tubes with both inner and outer boundaries clearly apparent were measured, and other tubes were ignored. All the tubes, up to a total of ten, with both boundaries present were measured in each growth. As a result some growths are represented by measurements on only one or two tubes, but no justification could be found for omitting them. In any case measurements were analysed by considering the entire sample, rather than individual growths. Ten was chosen as the upper limit because most growths had only ten or fewer suitable tubes. Where two distinct size-ranges occurred in the same growth, ten tubes were measured from each.

A plane section cut through tubes arranged more or less randomly will contain a range of sections of tubes from cross to longitudinal. Perfect cross sections are circular, because of the cylindrical shape of the tubes, but oblique sections are elliptical (Fig. 1). It can be shown that the smallest diameter of such an oblique section is a true diameter of the tube. All measurements have therefore been made on this smallest diameter. The tube thickness may have irregularities, so that estimation was sometimes necessary for measurements of the external diameter. However, it was possible in most cases to measure the two diameters along the same line.

For scanning electron microscopy, rock samples were prepared by smoothing rock slices on carborundum powders and polishing with a series of diamond laps, finishing with a 1 μm lap. This was followed by etching for 30 secs in 1 vol. % HCl. The slices were then attached to specimen stubs with a conducting paint, Durofix or double-sided sellotape, and were coated with gold-palladium in a vacuum-evaporator.

Samples of Recent algae were obtained from a variety of sources, either by personal collection or through the courtesy of other workers. These samples were stored at 3° C, in 0·8% glutaraldehyde buffered to pH 7·4, and were prepared for electron microscopy as follows:

1. Immersion fixation in 2·5% glutaraldehyde, buffered to pH 7·4 with KH_2PO_4 and K_2HPO_4, for two hours.
2. Washing in several changes of buffer.
3. Immersion in 1% OsO_4, in buffer, for 30 minutes.
4. Gradual transfer to water-free acetone.
5. Critical point drying.

The scanning electron microscopes (S.E.M.) used were Cambridge S2A models, operated at 18 KV at lower magnifications and at 28 KV to 30 KV at magnifications of 5000× or more. The final aperture diameters were 200 μm for lower and 140 μm for higher magnifications. Stubs were held at 30° to the electron beam to reduce the effects of charging, with a working distance of about 10 mm.

Historical review

Species of *Girvanella* have been described, under various generic names, from rocks of Upper Proterozoic (Korde 1973 : 212) to Middle Cretaceous (Colin & Vachard 1977) age. A list of species is given in Table 2.

Girvanella was first described by Nicholson & Etheridge (1878 : 23) as an agglutinating foraminiferan related to *Rhizammina algaeformis* Brady. They gave the specific name *problematica* to their fossil, for convenience, and provided the following diagnosis:

Generic characteristics: 'Microscopic tubuli, with arenaceous or calcareous (?) walls, flexuous or contorted, circular in section, forming loosely compacted masses. The tubes apparently simple cylinders, without perforations in their sides, and destitute of internal partitions or other structures of a similar kind'.

Specific characteristics: 'Tubes from 1-600th to 1-700th of an inch in diameter, not observed to taper, twisted together in loosely reticulate or vermiculate aggregations of a rounded or irregular shape, which seem to be mostly from 1-20th to 1-10th of an inch across'.

Nicholson (1888 : 22) gave a further description of the organism, but did not redefine it. Apart from assigning a different range of diameters to the genotype (16 μm to 40 μm) he added nothing to the original publication, and still believed the organism to have been a foraminiferan. This view was held by some workers for a long time, Rhumbler (1895) proposing a subfamily Girvanellinae of the Rhabdamminidae Rhumbler to contain the genus.

Seely (1885) described a genus of calcareous sponge, *Strephochetus,* from Middle Ordovician limestones in Vermont, and in 1886 Bornemann described *Siphonema* from Sardinian deposits of the same age. Bornemann compared his material with epilithic cyanophytes, and considered that *Siphonema* was related to them. Hinde (1887 : 227) recognized *Strephochetus* and *Siphonema* to be synonyms of *Girvanella,* but disagreed with both suggested affinities.

Rothpletz (1891 : 301) assigned *Girvanella* to the Codiaceae ((Trevis) Zanardini 1843) because of the dichotomous branching shown by some species, and its similarity to *Sphaerocodium* Rothpletz 1891. The latter has been assigned to the Siphonae, a taxon containing both the Codiaceae and Dasycladaceae (Endlicher) Cramer 1888. This assignment to the green algae was accepted by Brown (1894 : 203).

Wethered (1893 : 246) accepted that some forms of *Girvanella* appeared to have been plants, and might have been calcareous algae. In the discussion of this paper (p. 248), Reid suggested that the calcareous tubes typical of *Girvanella* were the result of inorganic encrustations on filamentous plants. Seward (1898 : 125) and Pollock (1918 : 255) compared *Girvanella* to the calcified sheaths of some Recent Cyanophyta, thus confirming Bornemann's (1886) opinion.

Pia (1927 : 37) placed *Girvanella* and similar genera in an artificial group, the Porostromata. This was accepted for some years. In 1935 Frémy & Dangeard proposed that the Jurassic species *G. minuta* Wethered should be renamed *Symploca jurassica*, because of its resemblance to the Recent species *S. hydnoides* Kutz. However, Johnson & Høeg (1961 : 54) expressed doubts about the assignment of *Girvanella* to the Cyanophyta, and suggested that it was a member of the Chlorophycophyta. This proposal seems to have been based on his own removal of many of the Porostromata to the Codiaceae, and also on the belief that Frémy & Dangeard had described *G. minuta* as a chlorophyte. Riding (1975 : 174) has restored these genera to the Porostromata. Dricot & Tsien (1977), in a discussion of the validity of the genus *Rothpletzella* Wood 1948, have pointed out the partial synonomy between *Girvanella* and *Sphaerocodium* Rothpletz 1891. Several of the species of the latter were therefore assigned to *Girvanella* by these authors, in part or completely (Table 2, p. 83).

Korde (1973 : 212) has mentioned several Upper Proterozoic and Lower Cambrian genera which appear to be girvanellids. The genera involved are *Nicholsonia* Korde, *Fistulella* Korde, *Botominella* Reitlinger (1959), *Kenella* Korde, and *Batinevia* Korde (1966). Mamet & Roux (1975) have commented on the resemblance between the last three and *Girvanella.* Korde (1973) proposes a new class of Rhodophyta, the Protobangiophyceae Korde, to contain these genera. But some of the descriptions of the protobangiophycean genera seem to bear little resemblance to the figures provided, and the reasons for the separation of these forms are not expressed in such a way that they can be evaluated.

Nicholsonia in particular seems to have been interpreted on the understanding that the original organism was a member of the Rhodophyta. Structures which are absent from the fossil are said to have been uncalcified. Korde's descriptions are not included in the systematic analysis below, as it is difficult to reconcile her accounts with other descriptions.

Riding (1977) has related the impregnated sheath of *Plectonema gloeophilum* Borzi, a modern species with rare branching, to *Girvanella*, and extends the range of the fossil to Recent times on this basis. However, the branching habit of *Plectonema* does not agree with the 'simple cylinders' definition of *Girvanella* (Nicholson & Etheridge 1878 : 23). The ultra-structures of the carbonate are also rather different, that of *P. gloeophilum* consisting of calcite needles in various orientations. *Girvanella* tubes comprise equidimensional micrite and radially-arranged needles, the structure having greater regularity and much lower porosity (Fig. 2).

The genus *Girvanella*

Further descriptive remarks can now be added to the original definition of the genus (Nicholson & Etheridge 1878). Growths vary in size from single tubes to clusters more than a centimetre across. Growths with many tubes may be almost circular in section, completely irregular, or in some intermediate form, and may have a core body such as a detrital particle or, more commonly, another fossil. The boundaries between growth and rock matrix may be distinct, eroded, micritized, diffuse or neomorphosed. Often the matrix seems to have neomorphosed more easily than the carbonate tubes. Fig. 3 shows a range of growth habits from the Stinchar Limestone. In addition to the problems of defining the genus *Girvanella* some confusion has arisen in its subdivision. A list of species is given in Table 2, pp. 82–84, in which there are about 40 Lower Palaeozoic taxa. Only a few of these have diagnoses not contradicting the generic diagnosis, as shown in Table 3, and many have indistinguishable characteristics.

The holotype of *G. problematica* Nicholson & Etheridge, the type species of the genus, has been destroyed. Wood (1957 : 23) discovered this and designated a neotype for the species. However, although he did not emend the generic diagnosis of Nicholson & Etheridge (1878), he redescribed the type species in a way which differs from the original generic diagnosis. This anomaly means that *Girvanella* and its type species *problematica* are still defined according to Nicholson & Etheridge (1878). Wood's neotype is kept in the British Museum

Table 3 Lower Palaeozoic species ascribed to *Girvanella* with characteristics contradicting the original generic definition; brackets indicate observations made from figures.

Simple cylinders	Branching	*(atratus)* *(brainierdi)* *effusa* *fragila* *grandis*	*incompta* *media* *mexicana* *moniliformis* *ocellatus*	*problematica** *p. lumbricalis* *p. typica* *prolixa* *(prunus)*	*pusilla* *ramosa* *sarmenta* *sibirica* *tasmaniensis*
	Constrictions	*conferta*	*effusa*	*problematica*	*ramosa*
Loose packing	High density	*conferta* *convoluta* *(effusa)* *incompta*	*(manchurica)* *media* *ocellatus* *problematica**	*prolixa* *pusilla* *(ramosa)* *sarmenta*	*(siluriana)*
	Adherence	*effusa* *fragila*	*incompta* *media*	*prolixa* *pusilla*	*ramosa* *sarmenta*
Septation		*conferta*	*problematica**	*prolixa*	

*as emended by Wood (1957).

(Natural History) collection, registration number V 34566, and since it does in fact conform to the original generic diagnosis, it is accepted here as the neotype of *Girvanella*.

Considerable information has accumulated since 1878 about both *Girvanella* itself and the Cyanophyta. Nicholson & Etheridge's (1878) diagnosis needs to be re-examined and related to this new body of information. To facilitate this, the characteristics used to define the genus will be considered: (1) microscopic; (2) tubular; (3) arenaceous or calcareous; (4) sinuous; (5) circular in cross section; (6) low growth density; (7) simple cylinders; (8) imperforate; (9) no septa or other internal structures.

Of these, points 1, 2, and 8 have never been disputed. Most species have been described as circular (point 5), but J. H. Johnson (1950 : 61) gave *G. texana* as 'nearly circular'. Wood (1963 : 26) described irregular tubes, attributing them to *post mortem* collapse. No non-calcareous tubes have been reported (3), although some associations with iron oxide or pyrite have been published (H. M. Johnson 1966 : 51; Lewis 1942 : 52). Playford *et al.* (1976 : 558) noted that bacteria are more likely to be responsible for such relationships than the algae themselves. Silicified *Girvanella* has also been described (Lewis 1942 : 51), but this example was a secondary replacement.

The hollow nature of the tubes (2) has never been questioned, and Lewis (1942 : 52) gives evidence for it. However, both branching and constrictions (7) have been described by several authors (Table 3). The figures provided in these cases commonly show tubes which cross or bend out of the plane of section, leading to misinterpretation (*cf.* H. M. Johnson 1966 : pl. 12). Septate girvanellids (9) have also been described, but these reports are the result of observation of refraction across grain boundaries within the cell space (Wood 1957 : pl. 5). Fig. 2, opposite, illustrates the causes of apparent branching, constrictions and septa.

Many authors have described growths with close-packed, adherent tubes, although Nicholson & Etheridge (1878) describe the genus as being loosely-compacted. In fact a great variety of growth densities (defined here as the ratio of tube volume to matrix volume in a growth) occurs in many populations, and the value of density as a generic or specific characteristic needs reconsideration in the light of population studies. The same applies to tube sinuosity (4). Some examples demonstrating the variability of single populations are given in Fig. 3.

Girvanella and Recent cyanophytes

Some modern Cyanophyta will calcify under natural conditions, when an excess of calcium is present, although they will not do so readily in culture. Lewin (1962) and Golubić (1973) have given reviews of the subject, and Pentecost (1978) has conducted a detailed study of cyanophyte calcification.

It is usually said that cyanophytes calcify only in freshwater environments, although many fossils, supposedly calcified cyanophytes, are primarily marine in origin. Monty (1977) has discussed the matter in terms of stromatolites. Some Recent forms do calcify in regions where storms may cover them with sea water from time to time, and further research may find fully marine forms which calcify.

Almost the only thing which seems to be common to the environments in which cyanophytes calcify is the high calcium level. Some calcium is clearly necessary, but

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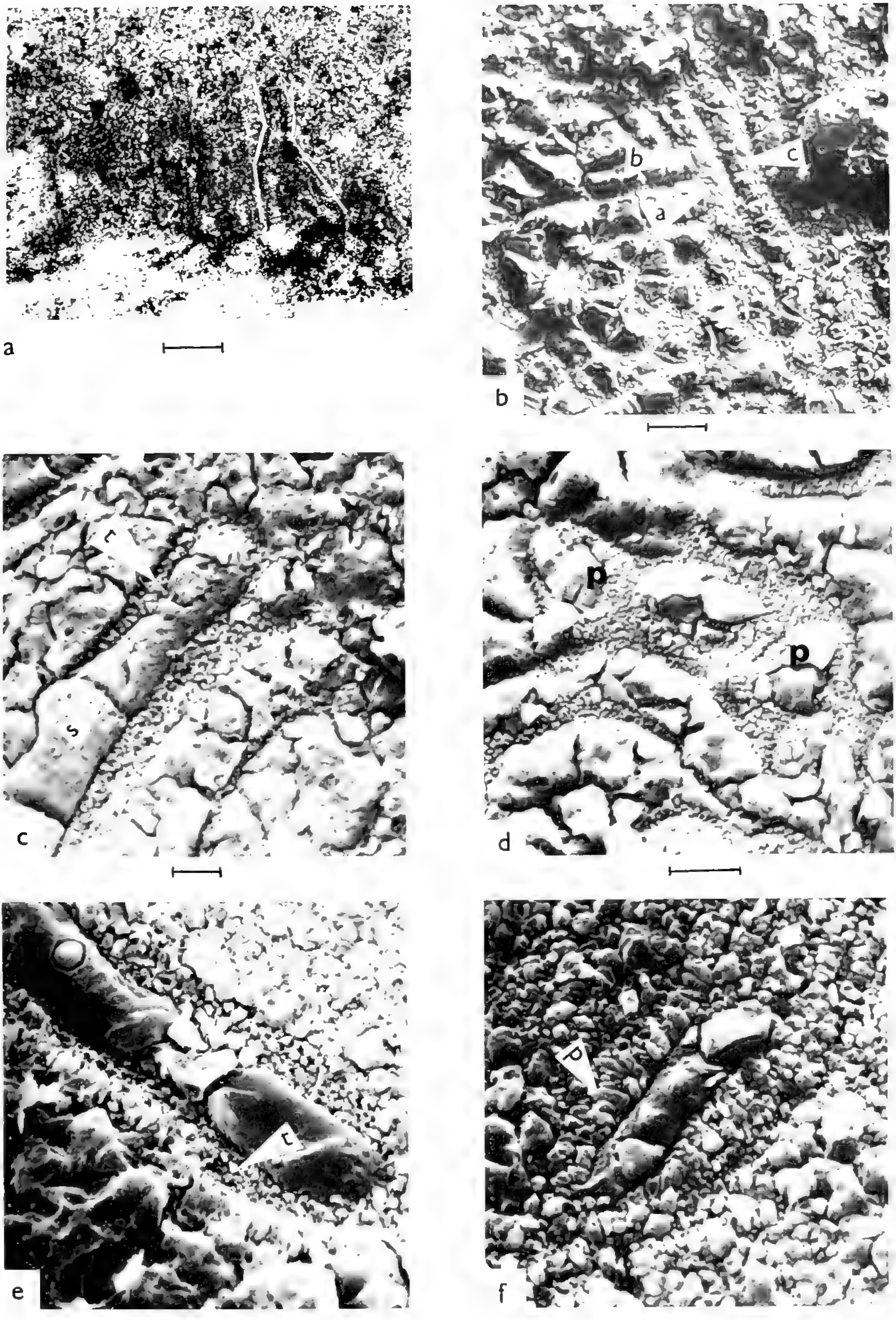
Fig. 2 Fine structure of *Girvanella* and *Rothpletzella*. (a), *Girvanella* with apparent branching. White lines mark tube directions. Bar = 7 µm. (V 60469). (b), *Girvanella* with apparent branching due to crossed tubes (SEM). Note the rounded ends of tubes a and b, against c. Bar = 10 µm. (V 60473). (c), apparent septa, marked s. The tube itself (t) comprises equidimensional micrite, but this is missing from the 'septa'. They are grain boundaries, lying across the tube axis. Bar = 5 µm. (V 60473). (d), tubes with a prismatic ultrastructure (p). Bar = 10 µm. (V 60473). (e), *Rothpletzella* with equidimensional micrite forming its tubes (t). Bar = 5 µm. (V 60103a). (f), *Rothpletzella* with radial prisms (p). Bar = 10 µm. (V 60103a).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blue-green algal deposits seem to occur only in waters which are saturated with it. Neither high light intensities nor warmth are essential, and water-flow rates vary considerably. These generalities apply to the group as a whole, however, and individual strains may be more exacting. This may be the cause of many of the difficulties met in laboratory studies of calcification.

It seems then, that the ecology of modern cyanophytes is of little help in the interpretation of fossil forms. That *Girvanella* had a wide ecological range implies only that several biologically distinct taxa were involved. The genus occurs in shallow-water marine limestones (from faunal evidence), and may be quite rare or may form 80% of the rock volume (Williams 1962 : 19). It is found with benthic faunas in calcareous muds or silts, and in reef environments. Often it is the only cyanophyte represented, but other porostromates may be present and calcified eucaryotes may also occur. Palaeocological evidence suggests growth in quiet or only moderately turbulent conditions, but such estimates are questionable. It is likely that uncalcified algal mats were present in the same environments, stabilizing sediments and preventing the development of current structures.

Modern cyanophytes may either impregnate or encrust their mucilaginous sheaths. Many organisms do both. The nature of the internal diameter of the carbonate tube depends on these differences. Distinguishing between them is therefore important: this matter is considered in more detail below. The carbonate itself is normally calcitic and low in magnesium, iron and strontium, although Monty & Hardie (1976 : 463) have described carbonates with 16 mole % Mg, formed in association with *Scytonema myochrous* (Dillwyn) Agardh. Modern cyanophyte carbonates are therefore stable in most cases, and are not subject to rapid diagenesis. However, since most modern calcifying blue-greens are freshwater organisms, comparisons with the predominantly marine *Girvanella* should be drawn with caution.

The fine structures of modern cyanophyte carbonates vary considerably, from the acicular type described by Gleason (1972 : 155) to the micritic textures figured by Schäfer & Stapf (1978 : fig. 4). Flajs (1977) describes the carbonates of three members of the Rivulariaceae as similar to those of *Chaetophora* (Chlorophyta). In these the filaments become encrusted with very fine calcite grains, which merge to form larger aggregates. Flajs believed all calcifying cyanophytes to follow this pattern. The close similarity between them and certain green algal carbonates, which he demonstrated, is of considerable interest.

Differences certainly occur from cyanophyte to cyanophyte, as shown in Fig. 4, but the differences lie in grain size and arrangement, rather than in grain shapes. Acicular carbonates like those described by Gleason (1972) or Krumbein & Potts (1978) are comparatively rare. There is no clear evidence that these ultrastructures can be used to distinguish cyanophyte genera in the biological sense, but some similarities within families seem to exist, especially if taken with other factors (Danielli in prep.). A description of the ultrastructure of *Girvanella* has, then, a place in the diagnosis of the genus. Some similarities are shown by the fine structures of *Girvanella* and *Rothpletzella* (Fig. 2, p. 89), emphasizing the close relationship of these two genera.

Early systematic studies of modern Cyanophyta were based on morphological and ecological grounds (see Geitler 1932). Drouet (1962, 1963) showed that cyanophyte morphology is very dependent on the environment of growth, and considerably condensed the number of taxa in his revised classification of the Oscillatoriaceae (Drouet 1968). The systematic study of Rippka *et al.* (1979) seems to be even more revolutionary, but will put

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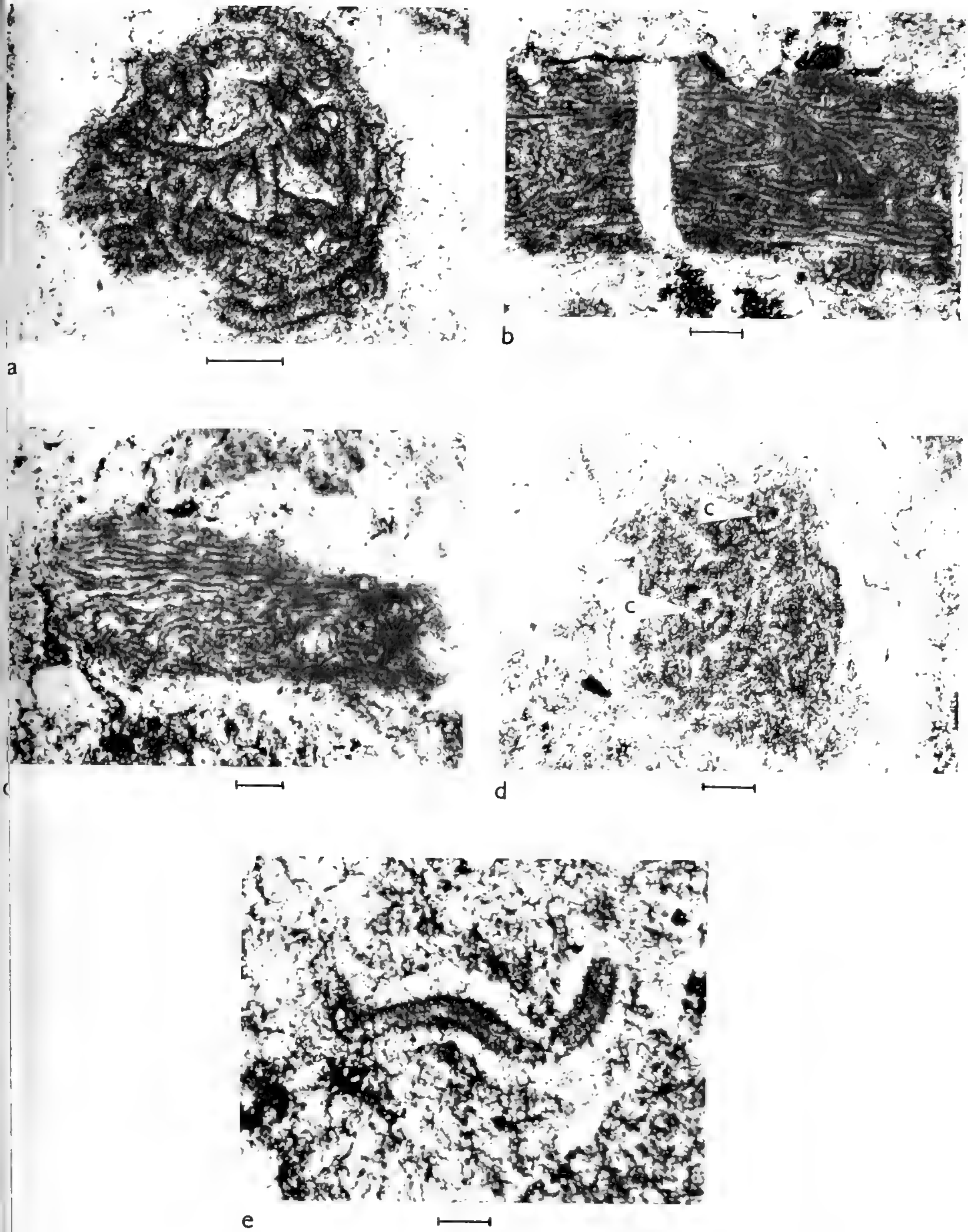
Fig. 3 Growth habits of *Girvanella* in the Stinchar Limestone at Aldons Quarry. (a), moderate density, variable parallelism and adherence. Bar = 20 μm. (V 15956). (b), elongate growth with external zone of subparallel adherent tubes, and internal zone of random adherent tubes, high density throughout. Bar = 100 μm. (V 60470). (c), subparallel tubes with lower density and adherence. Bar = 50 μm. (V 60471). (d), high density adherent tubes with random arrangement. Two tubes are in complete circles (c). Bar = 20 μm. (V 15965). (e), isolated tube with a cement overgrowth. Bar = 5 μm. (V 60472).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identification on a more objective basis. The organisms are cultured on standard media, so that a comparison of genotypes becomes possible. The method has been discussed by Whitton, Holmes & Sinclair (1978 : 64) and by Potts & Whitton (1980).

Elliott (1964 : 569) has described possible heterocysts in the Triassic form *Zonotrichites lissaviensis* Bornemann (1887). However, heterocysts and akinetes are not normally distinguishable in fossil material. H. M. Johnson's (1966 : pl. 6) example of the former in *Girvanella* may be neomorphic spar. In fossil algae, gross filament morphology is the principal tool available to the systematist. Thus whether or not a particular characteristic is useful should be decided on the basis of its biological nature. If a size or shape variation can be shown to have some direct relationship to the genotype of the organism, it may be of great value. Indeed, it is on this that identification by standard culture is based. If all the organisms tested give the same response under the same conditions, the assumption that they have the same genotype may be justified.

Point 1 in the list of *Girvanella's* generic characteristics (p. 88), is of descriptive value only. Most cyanophytes are microscopic[1]. Unless the calcification is incomplete, the structure is bound to be tubular (2), and no noncalcareous, mineralized forms have yet been reported (3). Some modern cyanophytes can approximate rectilinear growth (4), but it is not a consistent feature at generic level. It is also difficult to say when a curve is slight enough to be treated as incidental, except perhaps in a population study.

Some modern genera are habitually spiral (*Spirulina* Turpin); others are spiralled at times (*Oscillatoria* Vaucher) and many are never more than sinuous (*Rivularia* Agardh.). The characteristic seems to be both environmentally and genetically controlled. Comparison with *Oscillatoria* suggests that occasional spiralled filaments may be acceptable, but that populations with habitually spiralled filaments such as *G. problematica* var. *spiralis* Lewis should be excluded from the genus. Since procaryote cells seem to be either circular or oval in cross section (5), their trichomes are bound to have this shape. However, the carbonate tubes which form around them are not trichomes, and their inner surfaces may have several controls. If the carbonate is an impregnation, or a combined impregnation and encrustation, its inner surface may conform to the surface of the trichome. It will then be circular in section. No such restriction applies to the inner surface of an encrustation, which will more or less follow the surface of the sheath. Many cyanophytes have smooth sheaths with circular cross sections. However, the sheath may be irregular, or it may have a sculpture such as spiral or annular ribbing. This is probably an environmentally-determined character, in part if not entirely. It may also reflect the fine structure of the sheath itself. *Scytonema* Agardh., for example, has a strongly fibrillar sheath (Singh 1954). Unless the nature of the calcification is known, therefore, it would seem best to describe the calcareous tube of *Girvanella* as approximately circular in section, and perhaps to give an acceptable range of variation.

It has been suggested that the calcareous tube of *Girvanella* is an impregnated sheath (Seward 1898) but there is evidence for the presence of both impregnations and encrustations in the Stinchar Limestone girvanellids (Danielli 1977). It is possible that these should

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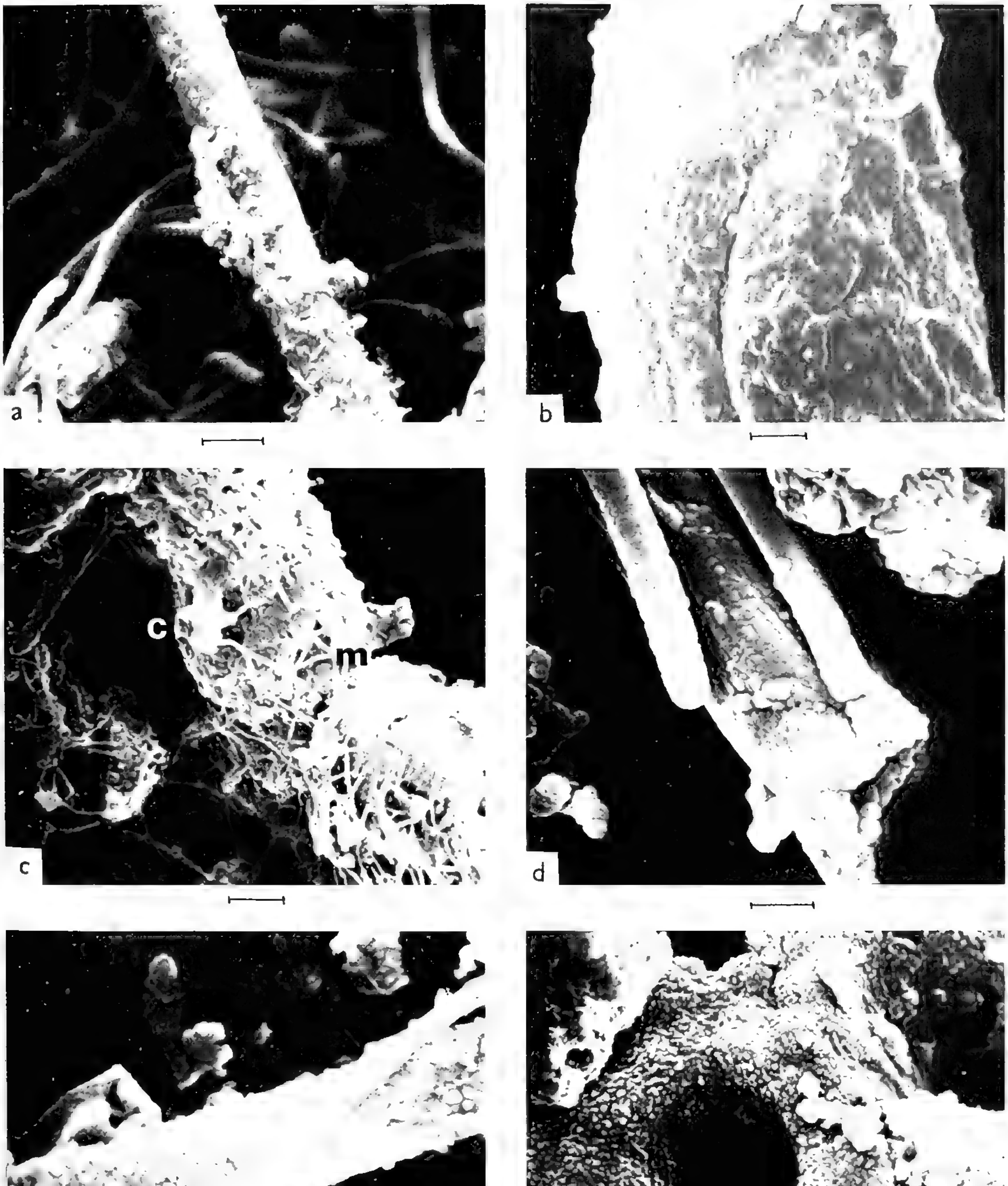
[1] Some bacterial carbonates are visible to the naked eye and resemble porostromates, but their importance in the fossil record is not yet known.

Fig. 4 Types of calcification in Recent blue-green algae. Several genera are shown, and grain size varies considerably, but the grain shapes are on the whole similar. (a), encrustation of equidimensional grains on a relatively smooth filament. Note the uncalcified background filaments. Bar = 15 μm. (b), impregnation, indicated by the granular appearance of the sheath surface. Bar = 2 μm. (c), embedding in a mass of mucus strands. c calcite grains, m mucus strands. Bar = 2 μm. (d), an empty but impregnated sheath which might be preserved as a porostromate fossil. Bar = 2 μm. (e), encrustation and impregnation of the same sheath, the two carbonates having similar textures. Bar = 1 μm. (f), a rivulariacean calcite. The trichome and sheath lay in the hollow, becoming encrusted with equigranular calcite. Organic matter has been removed with 14% NaClO in this case, exposing the micritic texture of the calcite. In the light microscope these tubes often appear unicrystalline owing to optical continuity of the grains. Bar = 50 μm.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be separated into two genera, although clear support for such a split cannot at present be obtained from modern organisms. *Rivularia,* for example, can both encrust and impregnate at the same time, and the two often have inseparable textures. In addition, the criterion of the internal to external diameter ratio, used for example by Riding (1977) to distinguish between them, does not hold in many cases. The impregnated sheath may be very thick in proportion to the protoplast diameter, and encrustations may be thin. These variations seem due mainly to ecological factors.

The cylindrical nature of the tubes (7) implies that the diameters are fairly constant along the tube axis, and that the structure is not branched. Some modern cyanophyte trichomes have a constant diameter (e.g. *Phormidium* Kuetz.), some taper (*Rivularia*), and some have pronounced constrictions at cross walls (*Nostoc* Vaucher). Whether or not this would be reflected in the carbonate again depends on the nature of the structure. A constricted tube would probably indicate that the filament it contained was also constricted, and would also be quite good evidence that the filament was simple, but a carbonate tube without constrictions gives no evidence either way.

Tapering would probably be reflected by the internal diameter of the tube, although not necessarily by the external diameter, if the tube were an impregnation. Since part of the carbonate of *Girvanella* tubes may well have been an impregnation, tapering might be expected to be apparent. It is then possible to say that the trichomes of *Girvanella* were probably not tapered.

The presence or absence of branching is used at generic level in the identification of modern cyanophytes (West & Fritsch 1927 : 454). It is not possible to separate false from true branching unless the trichomes are present, of course. Some porostromates, such as *Ortonella* Garwood 1914, have clear branching, but *Girvanella* is by implication an unbranched form (Dricot & Tsien 1977 : 232). Branching need not be frequent, so careful searches are necessary to establish its absence from any population.

Some modern cyanophytes have thin strips of sheath lying between the cells of their trichomes (*Nostoc piscinale* Kuetz.). Other forms often have fragmented trichomes, with sheath separating the fragments at more or less regular intervals (*Scytonema fulginosum* Tilden). It is theoretically possible for the strips of sheath to become impregnated with carbonate, producing a septate tube which could be preserved (9). However, no example of a septate *Girvanella* has been described which will support careful study.

Having scrutinized the original diagnosis of *Girvanella* above, it is clear that an emendation would be of some value. An attempt is offered below, taking these points into consideration.

Systematics

Kingdom **PROCARYOTAE** Buchanan *et al.*, 1974

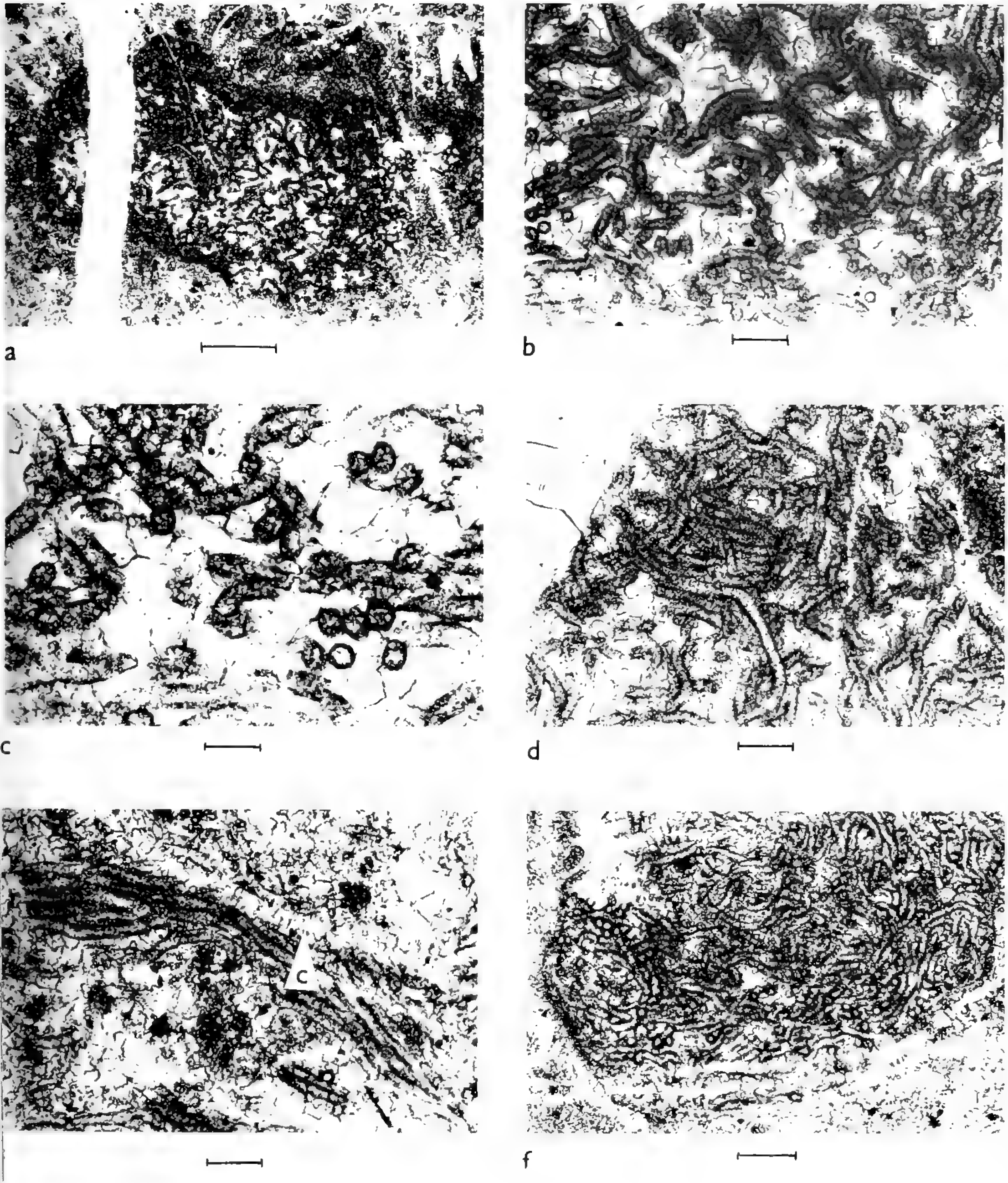
Division **CYANOPHYTA** Smith, 1938

Class uncertain

Family **POROSTROMATA** Pia, 1927

Genus ***GIRVANELLA*** Nicholson & Etheridge, 1878

Fig. 5 The neotype of *Girvanella*, and some contrasting growths in the same thin section, BM(NH) V 34566. (a), the growth which Wood (1957) designated as neotype of *G. problematica.* Note the low density central region, with denser growth at the boundaries. Bar = 55 μm. (b), a detail of (a), corresponding to Wood's (1957) figure, showing low density, moderate sinuosity, local parallelism and adherence. Bar = 100 μm. (c), detail of (b), with a variety of cell space textures. Bar = 50 μm. (d), part of the same growth showing variable sinuosity, density and parallelism. Bar = 100 μm. (e), another growth in the same section, with parallel, adherent tubes; note the cement overgrowth (c). Bar = 100 μm. (f), a third growth in the same slide, with thin sinuous tubes arranged more or less randomly. Bar = 200 μm.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[=*Argirvanellum* Rothpletz, 1916; *Batinevia* Korde, 1966; *Botominella* Reitlinger, 1959; *Fistulella* Korde, 1973; *Kenella* Korde, 1973; *Nicholsonia* Korde, 1973; *Siphonema* Bornemann, 1886; *Strephochetus* Seely, 1885; *Stromatocerium* Miller, 1882].

RANGE. Upper Proterozoic to Middle Cretaceous.

DIAGNOSIS. Microscopic tubular encrustations and/or impregnations of sheaths of filamentous organisms; filaments arranged at random or prostrate, rarely vertically; filaments single or in growths of variable size, shape and density; orientation parallel to random; filaments unbranched and slightly to highly sinuous; cell space approximately circular in cross section, sometimes compressed or with slight irregularities; cell space usually occupied by cement spar but sometimes micritic, cement developing either by growth from grains in the micritic tube or independently, as druses or equidimensional particles; aseptate micritic calcite tube comprising prisms or equidimensional grains, or both, the prisms with their long axes arranged perpendicularly to the filament axis and in a single layer, sometimes with smaller intercalated prisms.

NEOTYPE. The specimen shown on Fig. 5, after Wood (1957). Thin section kept by the Palaeontology Dept. of the British Museum (Natural History), London, reg. no. V 34566.

HORIZON AND LOCALITY. Stinchar Limestone (Ordovician, Lower Caradocian Series), Tormitchell Quarry near Girvan, Ayrshire, Scotland.

Specific subdivision

As Wood (1957) found, specific subdivision of *Girvanella* is a difficult problem. He drew a graph of internal diameters and obtained a bimodal curve for the sample he took from the

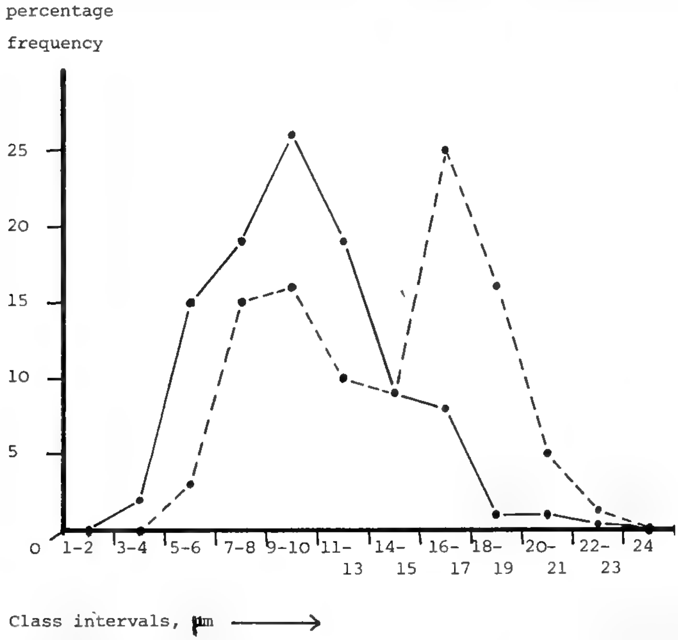


Fig. 6 Internal diameters of *Girvanella* tubes from the Stinchar Limestone. Plain line, Aldons Quarry (Danielli herein, n = 1060). Pecked line, Benan Burn and Tormitchell Quarry (after Wood 1957, with permission; n = 633).

Stinchar Limestone. The external diameters gave a less useful curve. Internal diameters from the sample collected for the present study gave a unimodal plot with a slightly longer range (Fig. 6). Wood's material came from several localities, and thus could have been derived from environments which differed in biological or biochemical factors but which are indistinguishable by modern geological methods. If this is so, the algae are likely to have been different in each. Even if the same species were present in all, several ecophenes may have been represented. The Aldons Quarry sample came from a single outcrop and is not therefore strictly comparable with Wood's.

Mamet & Roux (1975 : 137) surveyed the Carboniferous and Devonian species of *Girvanella*, and condensed the various taxa into four species. Their method of measuring from the published figures rather than the type material is questionable, but the results are of some interest. They based the four species on a graph of tube thickness plotted against internal diameter. Unfortunately, girvanellids in the Stinchar Limestone at Aldons Quarry do not conform to Mamet & Roux's method of subdivision. Nor does the method allow for the presence of a fifth species. The internal diameter and tube thickness of the Aldons sample are similar to those of Mamet & Roux, but the measurements are distributed over most of the graph and do not fall into clusters.

In a case like this reappraisal of the genus as a whole is necessary. One approach might be to reanalyse the previously-designated types, and reorganize them. However, as pointed out by Raup & Stanley (1971 : 177), many types do not adequately represent their species. Skevington (1973 : 43) has come to a similar conclusion in the case of graptolites, and Hughes, Drewry & Laing (1979 : 515) have regretted the type and synonomy arrangement of taxa under the rules of botanical nomenclature for a similar reason. Since a complete reassessment of the species of *Girvanella* would require a work of far greater length than this, and fundamental studies in greater depth, no more is intended here than to suggest a possible approach using the definition of the type species *problematica*. The species is taken as described by Nicholson & Etheridge (1878). The existing classification of *Girvanella* species has been investigated, but the value of *species inquirendae* in a systematic re-evaluation is open to question. It will be shown that some new basis for subdivision of the genus is needed, if the classification is to reflect the biology of the organisms.

The characteristics used by Nicholson & Etheridge (1878) give a good description of the fossil, and may be summarized as follows: (1) sheath diameter; (2) tapering; (3) parallelism; (4) density; (5) sinuosity; (6) growth shape; (7) growth size. No tapering species have been described (2). Indeed, since the generic diagnosis implies that the tube diameter is constant, the question might be considered out of place here. The density of the growths (4) has also been discussed under generic characteristics.

Points 3, 5, and 6 are concerned with the spatial relations between tubes. Authors delineating species have often described the sinuosity of tubes, and sometimes their degree of parallelism. Unfortunately no attempt has been made to define these numerically. Much the same can be said of growth shape and size. There is, however, some justification for this if one agrees with Maslov's (1949) view that they are environmentally-determined characteristics. This is likely to be the case, in view of the phenotypic plasticity of Recent filamentous cyanophytes (Desikachary 1970, Rippka *et al.* 1979).

We are left with point 1, sheath diameter. It has been used by many workers, in both definition and identification of species. The diameters of many of the species listed in Table 2, pp. 82–4, are compared in Fig. 7. The first problem encountered is the meaning of 'diameter'. As shown in Fig. 1 (p. 80) there are two diameters cd, ef to any cross section. In *Girvanella* they may differ by a factor of two or more. Not all authors of *Girvanella* species have explained which diameter they were giving.

The diameters shown have considerable overlap, and the ranges differ in length. Measurement of a single tube will not allow assignment of the tube to one species. If a number of tube diameters are known for a sample, questions of sample size and statistical significance are raised. Wood (1957) measured about 600 tubes, and found the range 5 μm to 22 μm for the Stinchar Limestone. Over 1000 were used in the present study, and a slightly wider range was obtained (Fig. 6). This might have been extended even further if 1500 tubes had been measured. Green (unpublished, 1959) conducted a statistical study of some Silurian girvanellids, but the conclusions were published without the basic data (H. M. Johnson 1966).

The external diameter is a function of the internal diameter and tube thickness. Its significance has been discussed by Wood (1957 : 26), who considered it to be unreliable because of its dependence on environmental factors. However, Mamet & Roux (1975) have shown that the relationship between tube thickness and internal diameter may be useful in classification.

Girvanellids in the sample taken from the Stinchar Limestone at Aldons Quarry agree with the generic definition of Nicholson & Etheridge (1878) in most respects. However, growth densities vary from 10% to almost 100% (Fig. 3). Strictly, the high density growths are not *Girvanella*, but in every other way the growths fit the definition. Since growth density is probably an environmentally-determined characteristic, there seems to be no reason for separating these forms as a different genus or species from the lower density forms.

The internal diameter from the Aldons Quarry sample ranges between 4 μm and 22 μm (the area indicated in Fig. 7). Some 26 species are contained in this interval, and it is overlapped by 10 others. It is possible that, if the sample size were larger, some of these species would lie completely within the Aldons range.

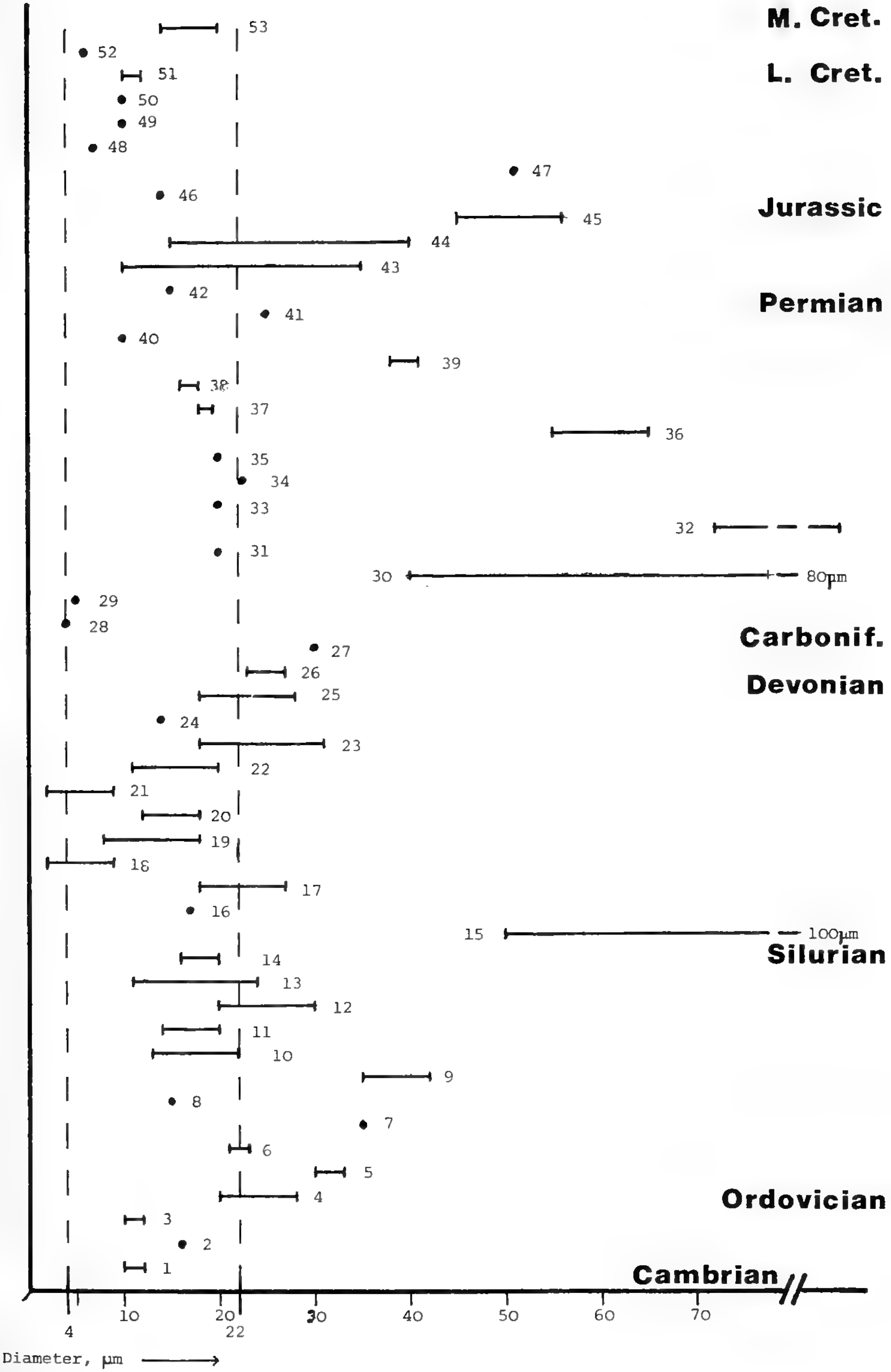
The external diameter of each tube was measured, and tube thickness was determined as half the difference between the two diameters. A range of 0·5 μm to 22 μm was found, which includes all those species whose definitions include a value for tube thickness. To illustrate the variability of the growths as well as that of individual tubes, Fig. 8 gives the internal diameter and tube thickness ranges found in some particular growths. While examples of the extreme values are rare, objections of a statistical nature can be made to the exclusion of specimens on grounds of rarity.

A study of *Girvanella* populations throughout its fossil record is evidently the next stage in this reassessment. The example of Rippka *et al.* (1979), in leaving this to the future, is followed here, but some aspects of the organism which might be considered are the detailed microscopic morphology in relation to the ecology of the organism, the nature of the carbonate tube and its relation with the enclosed trichomes, and the ultrastructure of the carbonate tube in relation to other Porostromates and to modern calcified cyanophytes.

The work of Drouet is applicable to the first of these suggestions. Though now his classifications are generally rejected, he did demonstrate the dependence of cyanophyte morphology on evironmental factors, describing ecological varients or ecophenes of, for example, *Schizothrix calcicola* (Ag.) Gom. (Drouet 1963). These varieties have essentially the same genotype. *Girvanella* comes from a wide geographical and temporal range, as well as a wide range of ecologies. There must be many genotypes represented, so that the ecophene approach will only be tenable in some circumstances. It might be used with advantage within a single outcrop, and preferably at a single horizon, for determining local variability within a population.

Huxley (1938) defines a cline as any variational trend in space. If the end members of a cline are separated from each other, they may develop into distinct species. In the case of fossil material especially, the full cline may not be preserved and the end-members may be taken for different taxa. Thus genotypic variation occurs along the cline. This picture, suggested by Dr M. A. Edington (personal communication), fits *Girvanella* a little better than does that of ecophenes.

Fig. 7 The diameters of *Girvanella* species. Ranges are given in chronological order, and keyed to Table 2, p. 82–4. Most authors give internal diameters, but some do not specify which they provide. Since the sparry cell space is often easy to see, it is likely that most of these undefined diameters are in fact internal. The range of values from the Aldons Quarry sample is indicated by two vertical broken lines. The variability of the lengths, overlapping positions, and lack of frequency distributions of the individual species makes the diameter of low value as a taxonomic criterion at present.


M. Cret.
L. Cret.
Jurassic
Permian
Carbonif.
Devonian
Silurian
Ordovician
Cambrian
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22
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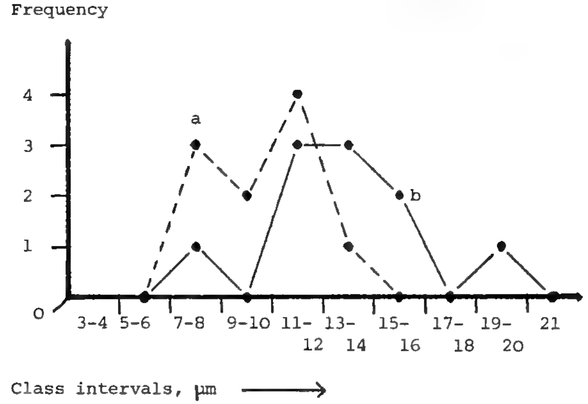
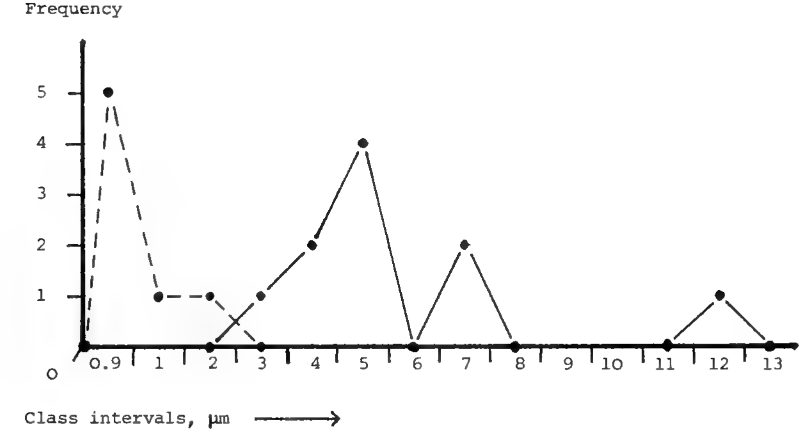
Diameter, µm



a) Internal diameter; a. N=10, b. N=10.



b) Tube thickness; a. N=7, b. N=10.

Fig. 8 Internal diameters (a) and tube thicknesses (b) for *Girvanella* growths in the Stinchar Limestone at Aldons Quarry. Plain lines, maximum range for single growth. Pecked lines, minimum range for single growth.

The study of clines requires sampling over substantial areas, since clinal variation is a geographical phenomenon. Therefore an investigation of *Girvanella* clines would require collection along the same horizon, over some kilometres if possible. Since no study of this kind has yet been published, it is not possible at present to decide whether *Girvanella* does or does not form clines.

The second suggestion for future studies concerns the carbonate tube. Its relationship to the original sheath of the organisms greatly affects the acceptable range of variation of characters such as the internal diameter. Unless such questions can be answered, these ranges must remain arbitrary.

Turning to the third suggestion, there is in fact some reason to doubt the value of ultrastructure as a taxonomic tool in the case of cyanophyte carbonates. Recent organisms show no clear relationship between carbonate fine structure and species or even genus. In addition the fossil porostromate *Rothpletzella gotlandicum* Wood 1948 appears to have a similar ultrastructure to that of *Girvanella* (Fig. 2, p. 89). Kobluk & Risk (1977 : 1077) have reported girvanellids with similar textures to those of the Stinchar Limestone forms. This apparent stability of the carbonate texture from place to place is interesting, but not very promising for specific subdivision.

The importance of population studies in work of this kind cannot be over-emphasized, especially with organisms that show such degrees of variation. In these cases a range of variation should be given for every characteristic.

Conclusions

The morphology of *Girvanella* has been subject to a good deal of misinterpretation. The genus has been discussed here in terms of modern cyanophytes, and the limitations of the fossil material have been outlined. Direct comparison can only be made at the level of filaments, since there is at present no unequivocal evidence concerning trichome shape, or number per filament.

The generic diagnosis of Nicholson & Etheridge (1878) has been emended to take account of this discussion, and the specific subdivision of the genus has been considered briefly. Studies involving sampling over wide areas, at a single horizon, are considered necessary so that the variation shown by the fossil can be investigated.

The position of the genus in relation to the groups of modern filamentous organisms is at present indeterminable, the only guide being the lack of branching shown by *Girvanella*. Russian scientists such as Kulik (1973 : 39) have defined species as members of the Hormagoneae and the assignment is very possibly correct, but care should be used in such determinations. The remarks made by Edhorn (1979) concerning the mobility of the filaments appear to present an over-extension of the evidence available from the fossil material and would be difficult to test. However, comparisons like that of Edhorn, between the growth habits of *Girvanella* and those of Recent organisms, may shed some light on the ecology of the fossil if applied with caution.

It is at present possible to say very little about the organisms concerned in the formation of *Girvanella* tubes. Population studies coupled with ecological work on the communities associated, and with sedimentology, may be useful in this connection. Since cyanophytes are important members of many modern communities, and are major sediment-producers at the present time, fossil forms might be expected to be of considerable palaeoecological value.

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[Principal references are in **bold** type; an asterisk (*) denotes a figure.]

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Centenary Miscellanea

To mark the centenary of the British Museum (Natural History) in 1981, this number of the *Bulletin* comprises nine short papers, each of which re-examines historical material in the collections of the Department of Palaeontology.

Contents

Reassessment of the Ordovician brachiopods from the Budleigh Salterton Pebble Bed, Devon

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Synopsis

The Ordovician part of the brachiopod fauna from the quartzite pebbles found in the Triassic Budleigh Salterton Pebble Bed, Devon, is reassessed, chiefly using the nineteenth-century collections made by Vicary, Valpy and others and originally figured by Salter and Davidson. Davidson's overlooked conclusion of two separate Ordovician ages is confirmed. The older Arenig has a bizarre fauna of large inarticulate brachiopods, and there is a younger and more abundant fauna of late Llandielo age. The European affinities of the fauna are confirmed and the taxonomy of the late Llandielo fauna (including some comparative material from France) is revised. The species *Corineorthis erratica* (Davidson), *Tafilaltia valpyana* (Davidson) and *Salopia? pulvinata* (Salter) are redescribed in detail, and other species placed in synonymy with them.

Introduction

The value of old collections is well demonstrated by the brachiopods and other shelly fossils found during the nineteenth century in pebbles from the conglomerates of Triassic age near Budleigh Salterton, Devon (Fig. 1). Although it was a Mr Carter who found the first fossils in the pebbles in about 1835, it was an enthusiastic amateur geologist, W. Vicary, who first made an extensive collection of the shells from about 1860, and brought them to the attention of the well-known palaeontologist J. W. Salter. Salter encouraged Vicary to give a short account of the rocks to the Geological Society of London (Vicary 1864). Salter (1864) appended a 'note on the fossils', containing descriptions and illustrations of 37 taxa of many phyla. Vicary's collection was bequeathed to the British Museum (Natural History) in 1903, and it was joined there in 1910 by the collection of another enthusiastic amateur, R. H. Valpy, after the latter's death.

Salter was astute in perceiving the central European affinities of the Budleigh Salterton fauna, which was quite unlike any of those faunas found elsewhere in Britain (apart from Cornwall) in rocks of the same age. Salter assessed this age as 'Lower Silurian' (i.e. Ordovician in modern terms), although he was puzzled by some shells which he interpreted as the oldest spiriferide brachiopods. The shells were subsequently reassessed by T. Davidson (briefly reported in 1866 : 67 and elaborated in 1870), the greatest of the nineteenth-century brachiopod workers. He then recognized that the pebbles, although all similar in their quartzite lithology, could be assigned to two separate ages, Ordovician and Devonian; it was the latter which included the questionable spiriferides. Davidson figured the brachiopod fauna in a series of publications (1866–71, 1870, 1881*a*). Davidson's collection from Budleigh Salterton, largely given to him by other collectors but containing many type specimens, was bequeathed to the Museum in 1885. Good specimens are extremely difficult to collect from the Budleigh Salterton Pebble Beds and thus the Museum

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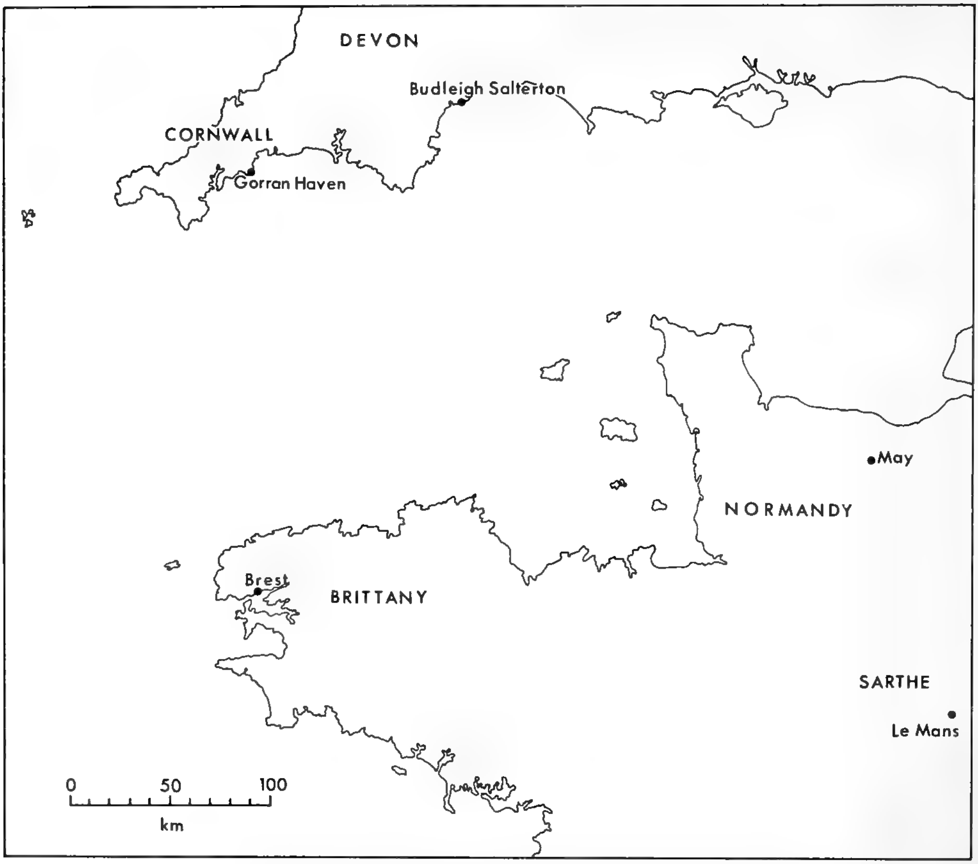


Fig. 1 Locality map showing the relative present-day positions of Budleigh Salterton, Devon, Gorran Haven, Cornwall and the Armorican Peninsula, France.

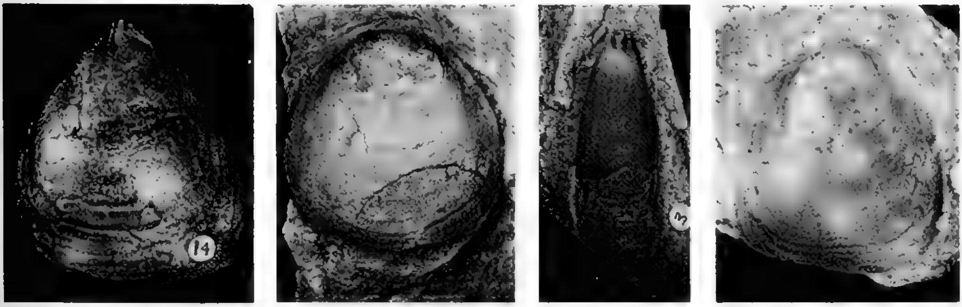
possesses the largest, and indubitably the most important, collection of brachiopods from that area, which has not been critically reassessed for a century. The present paper deals only with the Ordovician part of the fauna; the Devonian brachiopods will form the topic of a subsequent publication. Davidson, in a later review (1880 : 339), also realized that there were two separate Ordovician ages represented by the Budleigh Salterton brachiopods. The older of these he identified as 'Grès Armoricain – Lowest portion of Llandeilo', and the younger as 'Grès de May – Caradoc' (Davidson's stratigraphical terminology compared with modern usage can be found in Cocks 1978 : fig. 1). This important conclusion appears, however, to have been overlooked by all subsequent workers. The older horizon is represented only by the large inarticulate brachiopods and the younger by the more common pebbles dominated by '*Orthis budleighensis*'.

The Ordovician brachiopods found in the Budleigh Salterton pebbles are very similar to those found *in situ* in the Armorican Peninsula of Brittany and Normandy, France, and also to some extent in the Gorran Haven area of Cornwall (Fig. 1). Sadler (1974) has reviewed the Gorran Quartzites and their trilobite fauna, assigned to them a Llandeilo, possibly a late Llandeilo, age and (1974 : 74) recorded comparable trilobites from Budleigh Salterton pebbles. During the last 20 years much has been published on the Ordovician of the Armorican massif, the stratigraphy of which is now well known (see summaries by Babin *et* *al.* 1976 *a, b*). While a few French brachiopods have been revised recently (Melou 1973, 1975), most of the Armorican brachiopod fauna remains undescribed and we take the opportunity here of illustrating and measuring some brachiopods from Normandy, based on collections made by Sir R. I. Murchison, the founder of the Silurian system, which came to the Museum in 1911 with all the other foreign specimens of the Geological Society of London.

The Arenig Fauna

The brachiopod fauna of the Grès Armoricain in the Armorican Peninsula, France, was originally described (without illustrations) by Rouault (1850), and later revised and extended by Davidson (1880, 1881 *b, c*). Davidson's original French material, presented to him by Lebesconte, Guillier, Morière and others, is also now in the British Museum (Natural History), together with his notes and correspondence and the original drawings for the published plates. No primary work has been carried out since then on the brachiopod fauna, although new generic names were subsequently given to two of the species. Henry (1980) has revised the sparse Grès Armoricain trilobite fauna, which consists of *Ogyginus armoricanus* (Tromelin & Lebesconte), *Platycoryphe heberti* (Lebesconte) and *P. dangeardi* Henry, and endorsed the Arenig age deduced by previous workers. Although there is no internal evidence to be sure of the detailed age of the Grès Armoricain faunas within the Arenig, Dr R. A. Fortey has suggested to us that a middle Arenig age appears the most probable from an assessment of contemporary faunas elsewhere in transgressive situations comparable to that seen in the Grès Armoricain. Davidson's work (1880 on Brittany, 1881*b* on Normandy and 1881*c* on Sarthe) revealed the following brachiopods to be present in the French Grès Armoricain (with updated generic names):

	Brittany	Normandy	Sarthe
Ectenoglossa leseueuri (Rouault, 1850)	×	×	×
Lingulepis crassipyxis Havlíček, 1980			×
Lingulobolus brimonti (Rouault, 1850)	×	×	
Lingulobolus hawkei (Rouault, 1850)	×	×	
Pseudobolus ? *slateri* (Davidson, 1866)	×	×	
Tomasina criei (Davidson, 1881)			×



2 3 4 5

Figs 2–5 Inarticulate brachiopods of Arenig age from the Budleigh Salterton Pebble Bed. Fig. 2, B 21518 *Lingulobolus hawkei* (Rouault, 1850), × 1·0; the specimen is that figured by Salter (1864 : pl. 17, fig. 4) as *Lingula rouaulti* sp. nov., and was subsequently selected (Cocks 1978 : 12) as the lectotype of the latter species; W. Vicary Coll. Fig. 3, B 21504 *Pseudobolus*? *salteri* (Davidson), × 1·2; the lectotype (sel. Cocks 1978 : 13), originally figured by Davidson (1866 : pl. 1, fig. 28); W. Vicary Coll. Fig. 4, B 21516 *Ectenoglossa lesueuri* (Rouault, 1850), × 1·0; the specimen previously figured by Salter (1864 : pl. 17, fig. 1) and Davidson (1866 : pl. 1, fig. 3); W. Vicary Coll. Fig. 5, B 21514 *Lingulobolus brimonti* (Rouault, 1850), × 1·3; the specimen figured by Salter (1864 : pl. 17, fig. 2) and Davidson (1866 : pl. 1, fig. 21) as *Lingula hawkei* Rouault; W. Vicary Coll.

No Arenig trilobites have yet been noted in the Budleigh Salterton faunas, but the brachiopods *Ectenoglossa lesueuri* (Fig. 4), *Lingulobolus brimonti* (Fig. 5), *L. hawkei* (Fig. 2) and *Pseudobolus*? *salteri* (Fig. 3) are all known (Salter 1864, Davidson 1870, 1881*a*), and thus match exactly the Grès Armoricain inarticulate brachiopod fauna of Brittany and Normandy. The lack of illustrations in Rouault's original work led the first wave of subsequent revisers astray in their identifications of *brimonti* and *hawkei*. The attributions published by Salter (1864) and Davidson (1866, 1870) are thus in error, but this was rectified subsequently by Davidson (1880, 1881*a*) and led to the correct synonymizing of Salter's *rouaulti* (whose lectotype is refigured here, Fig. 2) with *hawkei*. Davidson's illustrations are so good that further redescription of the fauna is not given here, although the fauna as a whole could usefully be revised in the light of a thorough reappraisal of inarticulates and possibly bivalves of Arenig age from the whole central European area, including Bohemia and the Iberian Peninsula. Havlíček (1980) has described a comparable fauna from the Montagne Noire, southern France.

The Llandeilo Fauna

In contrast to the bizarre inarticulate fauna found in the pebbles of Arenig age, the Llandeilo age pebbles from Budleigh Salterton show an overwhelming dominance of articulate brachiopods, in particular the enteletacean previously commonly identified as *Orthis budleighensis* and which is now known to be *Tafilaltia valpyana*. The brachiopod fauna is not a diverse one, and consists of the three orthide species described in detail below, rare lingulides identified by Davidson as *Lingula morieri* Tromelin, 1876, and a single specimen, BM(NH) Palaeont. Dept. B 21525, identifiable as *Porambonites* sp. This last was figured by Salter (1864 : pl. 17, fig. 9) and identified correctly by him, even though it was later unaccountably placed in the synonymy of *pulvinata* by Davidson (1881*a* : 358). There are no other fossils on the same block, and thus it is just possible that the specimen could be of Arenig age; however this large (length 28·5 mm, width 39·2 mm) brachial valve appears to be more similar to Llandeilo and Caradoc forms of the genus. The specimen (B 21531) figured as *Terebratula* ? sp. by Davidson (1870 : pl. 4, fig. 11; 1881*a* : pl. 41, fig. 23) is a monoplacophoran resembling *Vallatotheca*, kindly reidentified by Dr N. J. Morris. There are also bivalves, gastropods, crinoids and trilobites in the late Llandeilo fauna, all awaiting revision apart from *Neseuretus tristani*, but all relatively uncommon when compared with the dominant brachiopods.

The fauna has its nearest geographical comparison with that from the Gorran Quartzites of the Gorran Haven area, Cornwall (Sadler 1974), sharing with it the trilobite *Neseuretus tristani* (Brongniart). However, the Cornish beds also yield a common large orthid (figured by Davidson, 1881*a*, as *Orthis calligramma* and to be revised by M. G. Bassett), which is not present in the Budleigh Salterton pebbles, and the other Cornish brachiopods include congeneric *Corineorthis* and heterorthids, but not species in common. The Budleigh Salterton Llandeilo pebbles probably have their closest faunal affinity with the fauna from the Grès de May Formation in Normandy. Detailed comparison is difficult, since the French brachiopod fauna has not yet been properly described, but the opportunity is taken here (see systematic section below) to demonstrate the specific identity of the commonest form at both Budleigh Salterton and in the Grès de May, *Tafilaltia valpyana* (Davidson). It is relevant to note that the same species (previously described as *Tafilaltia dalmanelloides*) is also present in the Llandeilo age Skalka Quartzite of Bohemia (Havlíček 1970). The age of this part of the Budleigh Salterton pebble fauna is almost certainly late Llandeilo, although the upper part of the Grès de May represents deposition which probably continued on into early Caradoc times (Babin *et al.* 1976*a* : 381).

Systematic Palaeontology

All the figured and quoted specimens are in the British Museum (Natural History) (B and BB). In general the specimens are well preserved, but the recemented quartzite lithology precludes the preservation of the very fine details of ornament.

Class **ARTICULATA** Huxley, 1869

Order **ORTHIDA** Schuchert & Cooper, 1932

Suborder **ORTHIDINA** Schuchert & Cooper, 1932

Superfamily **ORTHACEA** Woodward, 1852

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

Subfamily **PLECTORTHINAE** Schuchert & Le Vene, 1929

Genus ***CORINEORTHIS*** Stubblefield, 1939

Corineorthis erratica (Davidson, 1869)

(Figs 6–11)

1869 *Orthis Berthoisi* ? var. *erratica* Davidson : 233; pl. 32, figs 21–28.
1870 *Orthis Berthoisi* ? var. *erratica* Davidson; Davidson : 83; pl. 5, figs 13–16.
1881*a* *Orthis Berthoisi* var. *erratica* Davidson; Davidson : 356; pl. 41. figs 1–9.
1978 *Svobodaina* ? *erratica* (Davidson) Cocks : 74.

Description. Large dorsibiconvex to convexoplane orthide with obtuse cardinal angles and incipient development of weak plication; pedicle valve with subcircular to subpentagonal outline and averaging 83% as wide as long in 5 specimens; brachial valve averaging 80% as wide as long in 7 specimens, and between one-quarter and one-third as deep as long; ventral interarea slightly curved and apsacline, with prominent growth striations; open, wide delthyrium with conspicuous pedicle callist; short anacline dorsal interarea, with open notothyrium largely filled by posterior part of myophore; radial multicostellate ornament with 3 to 4 ribs per mm at 5 mm length; a few prominent concentric growth lines.

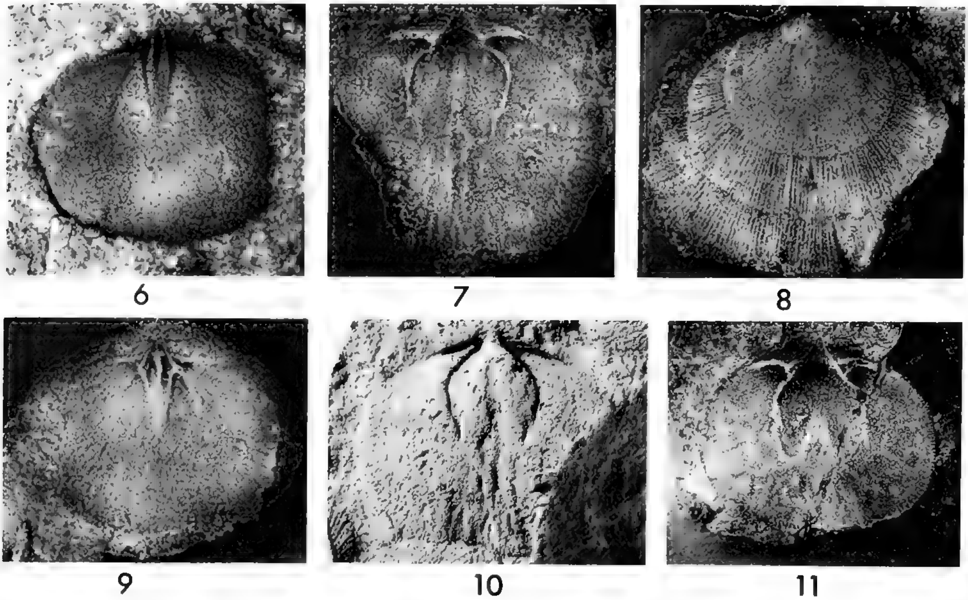
Teeth short, stout, and supported by dental plates extending anteriorly for up to 21% of valve length and diverging at about 90°; well-impressed ventral diductor muscle scars elongately bilobed, about 85% as wide as long, extending anteriorly for an average of just over 50% of valve length and enclosing elongate adductor scars which extend antero-medially to link with the vascular impressions.

Cardinal process simple, with well-developed triangular myophore and simple blade-like shaft extending anteriorly across the notothyrial platform onto median septum; elongate brachiophore bases average about one-quarter valve length, initially diverging for about two-thirds of their length, then converging across the flanks of the platform to merge anteriorly with the short median septum. Faint elongate muscle scars, about 85% as wide as long, expanding anteriorly, with maximum width in the mid-part of the valve, although the posterior pair of scars are most deeply impressed to form pits.

Material. Lectotype of *erratica* (selected Cocks 1978 : 74) B 20936 (Figs 7, 8, 10), external and internal moulds of a pedicle valve, originally figured by Davidson (1869 : pl. 32, figs 21–23); R. H. Valpy Collection, from late Llandeilo pebble in Trias, Budleigh Salterton Pebble Bed, Devon. Additional material in the British Museum (Natural History) : 11 brachial valves and 4 pedicle valves also from the Budleigh Salterton Pebble Bed. Specimens of *Corineorthis* also probably attributable to *erratica*, e.g. B 13289, are known from the Grès de May of St Germain, France.

Discussion. Examination of the material described as *Orthis berthoisi* var. *erratica* by

Davidson (1869) shows clearly that it is congeneric with material from Cornwall described as *Corineorthis decipiens* by Stubblefield (1939), itself recently recognized by M. G. Bassett as a junior synonym of *Orthis berthoisi* var. *cornubiensis* Davidson, 1881. Davidson (1881*a* : 355–7) also discussed the problem of *Orthis berthoisi* itself, which comes from the slates of La Couyère, Normandy (Rouault 1849 : 68; pl. 2, figs 4–4c). Topotype material of *berthoisi* (e.g. B 13233 in the Davidson Collection *ex* Tromelin), although severely crushed, leads us to agree with Davidson that *erratica* and *berthoisi* are not the same: until Rouault's types are revised, perhaps *berthoisi* is best regarded as a *nomen dubium*. The La Couyère slates are now known to form part of the Riadan Formation, which is late Ordovician in age (Babin *et al.* 1976*a* : 374).



Figs 6–11 *Corineorthis erratica* (Davidson, 1869) from pebbles of late Llandeilo age, Budleigh Salterton Pebble Bed, Devon. Figs 6, 9, B 20936 (additional brachial valve on lectotype block and latex cast of it), × 2·0. Figs 7, 8, 10, B 20936, latex cast of internal mould, latex cast of external mould and internal mould of pedicle valve, lectotype (sel. Cocks 1978 : 74), originally figured by Davidson (1869 : pl. 32, figs 21–23), × 1·5; R. H. Valpy Coll. Fig. 11, B 13284, latex cast of pedicle valve internal mould, × 1·5; T. Davidson Coll. *ex* W. Vicary.

Available statistical data indicate that *C. erratica* and *C. pustula* Williams, from the type Llandeilo area, although showing no significant differences in the outline of either valve or the shape of the cardinalia, do differ in their ventral diductor scars, which are more splayed in *erratica* (85% of length, compared with 62% in *pustula*). The coarse texture of the Budleigh Salterton sediments makes it hard to determine whether or not the internal pustules and characteristic exopunctae of *pustula* are present in *erratica*. *C. erratica* also has a better-developed myophore than *pustula*, presumably indicating a better-developed diductor attachment site to complement the larger ventral scars, and we continue to recognize them as two separate species. *C. erratica* has muscle bounding ridges which are laterally curved, in contrast to the straight ridges present in *C. cornubiensis*.

Superfamily **ENTELETACEA** Waagen, 1884

Family **HETERORTHIDAE** Schuchert & Cooper, 1931

Genus ***TAFILALTIA*** Havlíček, 1970

Tafilaltia valpyana (Davidson, 1869)

(Figs 12–23, 30, 31)

1864 *Orthis redux* Barrande; Salter : 294; pl. 17, fig. 7 (*non* Barrande, 1848).
1869 *Orthis redux* Barrande; Davidson : 224; pl. 28, figs 6–9 (*non* Barrande, 1848).
1869 *Orthis testudinaria* Dalman; Davidson : 226 *pars*; pl. 28, fig. 22, *non* figs 13–21, 23, 24 (*non* Dalman, 1828).
1869 *Orthis Valpyana* Davidson : 235; pl. 32, figs 29–33.
1870 *Orthis redux* var. *budleighensis* Davidson : 82; pl. 5, figs 9–12.
1870 *Orthis Valpyana* Davidson; Davidson : 83; pl. 5, figs 23–25.
1881*a* *Orthis budleighensis* Davidson; Davidson : 358; pl. 41, figs 12–20; pl. 42, figs 16–25.
1881*a* *Orthis Valpyana* Davidson; Davidson : 361; pl. 41, figs 21, 22.
1970 *Tafilaltia dalmanelloides* Havlíček : 20; pl. 4, figs 1–8.
1977 *Tafilaltia dalmanelloides* Havlíček; Havlíček : 115; pl. 11, figs 3–5, 7, 8.
1978 *Howellites ? budleighensis* (Davidson) Cocks : 65.
1978 *Heterorthina valpyana* (Davidson) Cocks : 74.

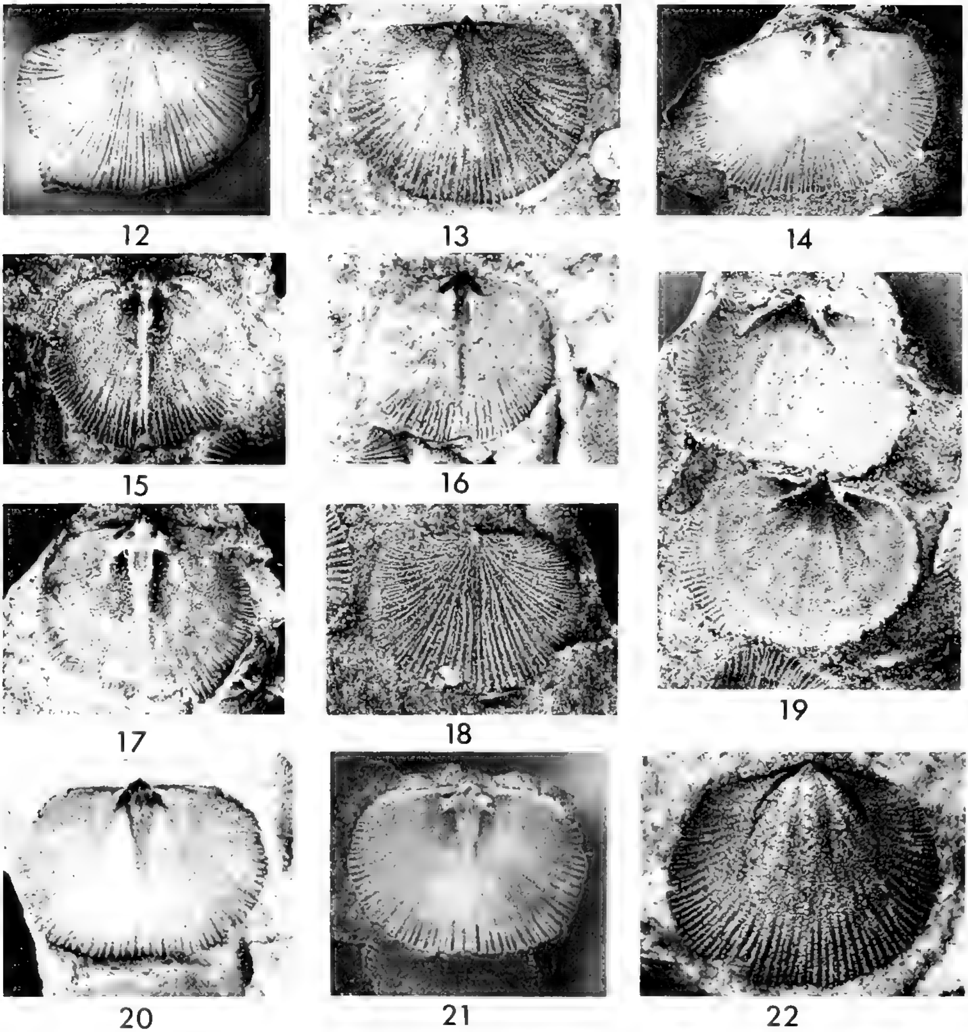
DESCRIPTION. Fairly small planoconvex to ventribiconvex transverse heterorthinid with brachial valve averaging 80% as long as wide in 46 specimens; pedicle valve averaging 83% as long as wide in 33 specimens and 25% as deep as long in 10 specimens; ventral interarea short, apsacline, with wide, open delthyrium, dorsal interarea short anacline, notothyrium completely filled by cardinal process; radial ornament of fine costellae, numbering 5 to 6 per mm 5 mm anteriorly of the umbo, which curve posterolaterally to merge with the hinge line.

Ventral interior with small teeth supported by low, widely-divergent dental lamellae extending laterally for about half the valve width and anteriorly for about one-quarter the valve length; pedicle callist well developed; muscle field large, usually poorly impressed anteriorly but averaging 56% of valve length and 99% as long as wide in 4 specimens in which the anterior edge was more strongly impressed; muscle field slightly flabellate with lateral margins of diductor scars less well developed than the median margins, which enclose poorly differentiated adductor scars; vascular canals, separated by ridges, can be quite deeply impressed.

Dorsal interior with well-developed, ponderous cardinal process with a raised posterior myophore, supported anteriorly by a low, broad shaft barely distinguishable from the supporting median septum; triangular posterior platform of myophore with prominent median ridge raised above lateral margins; brachiophores short and blade-like, with bases which average 17% as long as valve length and 64% as long as wide in 33 specimens; sockets narrow and well defined, and without fulcral plates; muscle scars elongate and variably impressed, quadripartite and averaging 46% of valve length and 85% as wide as long in 15 specimens.

MATERIAL. Lectotype of *valpyana* (selected Cocks 1978 : 74) B 21533, external mould (Fig. 12) and counterpart internal mould of a pedicle valve, the original of Davidson (1869 : pl. 32, figs 29–31); W. Vicary Collection, from late Llandeilo pebble in Trias, Budleigh Salterton, Devon. Additional material: over 300 specimens from other blocks in the Budleigh Salterton Pebble Bed in the Vicary and Valpy Collections, including B 21616, the lectotype of *budleighensis* Figs 15, 16). Also known from Perhaver Quartzite, Gorran Haven, Cornwall; the Grès de petit May, Normandy, France; and the Skalka Quartzite of Bohemia, Czechoslovakia, including the holotype of *dalmanelloides*, from Chrbina Hill, near Nenačovice (Havlíček 1970 : 20–21).

DISCUSSION. A few relatively large heterorthid specimens, distinguished as the new species *valpyana* by Davidson (1869), closely resemble the much more numerous and smaller form



Figs 12–22 *Tafilaltia valpyana* (Davidson, 1869) from pebbles of late Llandeilo age, Budleigh Salterton Pebble Bed, Devon. Fig. 12, B 21533, latex cast of external mould of a pedicle valve, lectotype (sel. Cocks 1978 : 74), originally figured by Davidson (1869 : pl. 32, fig. 29), × 2·0; W. Vicary Coll. Fig. 13, B 21524, internal mould of a brachial valve, Davidson (1869 : pl. 32, figs 32, 32a), × 1·8; W. Vicary Coll. Fig. 14, B 21509, latex cast of the internal mould of a brachial valve, × 2·0. Figs 15, 16, B 21616, latex cast and internal mould of a brachial valve, lectotype of *budleighensis* (sel. Cocks 1978 : 65), originally figured by Davidson (1870 : pl. 5, fig. 12 lower right), × 3·0. Fig. 17, latex cast of the interior of another brachial valve on the same slab as Figs 15 and 16, × 2·0. Fig. 18, BB 95940, latex cast of the external mould of a brachial valve, × 3·0; W. Vicary Coll. Fig. 19, B 21621, latex cast of two internal moulds of pedicle valves, × 3·0; W. Vicary Coll. Figs 20, 21, BB 95941, internal mould of a brachial valve and latex cast of it, × 2·4; W. Vicary Coll. Fig. 22, BB 95942, internal mould of a pedicle valve × 3·0; W. Vicary Coll.

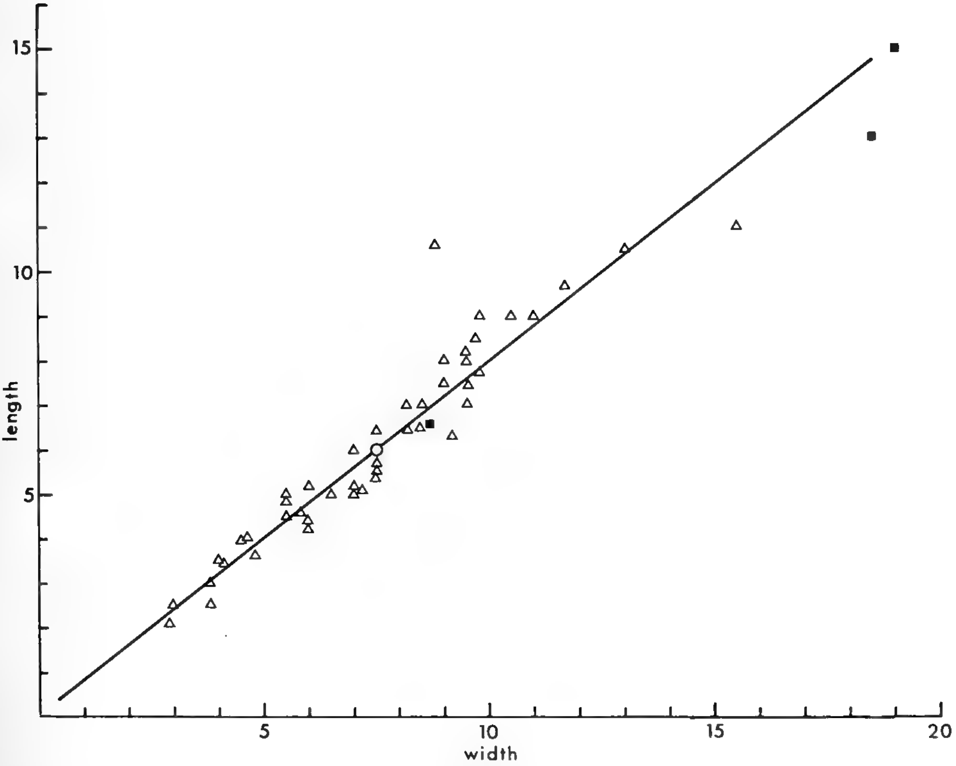
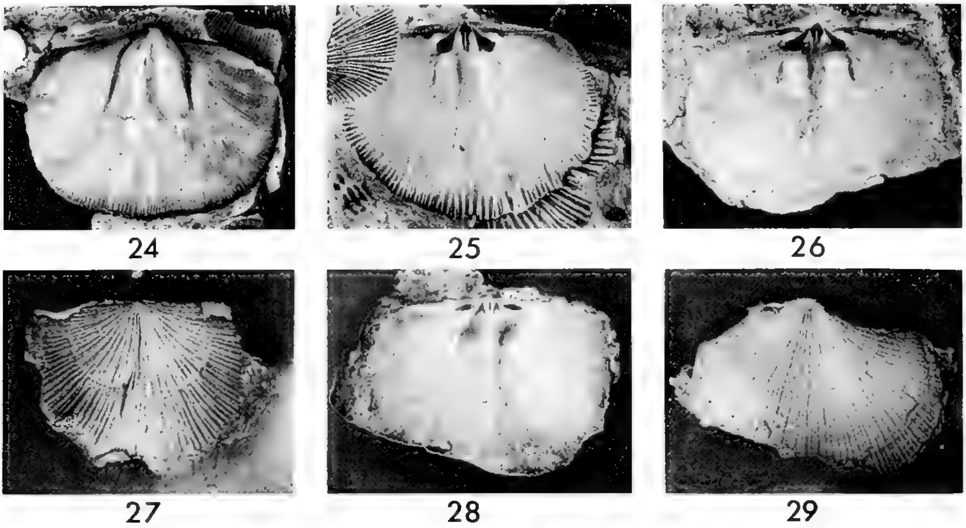


Fig. 23 Length–width measurements of brachial valves of *Tafilaltia valpyana* (Davidson, 1869), from pebbles of late Llandeilo age in Trias, Budleigh Salterton, Devon. The solid squares represent the three specimens figured by Davidson as *valpyana*; the open triangles represent 45 specimens, including the lectotype, of *budleighensis* from the same locality. The average (of the *budleighensis* sample) and regression line of the length on the width are also shown.

with which they occur. This smaller form had been recognized by Salter (1864), in his first descriptions of Budleigh Salterton fossils, as being similar to species from the Bohemian province, and he had identified it as *Orthis redux* Barrande, a species since made the type of *Drabovia* Havlíček, 1951. It was not until 1870 that Davidson felt he could formally separate the two forms, when he gave the Devon brachiopod the varietal name of *budleighensis*. We can now demonstrate (Fig. 23) that *valpyana* and *budleighensis* exhibit similar growth ratios, and so consider the better-known latter name to be a junior synonym.

The species can be readily identified as an heterorthid, and our initial reaction was to compare it with an early undescribed species of *Heterorthis* from the late Llandeilo of Dyfed, Wales (Addison 1974). Similarly, M. G. Bassett has assigned closely related material from Cornwall to the genus *Heterorthina*. However, comparisons between *valpyana* and *praeculta*, the type species of *Heterorthina*, whilst showing no significant difference in valve outline, relative length of muscle scars and dorsal cardinalia, do show a significant difference in the relatively greater depth of the pedicle valve ($5\% > p > 2\%$), and we have also noted that *H. praeculta* has more clearly differentiated and more deeply impressed ventral muscle scars, particularly towards their anterior. The opportunity is taken here to illustrate some topotype specimens of *Heterorthina praeculta* (Figs 24–29), including the lectotype (selected Cocks 1978 : 74) which has not been figured since its original illustration by Bancroft (1928:



Figs 24–29 Topotype specimens of *Heterorthina praeculta* Bancroft, 1928, from the Cheney Longville Flags (Caradoc: Marshbrookian), south side of road from Cwm Head to Marshbrook, Shropshire, Grid Reference SO 437896. Fig. 24, BB 9152, internal mould of a pedicle valve, lectotype (sel. Cocks 1978 : 74), originally figured by Bancroft (1928 : pl. 2, fig. 18), × 1·5; B. B. Bancroft Coll. Figs 25, 29, BB 7288, internal mould of a brachial valve and latex cast of the external mould, × 2·0; J. M. Hurst Coll. Fig 26, 28, BB 68827, internal mould and latex cast of a brachial valve, × 2·0; B. B. Bancroft Coll. Fig. 27, BB 72289, latex cast of the external mould of a brachial valve, × 3·0; J. M. Hurst Coll.

pl. 2, fig. 18). Although the cardinalia of *valpyana* resembles some variants of *Heterorthina kerfornei*, such as the specimen figured by Melou (1975 : pl. 23, fig. 5), other specimens of *kerfornei*, and indeed most *Heterorthina* generally, differ from *valpyana* in possessing a cleft shaft supporting the myophore (cf. Hurst 1979).

In our opinion, the species is best assigned to *Tafilaltia* Havlíček, a genus considered ancestral to *Heterorthis* by Havlíček (1977) and in its earlier species showing poorly differentiated ventral musculature, as in *valpyana*. The ponderous tripartite myophore and absence of chilidium is diagnostic of *Tafilaltia*, and indeed Havlíček (1970 : 17–21) included material from the Grès de May within his *Tafilaltia dalmanelloides*, which is accepted here, and is why we have suppressed the latter species as a junior synonym of *valpyana*. Comparisons between *valpyana* from Budleigh Salterton and apparently conspecific French material (Fig. 30) from the Grès de petit May, May, Normandy (B 85258), showed no significant differences in any of the nine characters tested, i.e. the outline of both valves (data for 23 brachial valves included in Fig. 31), the relative depth of the pedicle valve, the shape and relative length of the dorsal cardinalia, and the shape and relative length of both dorsal and ventral muscle scars. Similarly no significant differences in dorsal outline or shape and relative length of ventral muscle scars can be detected through comparisons made with Addison's unpublished statistics (1974: tables 14 and 15) of the small heterorthid mentioned above (*Heterorthis* sp. nov.) from late Llandeilo to early Caradoc sandstones of Lampeter Velfrey, Dyfed. However, this undescribed form differs from *valpyana* in its sharply-differentiated ventral muscle scars, and perhaps represents a direct link between *Tafilaltia* and better-known Caradoc *Heterorthis* such as *Heterorthis alternata* (J. de C. Sowerby) (see Williams 1963).

Fig. 30 *Tafilaltia valpyana* (Davidson, 1869) from the Grès de petit May, May, near Caen, Normandy, France. B 85258, part of a slab containing numerous external and internal moulds of both valves, × 3·0; Sir R. I. Murchison Coll. *per* Geological Society of London Coll., pres. 1911.

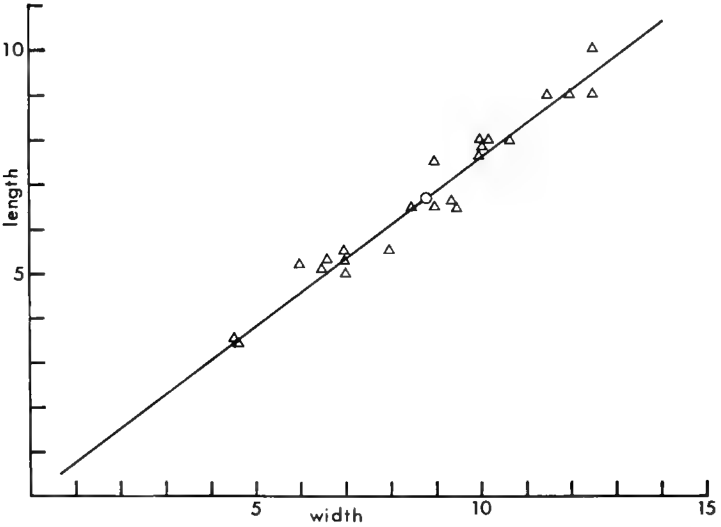


Fig. 31 Length–width measurements of 23 brachial valves of *Tafilaltia valpyana* (Davidson, 1869) from the Grès de petit May, May, near Caen, Normandy, France, all on slab B 85258 (Fig. 30). The average and regression line of the length on the width are also shown.

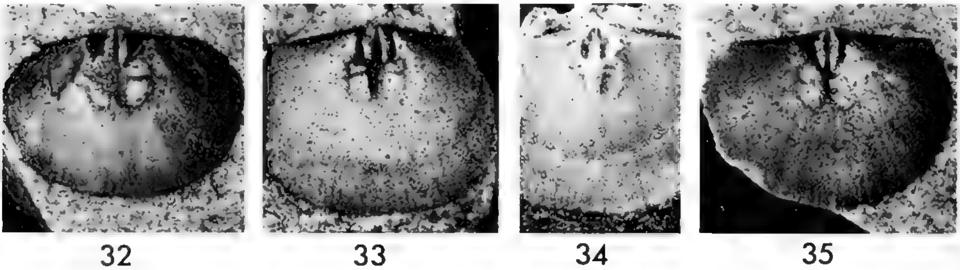
Family **LINOPORELLIDAE** Schuchert & Cooper, 1931

Genus ***SALOPIA*** Williams, 1955

Salopia ?pulvinata (Salter, 1864)
(Figs 32–35)

1864 *Orthis pulvinata* Salter : 294; pl. 17, fig. 8.
1870 *Orthis pulvinata* Salter; Davidson : 83 *pars;* pl. 5, figs 17, 19, ? fig. 18.
1881*a* *Orthis pulvinata* Salter; Davidson : 357; pl. 41, figs 10, 11.
1978 *Pionodema ? pulvinata* (Salter) Cocks : 80.

DESCRIPTION. Large, transverse linoporellid with brachial valve averaging 71% as long as wide (range 71–72%), and between 19 and 26% as deep as long in 3 valves. Dorsal interarea short, flat, anacline, with wide open notothyrium. Ornament poorly known, consisting of faint fine radial costellae. Cardinal process simple, blade-like, consisting of anteriorly widening shaft merging with notothyrial platform. Brachiophores short, with convergent bases extending forward for about one-fifth to one-quarter valve length; sockets narrow, with small curved fulcral plates. Dorsal adductor scars elongate and quadripartite, averaging 49% as long as valve (range 47–52%) in three valves, with anterior pair of scars larger than posterior pair. The muscle field is divided by a broad median septum. Pedicle valve unknown.



Figs 32–35 *Salopia ? pulvinata* (Salter, 1864) from late Llandeilo pebbles in Trias, Budleigh Salterton, Devon. Fig. 32, B 21523, internal mould of a brachial valve, lectotype (sel. Cocks 1978 : 80), originally figured by Salter (1864 : pl. 17, fig. 8), × 1·5. Figs 33, 34, BB 70910, internal mould of a brachial valve and latex cast of it, × 2·5; W. Vicary Coll. Fig. 35, B 13051, internal mould of a brachial valve, × 2·5; T. Davidson Coll. *ex* Winwood.

MATERIAL. Lectotype B 21523 (sel. Cocks 1978 : 80), the part and counterpart of a brachial valve (Fig. 32), figured Salter (1864 : pl. 17, fig. 8); from Ordovician pebble in Trias, Budleigh Salterton, Devon. Other material: two other brachial valves, B 13051 and BB 70940, both internal moulds only, from the same locality.

DISCUSSION. Only three brachial valves and no pedicle valve are known of *pulvinata*; although Davidson (1881*a* : 358) states that 'M. de Tromelin informs me that *O. pulvinata* occurs in company with *O. Berthoisi,* var. *erratica,* at Saint Germain-sur-Ille, La Bouëxiere, Champeaux (Ille-de-Vilaine), and in other places', no French material is available for comparison. In the absence of any pedicle valves the generic determination can only be provisional, hence the query, but the three brachial valves are certainly similar to *Salopia turgida* (M'Coy), as recently revised by Lockley & Williams 1981, particularly in their simple blade-like cardinal processes and quadripartite adductor muscle scars. However, *pulvinata* is more transverse (71% as long as wide, as compared with 88% for *turgida*), the brachiophores of *turgida* are relatively long in comparison with the quite short brachiophores of *pulvinata*, and the adductor muscle scars are more deeply impressed and less elongate in *pulvinata* than in *turgida.* A full revision of these species, and their relationship to the other species of *Salopia*, such as *S. globosa* (Williams, 1949), *S. triangularis* (J. de C. Sowerby, 1839) and the type species, *S. salteri* (Davidson, 1869) and its subspecies *gracilis* Williams, 1955, must await the discovery of pedicle valves at Budleigh Salterton or the collection of more material in France.

Acknowledgements

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Felix Oswald's Turkish Algae

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Synopsis

Algae from the Cretaceous and Caenozoic of Turkey, collected by Felix Oswald in 1898, are re-examined in the light of over eighty years of subsequent algal studies.

Introduction

The collections of the British Museum (Natural History) are incredibly rich, not merely in the major treasures of the national collection, but in original historical specimens, unique in their day, which were the foundations of so much that followed.

Algae are not usually attractive fossils when collected. Although studied by numerous nineteenth- and early twentieth-century microscopists, the organized development of algal studies generally as an important branch of micropalaeontology did not take place until after the second world war. It was largely initiated as part of the oil industry's researches at that time, to supplement their extensive pioneer use of Foraminifera. At the BM (NH), a separate subsection of fossil algae was not individualized from the fossil plants until 1969, when I was entrusted with this task.

Because of the extensive connections of the oil industry with the Middle East, the national collection of fossil algae contains much material from this area, mostly from sampling carried out between 1930 and 1960. It is therefore of interest to note the presence in the collections of a few Middle East samples collected in 1898, and recognized as algal at the very beginning of the present century.

Felix Oswald (1866–1958; obituaries by Swinnerton 1958, 1959) accompanied W. N. B. Lynch on his second tour of eastern Turkey (then known as Turkish Armenia) in 1898. Oswald's detailed geological observations in this then little-visited area were submitted as an academic thesis in 1905 and fully published with illustrations in 1906, in a book which he type-set and produced himself (Oswald 1906; preface). He acknowledges the help of R. Bullen Newton, then on the staff of the BM(NH), in connection with his palaeontology.

There are four relevant samples in the Museum's collections. They are of Lower Cretaceous, Palaeocene–Lower Eocene and Miocene (two) geological age; all but the second were figured by Oswald. Their re-study, and discussion, is set out below.

Discussion

1. Lower Cretaceous

Oswald (1906) : '*Munieria*'; plate facing p. 234 and pp. 236, 340. Buff-grey limestone from Akhveran, 42 km ESE of Bayburt (40° 15′ N, 40° 16′ E; eastern Turkey). Turkish Geological Map 1 : 800,000, Sheet 4, Erzerum (1943).

The large dasyclad in Oswald's original thin section was identified (probably by Bullen Newton) as a *Munieria* (Deecke 1883); the comparison given is with Hovelacque (1900 : pl. 46, fig. 2). This latter, however, does not show a *Munieria* but *Salpingoporella* sp.

Bull. Br. Mus. nat. Hist. (Geol.) **35** (3) : 125–129 Issued 29 October 1981

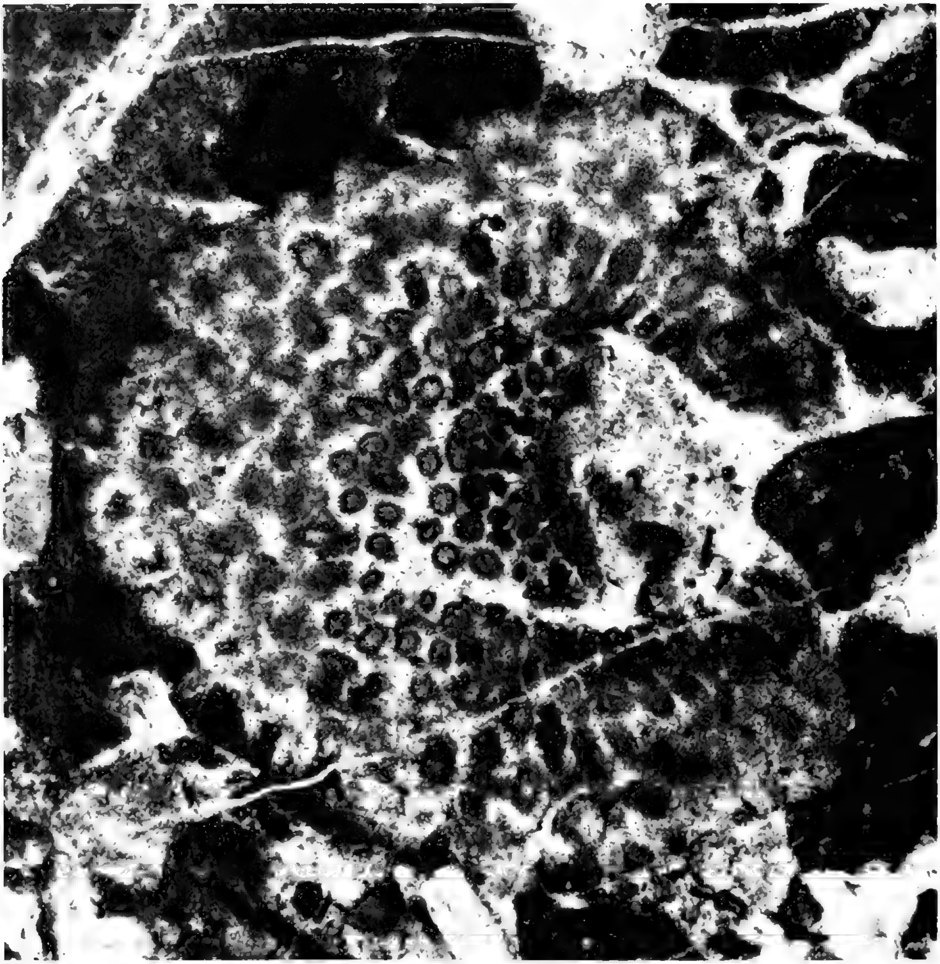

Fig. 1 *Euspondyloporella* sp. Oswald's original section, × 40. BM(NH) Palaeont. Dept., reg. no. V11063a.

(Conrad 1970 : 70, and personal communication). Oswald's actual section (refigured here, Fig. 1) shows a *Triploporella* or related genus; the section is oblique and of an individual showing pressure-displacement of the structure, so it is not precisely diagnostic. However, in one of further thin sections now prepared from the small original sample, another dasyclad section (uncrushed) was revealed, showing branches of a different form (Fig. 2). It seems unlikely that these two sections are of different taxa and they may well be of the same individual. It is stated of *Euspondyloporella duplicata* Sokač & Nikler (1973 : 23) that 'the primary [branches] are represented by two forms. In the club-shaped [top] portion of the alga, they are thin and tubular, slightly thickened in the distal part. Below the top, the primary branches consist of a handle occupying $\frac{1}{3}$ of the length, and of an elongated egg-shaped thickening occupying $\frac{2}{3}$ of the total length of the branch'. In the Oswald material, the original section shows the second pattern, and the new section the first. Further evidence for this determination lies in the large number of primary and small number of secondary branches, the spore-packed branches seen (when not replaced by infill calcite) and

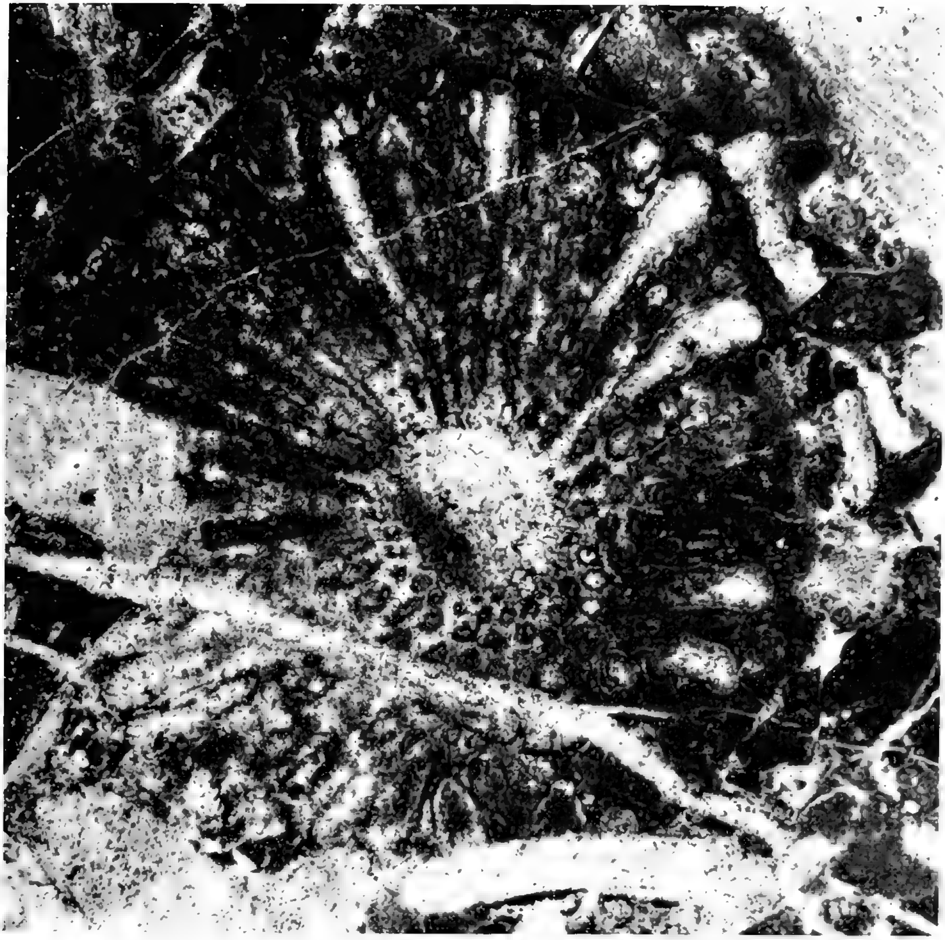

Fig. 2 *Euspondyloporella* sp.; a second section showing club-shaped branches from the apex of the thallus, × 30. Reg. no. V11063b.

gross dimensions, all shown both by Sokač & Nikler's Jugoslav type material and Oswald's Turkish material.

It would seem, therefore, that Oswald's dasyclad can certainly be identified as an *Euspondyloporella* (Triploporelleae), and probably as *E. duplicata*, though suitable additional sections would be necessary to confirm this.

The other accompanying organisms are a typical Tethyan Lower Cretaceous assemblage for this facies, which is widespread through the circum-Mediterranean and Middle East. They comprise the microproblematicum *Carpathoporella fontis* (Patrulius) (see Jaffrezo 1974 for the involved synonymy), the algae *Cayeuxia* sp. and *Solenopora* sp. and the problematic *Lithocodium aggregatum* Elliott. Bivalve and echinoid fragments occur. Oswald (1906 : 339, 340) stated that the algal limestone was succeeded by radiolarian limestone. South of the Turkish frontier, in the Lower Cretaceous of Iraqi Kurdistan, the organic Qamchuqa Formation (with algae) intertongues with the basinal radiolarian

Balambo Formation (Dunnington, Wetzel & Morton 1959 : 50, 230), and Oswald's Turkish account seems compatible.

The exact level of the type-material of *Euspondyloporella* in the Lower Cretaceous was given as probably Barremian–Aptian (Sokač & Nikler 1973 : 8). The Oswald sample, to which he assigned Hauterivian age, does not show orbitolines etc., and if therefore from a pre-orbitoline horizon, a Hauterivian–Barremian age seems likely.

2. Palaeocene–Lower Eocene

Oswald (1906) : '*Lithothamnion*'; pp. 249, 418. Dark-grey limestone from Chörak Khan, 45 km NW of Bayburt. Turkish Geological Map 1 : 800,000, Sheet 3, Sivas (1946).

'*Lithothamnion*' was for a long time used as a general term for a very wide variety of coralline algae, Recent and fossil. The examples in Oswald's rock are cylindrical units of the segmented coralline *Amphiroa*; probably a new species, but the rock and its fossil content are markedly affected by mineralization and diagenesis – Oswald refers to the rock as a marble (Oswald 1906 : 248, 418) – and most examples of the fossil are obscured by this. Associated are fragments of *Archaeolithothamnium* sp., ? *Pycnoporidium*, ? *Elianella* (*Parachaetetes* auctt.), and what from outline and traces of structure remaining is probably the feather-alga, *Distichoplax biserialis* (Dietrich) Pia. Molluscan and echinoid debris is also present.

This is probably a Palaeocene–Lower Eocene assemblage; a better-preserved sample could confirm this. All of these genera and species occur in rocks of that age in northeastern Iraq, south of the Turkish frontier, and so Oswald's assigned age of Middle–Upper Eocene can be modified. His '*Lithothamnion*' is an *Amphiroa* sp. (Fig. 3) showing wide peripheral perithallus bordering the distinctive zones of the medullary hypothallus, and it is not the same as the Iraqi Palaeocene *Amphiroa elliotti* (Johnson 1964). The Turkish species is not formally described as new by reason of the preservation.

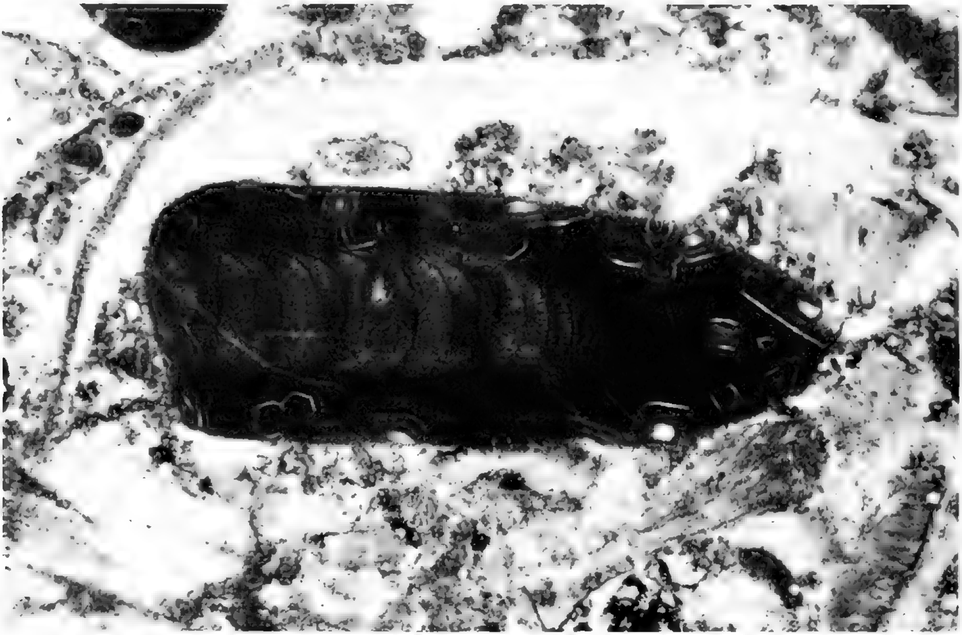

Fig. 3 *Amphiroa* sp.; original section of Oswald, × 50. Reg. no. V11064a.

3. Miocene

Oswald (1906): '*Lithothamnion ramossissimum* Reuss'; p. 52 and facing pl., fig. 9; p. 452. Light-brown limestone from Madrak, 19 km SSE of Erzerum. Also p. 81 and facing pl., fig. 1; p. 453. Creamy-pink limestone from Kanjean, 48 km north of Malazgirt. Malazgirt (39° 09′ N, 42° 30′ E) is 138 km SE of Erzerum. Turkish Geological Map 1 : 800,000, Sheet 4, Erzerum (1943).

Specimens from these two samples are preserved in the collections of fossil bryozoa at the BM(NH), reg. nos D 7958–7967 incl. The thin sections shows a rich algal–bryozoan assemblage similar to that of the European Vienna-Basin Miocene (Leithakalk), the algal microflora of which was revised in detail by Conti (1946). Oswald's figured Madrak specimen appears to be *Lithophyllum piai* Conti and his Kanjean specimen *Palaeothamnium archaeotypum* Conti.

Conclusions

It is noticeable how, in spite of the relatively rudimentary knowledge of fossil algae available at the beginning of this century, Oswald assigned his material to approximately the right geological ages. He did not, of course, depend solely upon the algae; stratigraphy and other fossils were available. What is remarkable is his thoroughness in doing all that could be done to determine the algae, then regarded as of very little value. Modern sampling of these localities would yield more and perhaps better-preserved materials, but his pioneer effort is noteworthy.

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J. A. Moy-Thomas and his association with the British Museum (Natural History)

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Introduction

The British Museum (Natural History), as a national institution for the repository and care of natural history specimens and furtherance of their understanding, owes its efficiency not only to those employed there but also to that very large body of dedicated amateurs and professional scientists who collect, donate and work on the collections. Over the last hundred years their contributions have been very significant and there has been a history of close collaboration. For instance, Richard Lydekker (1849–1915), who worked for the Indian Geological Survey, compiled the catalogues of the Museum's collections of fossil mammals, reptiles and birds. A. W. Wrigley (1885–1953), a draughtsman, worked closely with Museum staff to produce many papers on Tertiary molluscs and Eocene foraminifera.

It seems appropriate in this, the Museum's centenary year, to acknowledge the contributions made by our non-Museum colleagues. One such was J. A. Moy-Thomas, who was closely associated with the fish section immediately prior to the second world war. His association with the Museum was unfortunately brief, but during those few years he collected and examined a variety of interesting fossil fishes in our collections and, above all, typified that essential collaboration between Museum staff and others which has so often proved rewarding.

J. A. Moy-Thomas

James Moy-Thomas, eldest son of Mr and Mrs Alan Moy-Thomas, was born in 1908. Billy, as he was affectionately known, was sent to Harrow from whence he obtained an open scholarship to Christ Church, Oxford. After three years of study he was awarded a first class honours degree in zoology in 1930. The following session he remained up at Oxford and attended classes in geology. For most of this period his tutor was Dr G. de Beer, with whom he was later to form a close friendship. In the summer of 1932 at the instigation of de Beer he visited the Zoology Department of the University of Glasgow. There he enjoyed the hospitality of Professor Graham Kerr and was encouraged to re-examine developmental stages of *Polypterus*, making use of the specimens brought back by the late John Samuel Budgett, including the material used by Kerr himself in 1907. Moy-Thomas's work on *Polypterus* was published in 1934. In the meantime he worked as an assistant to Professor Walter Garstang at Leeds where he met and married Miss Joy Mitchell.

This period also saw the publication of his first paper, in collaboration with T. H. Harrison of Pembroke College. It consisted of a short note to *Nature* on the St Kilda house mouse. Two more papers followed in 1933 and in the ensuing years he published a further 34 papers. He returned to Oxford in the summer of 1933 to the post of University demonstrator in the Department of Zoology and Comparative Anatomy. This was in essence

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a research fellowship and in his first year back at Oxford J. A. Moy-Thomas attended various lecture courses, including those of Mr J. Z. Young who was later to become a close friend. During the next seven years he also became a good friend and colleague of Dr E. I. White of the British Museum (Natural History), and they both frequently attended meetings of the newly-formed Tetrapods Club (a dining club in London, founded in 1930 for those interested in vertebrate zoology). E. I. White introduced him to Sir Arthur Smith-Woodward (erstwhile keeper of the Department of Geology) who in 1935 gave Moy-Thomas permission to use his many unpublished notes on fossil fishes.

In 1936 Moy-Thomas shared the Rolleston Memorial Prize with B. G. Maegraith (a fellow of Exeter College) and in the following year he was re-elected to the post of University Demonstrator and lecturer. Shortly afterwards he became the first holder of the E. T. Browne Fellowship at Queen's College.

In each of the years 1935, 1937, 1938 and 1940 he received small sums of money from the Godman Exploration Fund (£20 in 1935, £30 in the subsequent years) to enable him to collect fossils for the British Museum (Natural History). He was a diligent collector with infinite patience who furnished the Museum with some 127 specimens of fossil fishes (49 in counterpart), mainly from Glencartholm, only 9 of which were purchased. On many of his collecting trips he was accompanied by his wife but at Glencartholm in 1933 he was helped by Mr W. S. Bullough (later Professor of Zoology at Birkbeck College, London). Ironically it was Bullough who found the specimens of *Tarrasius* on which Moy-Thomas's 1934 Zoological Society paper was based.

In 1939 Moy-Thomas joined the English–Norwegian–Swedish (E.N.S.) expedition to Spitzbergen (not Greenland as is erroneously reported in his obituary notices) which was the result of an intimate collaboration between the British Museum (Natural History), the Paleozoological Department of the Riksmuseum in Stockholm and the Paleontological Museum in Oslo (Fig. 1). The initiator was Professor E. A. Stensiö and the expedition was financed by all three countries. The English members were Dr E. I. White, J. A. Moy-Thomas, J. Brough and W. N. Croft. The Norwegians were Professor A. Heintz, Sven Føyn and the student Aarhus. The Swedish members were Professor E. A. Stensiö, leader of the expedition, E. Jarvik and G. Wängsjö, and they were accompanied by Dr N. Della of Riga.

At the beginning of the war Moy-Thomas started in the intelligence service but soon volunteered for flying work. Having successfully completed his tour of operations as a night fighter observer/navigator he was posted to R.A.F. Defford which was a non-operational unit concerned with the development and pre-service testing of air interception apparatus (airborne radar). This apparatus was being developed by the Telecommunication Research Establishment (T.R.E. Malvern). Here, together with Professor Derek Jackson F.R.S. (Spectroscopy, Oxford), he flew as a radar observer in Mosquitoes and Beaufighters. Moy-Thomas was killed in a motor accident while on duty on February 29, 1944.

He was a sociable person with a great gaiety, sense of humour and zest for life. Everyone with whom he came into contact seems to have liked him. He was a very good golfer (handicap 3), enjoyed a game of darts and was an avid stamp collector. At Oxford he is remembered as a most successful teacher and tutor and at the British Museum (Natural History) as an endearing character with a sense of humour and a first-class memory. He greatly admired both Professors W. Garstang and E. S. Goodrich and for the latter he erected the genus *Goodrichia* (a large shark from Glencartholm) in 1936. The name was unfortunately pre-occupied (by a mollusc) and it was subsequently changed posthumously to *Goodrichichthys* (Moy-Thomas, 1951).

During his short career J. A. Moy-Thomas worked mainly on fossil fishes (32 papers), particularly shark-like forms and palaeoniscids. However, he still found time for experimental work and as late as 1940 was examining the dermal bones of the skull of the trout in an effort to determine whether or not their development was influenced by the neuromast organs. Although one of his longest papers was on coelacanths perhaps his most notable was on *Palaeospondylus.*

Fig. 1 J. A. Moy-Thomas (left) shown here with W. N. Croft (1915–1953, a palaeobotanist in the British Museum (Natural History)) during the English–Norwegian–Swedish expedition to Spitzbergen (1939). Croft, like Moy-Thomas, died at a young age. He collected a large number of Old Red Sandstone fishes and Devonian plants for the Museum.

Interpretation of *Palaeospondylus*

Genus ***PALAEOSPONDYLUS*** Traquair, 1890

Fig. 2A–C

TYPE SPECIES. *P. gunni* Traquair, 1890.

Towards the end of his short career Moy-Thomas turned his attention to *Palaeospondylus gunni* Traquair, an enigmatic fossil from the Middle Old Red Sandstone of Caithness. This little fossil, barely reaching 60 mm in length, has been a palaeontological conundrum since its first description by Traquair (1890); Dean (1904 : 425) remarks '*Palaeospondylus*, like Gloster, seems to have been born to bite the world'. Two Caithness men, Alexander and Marcus Gunn, 'delivered' *Palaeospondylus* into the scientific world by bringing it to the attention of Traquair. Their collecting efforts at Achanarras were recognized by Traquair who named it after them. *Palaeospondylus* has certainly had a 'bite' at many palaeontologists and zoologists, who have reacted by referring it to one or other of the many fish groups or, in some cases (Gill 1896; Dean 1898, 1900), to specially-erected classes or subclasses. When first described *Palaeospondylus* was regarded as an agnathan and this opinion received some initial consensus (Traquair 1890, 1893*a*, 1893*b*, 1894, 1897; Howes 1892; Woodward 1892, 1898; Dean 1895; Stensiö 1927; Bulman 1931; Ayers 1933; White 1935). This consensus was challenged on numerous occasions. Sollas & Sollas (1903) suggested it to be an elasmobranch. Kerr (1900) and Miller (1930) compared it to a larval dipnoan, Dawson (1893) to a larval amphibian, Kyle (1926) to a larval herring, Dean (1904) to a holocephalan, and Jarvik (1980) regarded it as a larval *Osteolepis.* Huxley, it is said (Dean 1900), thought it to be a larval *Coccosteus* while Dean (1896, 1898, 1900) and Abel (1912) regarded it as a larval arthrodire. Finally, Moy-Thomas (1940) crystallized its placoderm relationships by suggesting it to represent a stegoselachian (a naked placoderm). Most modern text books (e.g. Parker & Haswell 1963, Romer 1966) deal with *Palaeospondylus* as an appendix to the placoderms.

Customarily, uncertainty about relationships of fossils arises from material which is poorly preserved or scanty, or both. But *Palaeospondylus* is known by, literally, thousands of specimens, almost all of which have been found at a single slate quarry on Achanarras Hill where it is distributed through several beds (Rayner 1963). At least one specimen was found in contemporaneous strata at Niandt (Traquair 1909) and a further example in the Sandwick Fish Bed at Cruaday Hill, Orkney (Trewin 1976). The Museum collections contain some 450 specimens. It is true that many are poorly preserved, leading Traquair (1890 : 485) to describe the head as a 'flat crushed mass of bony bars'. Other specimens, however, are preserved almost as well as other representatives of the Achanarras fish fauna (*Coccosteus, Homostius, Cheirolepis, Cheiracanthus, Mesacanthus, Rhadinacanthus, Diplacanthus, Pterichthyodes, Dipterus, Osteolepis, Glyptolepis*), the relationships of which have rarely been in doubt. *Palaeospondylus* has also been the subject of various preparation techniques, examples of which are in the Museum's collections. Sollas & Sollas (1903) used *Palaeospondylus* as one of their first experimental materials to produce wax-plate reconstructions (P.9856, P.9859–61). Bulman (1931) produced whole mount preparations (P.16120–5) and one specimen (P.22393) has been prepared by the acid transfer technique of Toombs & Rixon (1950). So the plea that the material is poor or insufficient fails in this case.

We suggest, instead, that the problem with *Palaeospondylus* is one generally inherent in fossils: that is, they are data 'in search of interpretation' (Nelson 1978 : 329). There are three main aspects to this problem. The first is incompleteness, in the sense that only the hard parts or a limited amount of the soft parts are preserved, thus reducing the amount of comparative information available for interpretation. Secondly, 'a fossil is meaningless until it can be interpreted in the light of a Recent model' (Patterson 1977 : 621). Finally a fossil is, by its very nature, in danger of being furnished with an ancestral status by over-zealous palaeontologists. The problems posed by *Palaeospondylus* fall into all three categories. The last-mentioned area was particularly characteristic of the early studies of *Palaeospondylus,* as the following remarks made by Dean (1904) show: 'For if the remains of *Palaeospondylus* are so poorly preserved that they cannot be definitely described, why do we continue to add papers to the troublesome literature? The only possible excuse is that the creature is seductive, full of suggestions as to the origin of the gnathostomes, and the mode of evolution of the jawless vertebrates.'

We shall begin by examining the earliest theories of the relationships of *Palaeospondylus* with the agnathans. Traquair (1890) noted the similarity in the shape of the head between *Palaeospondylus* and *Myxine* and, considering the period in which Traquair was working, it is not surprising that a relationship between the two should have been suggested. Toward the end of the nineteenth century palaeontology, through its concern with time, was beginning to emerge as the 'authority' on questions of phylogeny. Darwin predicted that, were the fossil record more carefully examined, progenitors of modern groups and links between groups would be found. So, one searched the rocks for suitably primitive and stratigraphically suitable candidates. *Palaeospondylus* was judged to be such an approximation to an ancestor of modern agnathans or, more specifically, to myxinoids (Traquair 1890; Bulman 1931). *Palaeospondylus* is naked like modern agnathans and was originally thought to have no jaws or fins. Its nakedness made it a better candidate than other jawless vertebrates—the heavily armoured heterostracans and osteostracans.

Several characters have been used to suggest relationship between *Palaeospondylus* and Recent agnathans: 1 – no jaws (Traquair 1890, 1893*a, b,* 1894; Stensiö 1927); 2 – no limbs (Traquair 1890, 1893*a, b,* 1894, 1897; Woodward 1892; Stensiö 1927; Bulman 1931);

3 – cirri surrounding a circular opening at the anterior end of the head, interpreted as a mouth (Woodward 1892; Traquair 1893*a*) or a nasal opening (Traquair 1893*b*, 1894; Stensiö 1927; Bulman 1931); 4 – single median recess at the anterior end of the cranium, interpreted to house a single nasal organ (Woodward 1892; Traquair 1893*b*; Stensiö 1927; Bulman 1931); 5 – V-shaped branchial pouch supports behind the head (Bulman 1931); 6 – dichotomized radials (often incorrectly referred to as fin rays) in caudal region (Traquair 1894); 7 – protocercal tail (Traquair 1893*a*, *b*, 1894, 1897); 8 – no discrete ossifications in the braincase (Traquair 1894).

Characters 1 and 2 are primitive, present in any non-gnathostome, and are not therefore agnathan characters any more than they are echinoderm or nematode characters. If the 'mass of bony bars' lying on the (presumed) ventral surface are not evidence of visceral arches then what are they? Three interpretations have been offered; that they are labial cartilages (Woodward 1892), that they are, in fact, ridges on the underside of the neurocranium and represent interbranchial ridges similar to those in cephalaspids (Stensiö 1927), or that they are remains of various cartilages supporting the tongue as in myxinoids (Bulman 1931). Most authors agree, as do we, that the 'bony bars' are visceral structures and that many are free or articulate with the braincase. This would seem to rule out any comparison with either lampreys or hagfishes, in which the visceral skeleton is unjointed and continuous with the neurocranium. Only gnathostomes show a jointed visceral skeleton which articulates with the neurocranium.

Character 3 has been commonly used for suggesting agnathan relationships, particularly with myxinoids. The more popular interpretation is that the 'cirri' (rostralia) surround a circular opening which represents a single nasal opening. Only hagfish, amongst agnathans, have a series of rostral cartilages (of different lengths) reaching in front of the nasal region. *Myxine* also has a row of cartilaginous rings around the nasal tube (Cole 1909 : fig. 1). Moy-Thomas (1940) examined several well-preserved specimens (P.22394, P.22401, P.22410) and found that considerable variation exists between individuals in the size and, to a lesser extent, the number of 'cirri'; he suggested that these together represented a fenestrated capsule(s). We would concur with this interpretation.

As to character 4, a median recess at the anterior end of the cranium is found in a variety of craniate embryos and is not an agnathan character. Character 5 is an interpretation of structures which have been otherwise interpreted as pectoral girdles and/or fins (Moy-Thomas 1940; Dean 1896). Character 6 is also found in elasmobranchs and lungfishes (Fürbringer 1904) and character 7 was shown to be a mistaken observation (Traquair had restored the tail upside down). The tail is now regarded as being asymmetrical with a slightly larger lower lobe. In any event, a protocercal tail is found in Recent lungfishes (Miller 1930).

Character 8 is difficult to evaluate since the nature of the preserved material is not clear. Microscope sections show no structure and the chemical composition, like that of other fossils from Achanarras, 'now consists of coal' (Sollas & Sollas 1903 : 273). The skeletal material has been interpreted as bone (Traquair 1890), or as calcified cartilage (Traquair 1839*a*), but there is no evidence to favour either of these suggestions.

So, in our opinion, not one piece of evidence has been produced suggesting *Palaeospondylus* to be an agnathan and interpretation on an agnathan model (hagfish or lamprey) is not justified. The presence of ring centra would also militate against agnathan relationships. Hagfish have no chondrification or ossification around the notochord, lampreys have cartilaginous dorsal arcualia and the only evidence of a vertebral column in ostracoderms is the impressions of (presumably) neural arches in some cephalaspids (Janvier 1980). The presence of ring centra in *Palaeospondylus* as an agnathan ancestor was explained by assuming that absence of skeletal ossification is a derived condition of Recent agnathans. We do not wholly share this view. Hagfishes, which we regard as the sister group of lampreys and gnathostomes (Løvtrup 1977; Hardisty 1979; Janvier & Blieck 1979), never possessed bone or paired fins in their history. This might also be true of lampreys, in which case we would regard lampreys and anaspids as the sister group of osteostracans and gnathostomes (Janvier, personal communication).

We accept that *Palaeospondylus* has visceral arches, albeit they are difficult to interpret, and agree with Moy-Thomas (1940) that there is evidence for both pectoral and pelvic fins. We therefore believe that *Palaeospondylus* is either the sister-group of gnathostomes or a member of some gnathostome subgroup. Several suggestions have been offered (p. 134). Sollas & Sollas (1903) considered it to be an elasmobranch but one that 'proceeded in its subsequent development along an independent course, losing its limbs, if it ever possessed them, and acquiring a highly organised vertebral column, homoplastic in character with that of cyclo-spondylous Selachians' (1903 : 290–291). The main reason given by these authors for elasmobranch affinities is the general similarity in the shape of the head: the eye is situated immediately in front of the otic capsule, and there is a saddle-shaped ledge on the ventral surface of the neurocranium, marking the position of the pituitary body. We find nothing particularly elasmobranch about these features: we cannot confirm the presence of a 'saddle-ledge' but note that the ventral profile of *Squalus* is very similar to that of larval *Acipenser* and *Neoceratodus* (de Beer 1937). The particular shape of the ventral profile may thus be no more than a general early ontogenetic feature of gnathostomes. Dean, in perhaps light-hearted mood (1904 : 425), suggested that *Palaeospondylus* is a holocephalan. He based this suggestion on four characters: continuous dorsal fin (no evidence), protocercal tail (incorrect observation), ring vertebrae (known elsewhere – chondrichthyes, larval teleosts, sarcopterygians) and a huge head.

Moy-Thomas regarded *Palaeospondylus* as an adult and to be a stegoselachian, a group of placoderms in which there is little development of armour – Stensioellidae and Rhenanida. He chose to make comparisons with these but also with acanthodians, presumed close relatives of placoderms (Watson 1937), and arthrodires. Moy-Thomas's model was therefore a placoderm + acanthodian morphotype (an aphetohyoidean, established by Watson as a grade group). Moy-Thomas mentioned eight characters to support his argument, citing precedents within selected placoderms and acanthodians: 1 – heterocercal tail; 2 – anterior position of the pelvic fins (like *Pseudopetalichthys* and *Rhamphodopsis* – a ptyctodont); 3 – ventral mouth and small size of lower jaw; 4 – palatoquadrate ossified in more than one piece in which the 'tauidion' (Sollas & Sollas 1903) represents the medially united anterior ossifications; 5 – ring-like centra (*Gemuendina* and *Pseudopetalichthys*); 6 – short occipital region (like *Jagorina*, but most placoderms have long occipital regions); 7 – well-developed rostral region (like *Nessariostoma*); and 8 – hyomandibular not supporting jaws (but the hyomandibular is involved in jaw suspension of most placoderms (Miles 1971) and the jaw suspension of acanthodians is known to have a suspensory hyomandibular (Miles 1973)). Once again, all these characters can be matched outside placoderms and acanthodians and we find no placoderm characters in this list.

Jarvik (1980) has recently suggested that *Palaeospondylus* is a larval *Osteolepis*. His argument is in two stages. He first notes the similarity between *Palaeospondylus* and anuran tadpoles (presence of ossified ring-like centra and external shape of the tail). He then argues (1980 : 218) that '. . . because osteolepiforms have been shown to be close to the ancestry of the Anura it is tempting to suggest that *Palaeospondylus* may be a larva of *Osteolepis macrolepidota*, an osteolepiform which is also common in the flagstones at Achanarras'. To this we would make three comments: the similarities between anuran tadpoles and *Palaeospondylus* are not unique; immediate relationship between anurans and osteolepiforms is not beyond doubt (Rosen *et al.* 1981); *Osteolepis* is very rare at Achanarras, there being only approximately 16 specimens known (Trewin, personal communication).

One of the most distinctive structures of *Palaeospondylus* are the so-called 'post-occipital lamellae' which are readily visible and which, we believe, offer a clue about relationships. The 'post-occipital lamellae' are represented by a pair of rods which lie on either side of the anterior centra. Amongst living fishes there are very few comparable structures. Moy-Thomas regarded them as part of the branchial arch series although 'why they are so much enlarged is still a mystery' (1940 : 401). In this he finds agreement with Dean (1896) and Sollas & Sollas (1903). Other interpretations include: parachordals (Jaekel 1927), pronephric lamellae of cephalaspids (Stensiö 1927), the posterior lingual cartilage of a myxinoid

(Bulman 1931), a rudimentary dorsal shield (Woodward 1892), elements of a shoulder girdle (Kyle 1926) or a cranial rib of a dipnoan (Kerr 1900).

The last interpretation seems particularly promising to us since the comparable structures in Recent dipnoans are so similar in shape and position, and are distinctively large. The structures in question have rounded, presumably articulatory, heads (Fig. 2B) and always lie against the posterior edge and slightly on the ventral surface of the neurocranium. This was therefore their position in life. They are associated (? articulated) with smaller, angulated structures (branchial arches – Sollas & Sollas 1903, Moy-Thomas 1940), which may be interpreted as occipital neural arches. Our comparisons of cranial ribs seem most favourable with *Protopterus* and *Lepidosiren* (Agar 1906 : figs 9, 16).

We agree with Kerr (1900, 1919) and Miller (1930) that these enlarged structures are cranial ribs and this allows us to interpret *Palaeospondylus* as a lungfish. Our interpretation of the visceral structures is given in Fig. 2B and is based on comparisons with the illustrations of lungfish larvae provided by Agar (1906), Kerr (1919) and Fox (1965). The many specimens of *Palaeospondylus* show considerable variation but we have found it impossible to relate differences in structure to absolute size. This is chiefly because the several visceral elements are very difficult to interpret; it is not easy to decide where there are points of articulation or, in some cases, whether an element is separate or not. Diagenesis must have affected such an obviously delicate animal. For this reason we do not intend to describe the skull. Instead we will simply point out several important areas of agreement and disagreement between the restoration given here and those offered by Moy-Thomas (1940 : figs 2, 4). We agree that the 'rostralia' are expanded distally and that they may be fused distally, thereby forming together a fenestrated capsule. The resemblance between this and (partially macerated) nasal capsules of *Lepidosiren* was noted by Kerr (1900) and Miller (1930 : fig. 5). The 'tauidion' (Sollas & Sollas 1903) is a prominent structure which we compare to a dipnoan vomer. We agree that the paired elements which lie beneath the otic capsules and converge anteriorly are ceratohyals (always large in dipnoans and urodeles), and that the small unpaired element immediately behind the anterior ends of the ceratohyals is a basibranchial. We disagree with Moy-Thomas over the interpretation of those visceral elements anterior and lateral to the otic capsule. These have been the most problematical elements, interpreted differently by Sollas & Sollas (1903), Bulman (1931) and Moy-Thomas (1940). We believe that the 'hyomandibular' is nothing more than the thickened edge along the anterolateral margin of the otic capsule and may be compared to the otic process of the palatoquadrate; that the 'gammation' and posterior trapezial bar of Sollas & Sollas (1903) compose a single element (specimen P.22392) representing the quadrate region of the palate; and that the 'anterior trapezial bar', 'pregammation' and perhaps the 'hemidome septum' are palatal elements. Since the last-mentioned elements are the most variable they might represent developing tooth ridges (cf. Kerr 1919 : fig. 164c).

Like Moy-Thomas, we consider that the palatoquadrate is fused to the neurocranium and find it interesting that Moy-Thomas chose to make his comparison of the skull with the urodele *Hynobius*. Identification of the lower jaw is difficult. It is possibly represented by the outer curved element, representing a Meckelian ossification/chondrification which forms the outer edge of the 'hemidome'. This is expanded posteriorly and articulated with that element identified here as the quadrate. Anteriorly it curves to meet its antimere immediately in front of the vomer, as it would in a dorsally flattened head.

Moy-Thomas rejected dipnoan affinities of *Palaeospondylus*, chiefly on the ground that he considered it to be an adult. He noted the existence of centra and the advanced degree of ossification. The nature of the skeleton has never been established beyond the fact that it is chemically like coal. Centra are known in larval teleosts—indeed, this was one of the reasons that led Kyle (1926) to consider it as a larval herring. If *Palaeospondylus* were an adult we find it unlikely that fin rays would be absent, that any trace of dermal covering would be absent, that the girdles would be such insignificant structures and that the neurocranium would be so open and trough-like dorsally. These features are those of larvae.

The logical conclusion is that *Palaeospondylus* is a larval *Dipterus*, the only lungfish

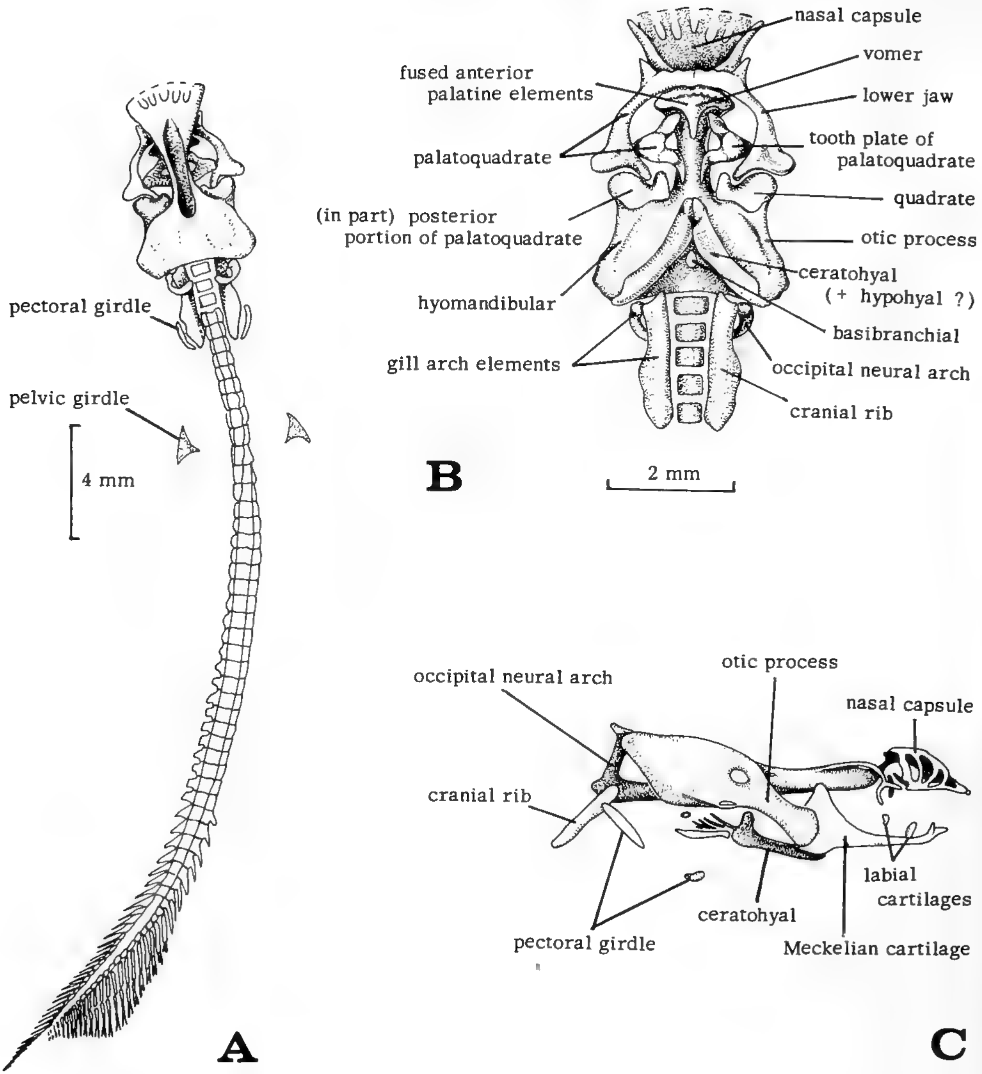

Fig. 2 A, reconstruction of *Palaeospondylus*. Skull in dorsal view, posterior portion of trunk and tail twisted to appear in right lateral view. Based on Moy-Thomas (1940 : fig. 7), skull redrawn. B, restoration of the head of *Palaeospondylus* in ventral view. Labelling on right-hand side represents our interpretation, that on the left Moy-Thomas's. C, *Lepidosiren*, stage 38. Reconstruction of the head of the embryo in lateral view, tooth plates omitted. After Agar (1906 : pl. 3, fig. 16).

present in the fauna. Centra are not normally recorded for *Dipterus* but Jarvik (1952) records them and specimen P.10613 shows centra in at least the tail region. The tail of *Dipterus*, unlike that of many Dipnoans, is also asymmetrical. We can, however, suggest no morphological character which would refer it specifically to *Dipterus*.

We recognize that our interpretation of *Palaeospondylus* fossils, even at such an elementary level as deciding whether a structure is fused or articulated, is governed by our initial choice to use a particular model. Such is the nature of palaeontology. The difference between our attempt and those of most other workers who have considered *Palaeospondylus* (with the exception of Kerr) is that we have attempted to identify a synapomorphy with a Recent group, rather than rely on obviously primitive features (as did Traquair and Bulman), features which are not characters of groups (Moy-Thomas) or use other fossil groups as models (Stensiö). We leave *Palaeospondylus* as larval dipnoan to 'seduce' or to 'bite' other palaeontologists.

Jamoytius and *Moythomasia*

Two genera of fossil fishes have subsequently been named after Moy-Thomas. The first was *Jamoytius* by E. I. White in 1946 and the second *Moythomasia* by W. Gross in 1950.

Genus ***JAMOYTIUS*** White, 1946
Fig. 3

DIAGNOSIS. See White 1946.

TYPE SPECIES. *J. kerwoodi* White 1946.

REMARKS. When first described by White (1946 : 93) the naked *Jamoytius* was considered not only as a likely ancestor for amphioxus but also for the Craniata. White consequently erected the new order Euphanerida to incorporate it. These suggestions, however, did not meet with universal favour and *Jamoytius* was subsequently regarded as a larval thelodont by Wängsjö (1952 : 566) and as an anaspid by Robertson (1953 : 734). Smith (1957 : 394) and Stensiö (1958 : 239) concurred with Robertson and suggested that 'the carbonized remains of the body muscles (myocommata)' were scales. Tarlo (1960 : fig. 5), after a re-examination of the holotype, not only confirmed both Smith's (1957) and Stensiö's (1958) contentions but also claimed the presence of ridge scales. More recently Newth (*in* Young 1962 : 128) has suggested it to be the ammocoete larva of an ostracoderm and Wickstead (1969 : 422) that it corresponded to a metamorphosing amphioxus. Ritchie (1960, 1968) has published accounts based on new material, in which he claimed to have confirmed the presence of scales.

Jamoytius kerwoodi White 1946

1946 *J. kerwoodi* White : 89.
1960 *J. kerwoodi* White; Tarlo : 113, fig. 5.
1960 *J. kerwoodi* White; Ritchie : 647, fig. 1.
1968 *J. kerwoodi* White; Ritchie : 26; pls 3–6.

DIAGNOSIS (emended). A naked cyclostome with diphycercal tail and branchial basket.

REMARKS. We cannot find any trace of scales on the specimens examined (BM(NH) and Royal Scottish Museum). Furthermore, the carbonized remains bear no resemblance to anaspid scales. The so-called scales seen by Ritchie (1960, 1968) were only observed by him after the specimens had been treated. No such structure is visible on any specimen we have examined and we suggest that both Tarlo (= Halstead) and Ritchie were mistaken in their observations. Futhermore, no good evidence has been presented against regarding the segmental structures as the remains of body muscles. In no specimen is there anything more than carbonized remains and occasionally a rather amorphous, tarry, surface structure.

There is likewise no evidence for a lateral fin fold either on the holotype (cf. White 1946 : fig. 1) or on RSM 1966. 3.1 (cf. Ritchie 1968 : pl. 4).

In our estimation the fossil looks very similar to the present-day lamprey and like it has a branchial basket (Fig. 3) with horizontal struts and a diphycercal tail. The branchial basket has no more than seven openings and the appearance of paired structures (eyes) and an annular cartilage argues against it being a larval amphioxus.

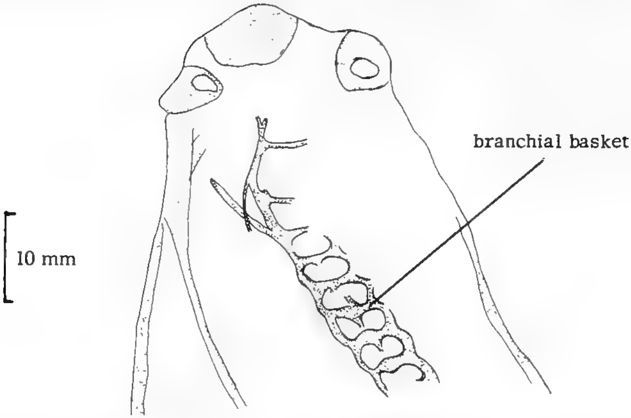

Fig. 3 *Jamoytius kerwoodi* White. Sketch of anterior portion of head as preserved in BM(NH) P.47787, showing the lamprey-like branchial basket.

Genus *MOYTHOMASIA* Gross, 1950

[= *Aldingeria* Gross 1942 : 431, *non* Moy-Thomas 1942]

DIAGNOSIS. See Gross, 1942 : 431.

TYPE SPECIES. *M. perforata* (Gross).

REMARKS. The name *Aldingeria* was first used by Moy-Thomas in October 1942 for a Carboniferous palaeoniscid from East Greenland. Two months later in December of that year the same name was used by Gross (1942 : 431) for a very different palaeoniscid from the Upper Devonian of the Baltic. When Gross realized that *Aldingeria* Moy-Thomas took priority over *Aldingeria* Gross he replaced his genus with the name *Moythomasia* (Gross 1950 : 145) in honour of the British palaeontologist.

When first described by Gross, *Moythomasia perforata* appeared to be just another palaeoniscid. Fortunately, however, this genus also occurs in the calcareous Devonian rocks of Australia (*M. durgaringia* Gardiner & Bartram 1977) and it has turned out to be far more interesting than ever Gross could have imagined.

Moythomasia durgaringia Gardiner & Bartram 1977

DIAGNOSIS. See Gardiner & Bartram 1977 : 238.

REMARKS. This species closely resembles *Mimia toombsi* Gardiner & Bartram, from which it only differs significantly in having a short ascending process.

Moythomasia is regarded as the sister-group of the Actinopteri (Rosen *et al.* 1981), sharing with them a differentiated propterygium in the pectoral fin, a pelvic fin exclusively supported by preaxial radials, fringing fulcra, ganoid scales, acrodin caps on marginal teeth, an endopterygoid, a dentary with a sensory canal and the absence of the jugal/infraorbital canal junction. *Moythomasia* and *Mimia* do not possess a stem to the parasphenoid, or a process on the post-temporal. The ventral fissure and otico-sphenoid fissures were cartilage-filled and not completely bridged by dermal bone (i.e. the parasphenoid), and the lateral occipital fissure is perichondrally lined in both. All of these features suggest that these two genera are the sister-group of all other actinopterygians, with the exception of *Cheirolepis* which lacks acrodin caps on its teeth and fringing fulcra, and *Polypterus* which lacks fulcra and ganoid scales.

Conclusion

During Moy-Thomas's life-time significant advances were made in our understanding of fossil fishes. New methods of examining fossils were introduced, including acid preparation, the use of fine dental hammers, serial sectioning and microscope examination under liquids of varying refractive indices. And there was also a concomitant influx of literature. Perhaps Moy-Thomas's most important contribution was to summarize this information in the light of his own research, and to embody it in his book *Palaeozoic Fishes* (1939). Beyond this, however, he was typical of those numerous individuals who rightfully use this National Museum. We hope that the next hundred years will produce as many fruitful collaborations as the last.

Below, we print a complete bibliography of Moy-Thomas's contributions.

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Burials, bodies and beheadings in Romano-British and Anglo-Saxon cemeteries

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Synopsis

Five late Romano-British sites, Cassington, Queensford Mill, Radley, Stanton Harcourt and Curbridge, all within a restricted area of the upper Thames valley, have produced over 200 extant skeletons. These have provided information for a study of the population, its health and its burial practices. Details of each individual are tabulated. The age at death, average adult height and frequency of some non-metric variables are given. Health is considered in detail: dental health, injuries, frequency of fractures, the incidence of osteo-arthritis and the occurrence of other disease, including the earliest recorded case of tuberculosis in Britain and an early example of possible osteosarcoma.

The association of decapitated and prone burials in three of the cemeteries is noted and considered in a survey of the recorded instances of both practices in Romano-British and Anglo-Saxon cemeteries.

Introduction

Students of early British populations consulting the collection of the Subdepartment of Anthropology of the British Museum (Natural History) may be surprised to find some of the boxes labelled 'Oxford Collection'. The origins of this collection go back to the mid-nineteenth century, when George Rolleston, Professor of Human Anatomy at Oxford, assembled a large collection of skeletons from all over the world. The British archaeological material was derived from all parts of the country, but particularly from local sites. Rolleston's contemporaries rescued material from quarries and railway cuttings, and carried out their own excavations, especially on visible monuments such as barrows. Rolleston himself was no mean antiquary and retrieved much material. The tradition of personal involvement was continued by his successors in the Department of Human Anatomy, Dudley Buxton and Miss Beatrice Blackwood. E. T. Leeds, Keeper of the Ashmolean Museum, and his colleagues contributed remains from several cemeteries, and the Department received bones from other archaeologists. Thus the collection continued to grow. In the late 1940's, the major part of this collection, an outstanding group of skeletal material, well catalogued and organized, was given to the British Museum (Natural History) where it became known as the 'Oxford Collection'.

The bones from two excavations, Cassington and Radley, have never been published, and these, together with some from more recent excavations at Curbridge, Stanton Harcourt and Queensford Mill, provide a sample of over 200 individuals from a restricted area of the upper Thames valley attributed to the late Romano-British period (third to early fifth centuries AD). These have provided information for the study of the population, its health, and its burial practices, particularly decapitation and prone burial. Both of these practices occur not

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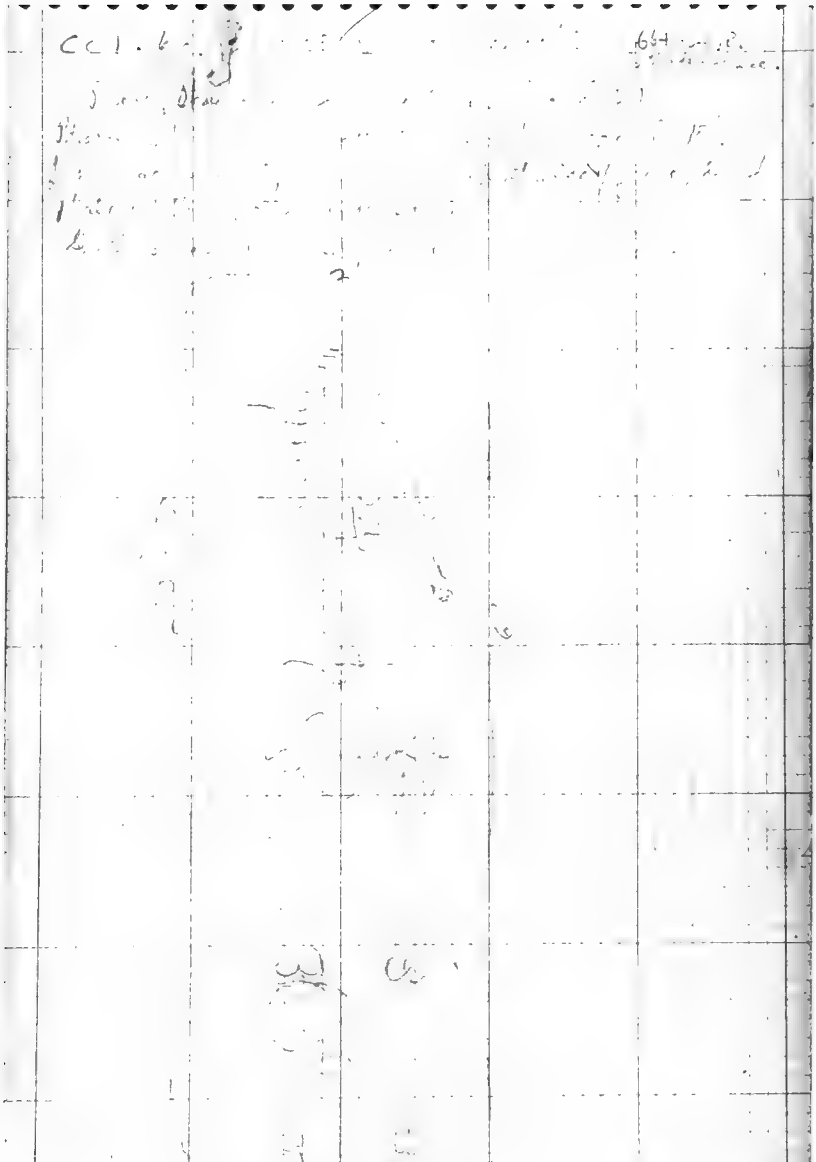

Fig. 1 Decapitated and prone burial from Cassington as depicted in Captain Musgrave's field notebook. Original notebook in Ashmolean Museum, Oxford. Reproduced with permission.

uncommonly in southern England in late Romano-British times, and are recorded also in pagan Anglo-Saxon cemeteries. The significance of these practices is considered in the light of other examples noted from the literature. While decapitation has been discussed recently (Clarke 1979 : 192–193, 372–375; MacDonald 1979 : 414–421) prone burial and its association with decapitation has received little comment. The study of a group from a limited area increases knowledge of both practices without, perhaps, adding to the range of possible explanations for them.

The sites

At Cassington several burials were examined in the early 1930s by Leeds and others, but most of the bodies were retrieved by Captain Musgrave and Miss Blackwood in 1935 during the construction of the Oxford bypass. Over 100 skeletons were found, in a cemetery of unknown size, and the remains of 72 were added to the Oxford Collection, the rest being reburied. 60 are still available, although three which were sent, in 1932, to the University of Albuquerque, New Mexico, in exchange for Pueblo Indian remains, have not been examined. Information is available from the Oxford Catalogue and from Musgrave's notes and drawings of the skeletons in the graves (Fig. 1). Only brief notes have been published, probably by Leeds (*JRS* 1937 : 237)[1]. In the following descriptions the skeletons are generally referred to by the numbers given in the field by Musgrave. In a few cases, where there is no field number, the Oxford Collection Catalogue number has been used. The concordance between the two systems is given in Appendix I, p. 170.

At Radley a complete small cemetery of 35 graves was hastily excavated in 1945 by R. J. C. Atkinson, in advance of gravel digging. A report of the excavation, though not of the human remains, was published (Atkinson 1952 : 32–34) and most of the bones were deposited in the British Museum (Natural History). Unfortunately the bones themselves were not numbered, labelling was inadequate, and in several instances two or three skeletons are confused. While generally the postcranial bones appear to be consistent with the skulls bearing the same number, these numbers cannot be correlated with the numbered graves on the site plan, making studies of spatial distribution impossible. The remains of at least 31 people are available for study.

Recently rescue excavations have been carried out by the staff of the Oxfordshire Archaeological Unit. At Curbridge, graves containing 21 individuals, on the line of the Witney bypass, were investigated in 1975 by R. A. Chambers (1976 : 38–55; 1978 : 252). In 1978, at Stanton Harcourt, part of a cemetery threatened by gravel quarrying was excavated by N. McGavin. The excavation report with a brief note on the remains of the 36 individuals is published (McGavin 1981). At Queensford Mill a rapid rescue excavation of part of a very large cemetery took place in advance of gravel extraction in 1972 (Durham & Rowley 1972 : 32–37). A summary of the information about the human remains has been published (Harman, Lambrick, Miles & Rowley 1978 : 4–6).

Decapitated bodies were discovered in the first four cemeteries, and in three of those prone burial also occurred.

All five cemeteries, Cassington, Radley, Stanton Harcourt, Queensford Mill and Curbridge are considered in detail, while other smaller groups from the same area but which do not contribute to the general survey of the population are considered in the comment on burial practices.

The preservation of the bones from Cassington, Radley, Stanton Harcourt and Queensford Mill, all gravel sites, was generally good, though some from Cassington and Radley had suffered when the topsoil was stripped from the sites. The graves at Radley were shallow and many of the skulls were damaged. The skeletons at Curbridge were buried shallowly in clay and their condition varied; some were well preserved but others were badly decayed. Most of

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[1] A key to references in this form, more familiar to workers in archaeological subjects, will be found at the beginning of Appendix VI, p. 184.

the skeletons from Stanton Harcourt and Queensford Mill were reasonably complete; some from Curbridge were incomplete owing to fragility and decay; some from Cassington were complete though many were represented by the skull, pectoral and pelvic girdles and all limb bones, or only a selection from these; at Radley most of the skeletons are represented by the skull, pelvic girdle and all limb bones.

The populations: normal variation

Appendices I–V (pp. 170–183) show the primary information deduced about each skeleton from the five cemeteries considered.

The sex of adult individuals was decided where possible from the relevant features of the skull and pelvic girdle and from the size and ruggedness of the skeleton as a whole. The age of individuals has been assessed from the state of epiphyseal fusion and of tooth eruption, and the degree of tooth wear, based on the criteria given by Brothwell (1963 : 59, 60, 69) and from the length of the diaphyses in the case of juveniles, using the chart prepared by Miss R. Powers. The height of adults has been calculated where possible from the lengths of the long-bones, using the regression formulae of Trotter and Gleser (Brothwell 1963 : 102). The state of dental health is indicated by showing the incidence of caries, abscess and ante-mortem tooth loss. Where possible the presence of normal variations in the skeleton, such as metopism, wormian bones and vertebral anomalies, has been noted, and in the tables both these and any evidence of disease or injury are listed.

Table 1 shows the number of skeletons from each site arranged according to age and sex, and from all sites combined. At Cassington there are almost twice as many males as females, while at Queensford Mill the males are outnumbered, though less dramatically. The discrepancy at Cassington seems too great to be accounted for by the relatively small sample size; both here and at Queensford Mill it could be explained as a result of segregated burial in a partially excavated cemetery, though the spatial distribution of 53 adult burials of known sex from the latter site does not show segregation.

It is clear that children are under-represented in all the cemeteries. At Queensford Mill only one infant of less than a year was found, and this appeared to be a premature baby accompanying the mother, not an independent burial. This is true also of one infant from Cassington, two (possibly twins) from Curbridge, and one from Stanton Harcourt, thus reducing the number of independent infant burials by half. Infant burials are not uncommon on occupation sites, and have occurred in relatively large numbers on nearby sites such as Mount Farm, Berinsfield (Lambrick, in preparation) and Barton Court Farm, Abingdon (Miles, in press). While this may account for the deficiency of young children, the extreme paucity of burials of children under fifteen years in all cemeteries save Queensford Mill is remarkable. It is possible that infants and children buried in shallow graves may have been removed with topsoil, unknown to the excavators, but this was unlikely at Stanton Harcourt. At Queensford Mill, excavated in similar circumstances to the other cemeteries, a significantly larger proportion of child burials was found, and this seems to be a real difference between that cemetery and the others. No segregation according to age was noted at Queensford Mill. While this may have occurred at Cassington, Curbridge or Stanton Harcourt, Radley was completely excavated, and any children's corpses from that community must have been buried elsewhere.

Since neither the true proportion of child to adolescent deaths nor the age of those regarded as 'over 40' or 'over 45' is known, it is not possible to calculate average age at death, but it can be observed that of those surviving beyond the age of 20 who could be aged with more accuracy than the mere term 'adult', 69 were males and 70 females: 50% of the males survived beyond the age of 40 years, but only 40% of the females. The difference may be due to a higher female mortality during child-bearing years. Extreme tooth wear and loss and some pathological conditions suggest that some individuals survived considerably beyond the age of 40 years.

Table 1 Distribution of individuals according to age and sex.

		Age in years												
Site	Sex	0		5	10	15	20	25	30	35	40	45 +	Adult	Total
Cassington	♂	–	–	–	–	–	3	–	4	1	1	8	25	42
	♀	–	–	–	–	1	1	2	–	2	2	5	9	22
	?	–	3	1	–	1	–	1	1	–	–	–	–	7
	Total	–	3	1	–	2	4	3	5	3	3	13	34	71
Curbridge	♂	–	–	–	–	–	1	–	–	2	–	2	1	6
	♀	–	–	–	–	–	–	–	–	1	–	2	2	5
	?	–	2	–	–	1	1	–	–	–	–	3	–	7
	Total	–	2	–	–	1	2	–	–	3	–	7	3	18
Queensford Mill	♂	–	–	–	–	–	2	3	5	2	–	10	1	23
	♀	–	–	–	–	3	7	4	6	1	1	8	4	34
	?	1	7	6	5	1	–	–	–	–	–	2	2	24
	Total	1	7	6	5[2]	4	9	7	11	3	1	20	7	81
Radley	♂	–	–	–	–	1	1	–	2	–	–	8	5	17
	♀	–	–	–	–	1	3	–	–	1	–	7	2	14
	?	–	–	–	–	–	–	–	1	–	–	–	–	1
	Total	–	–	–	–	2	4	–	3	1	–	15	7	32
Stanton Harcourt	♂	–	–	–	–	–	1	6	1	1	–	5	1	15
	♀	–	–	–	–	1	5	2	2	–	–	2	3	15
	?	–	3	–	–	1	–	–	–	–	–	–	2	6
	Total	–	3	–	–	2	6	8	3	1	–	7	6	36
All Cemeteries	♂	–	–	–	–	1	8	9	12	6	1	33	34	103
	♀	–	–	–	–	6	16	8	8	5	3	24	20	90
	?	1	15	7	5	4	1	1	2	–	–	5	4	45
	Total	1	15	7	5	11	25	18	22	11	4	62	58	238

[2] In more detail child mortality at Queensford Mill was as follows: Foetus of 7–8 months *in utero*, 1. 1–2 years, 2. 2–3 years, 1. 3 years, 2. 3–4 years, 1. 4–5 years, 1. 5–6 years, 1. 6 years, 1. 7–8 years, 3. 9–10 years, 1. 10 years, 1. 12 years, 2. 13–14 years, 2.

The average height of 62 males was 5′6¾″ (1·70 m) and of 60 females 5′2½″ (1·59 m), a little shorter than the modern British averages; the female figure is biased by the large proportion of very small individuals found at Queensford Mill, where of 21 females whose height could be calculated, eight were between 4′10″ (1·47 m) and 5′0″ (1·52 m).

Several skeletal variables have been noted. The incidence of lambdoid wormian bones is high in Romano-British populations – 71% (Brothwell 1963 : 96); in the five cemeteries considered here it is 51%.

At Cassington, 14 of 29 possible cases have lambdoid wormians. Two of these also have an open metopic suture, but a third with this feature has no wormian bone. Nine individuals have the right arm longer than the left, probably not noticeable during life. Three of these also have minor sacral anomalies; incomplete fusion of the first sacral vertebra, or spina bifida occulta of the sacrum. Another individual has a sacralized fifth lumbar vertebra, and another, congenital fusion of two cervical vertebrae.

At Radley, 10 of 16 possible individuals have lambdoid wormian bones, and of these three also have a wormian on the right side, in the suture between the temporal and occipital, just below asterion. This rare anomaly occurs in four of sixteen individuals in whom this part of the skull was observed. There is also one sagittal wormian bone and one case of an open metopic suture. Two vertebral anomalies occur; a sixth lumbar vertebra, and a sacralized lumbar vertebra. Atkinson notes that at Radley the graves fall into two groups, an eastern and a western group, with very slightly different orientations: he suggests that this may reflect custom, or a difference in date, or possibly family grouping, and it is unfortunate that it is no longer possible to correlate the skeletons with the graves, as anomalies of the type described might support the hypothesis of relationship.

At Curbridge, three of ten possible individuals have lambdoid wormian bones, and a fourth has an inca bone. There are four cases of open metopic sutures, two of which also have lambdoid wormians. All the persons decapitated have open metopic sutures.

At Stanton Harcourt, 14 people have lambdoid wormian bones of a possible 21, and these include all three cases of an open metopic suture. There seems to be a correlation between the presence of lambdoid wormian bones and coffin nails; while this may suggest family relationship between those people buried in coffins, the incidence of lambdoid wormians is so high that such a conclusion may be unwarranted. There are five cases of congenital fusion of two vertebrae, usually cervical. This is a remarkable frequency of a fairly rare anomaly that tends to be familiar. Two individuals have an extra lumbar vertebra.

At Queensford Mill, in a possible 44 individuals, lambdoid wormian bones occur in 17, of whom two also have coronal wormian bones, two have sagittal wormian bones, two have inca bones and one has an open metopic suture. Two other people have inca bones, and another has a sagittal wormian bone, and in addition an open metopic suture; this occurs in another two individuals who have no other cranial anomalies. Vertebral anomalies occur in eight individuals of 40 with reasonably complete and well-preserved vertebral columns. Three have separate neural arches on the fifth lumbar vertebra; one of these also shows sacral spina bifida occulta, and a second individual showing this has a cleft neural arch on the fifth lumbar vertebra. Another person has a separate neural arch on the fourth lumbar vertebra, and cleft neural arches occur in a further two individuals, one in the first cervical vertebra, and one in the eleventh thoracic vertebra, a very unusual site. One woman had congenital fusion of two cervical vertebrae.

While it is clear from the above that some skeletal anomalies overlap others, and that their incidence varies, it is only in one instance that valuable information is provided; at Curbridge, where all three persons who had been decapitated had an open metopic suture, which strongly suggests that they were quite closely related.

Total congenital absence of the third molars occurred in four of a total of 58 complete pairs of maxillae and mandibles; four have one absent, two have both lower teeth absent, one has both uppers absent, and one has three absent. Other incomplete jaws show one or two third molars absent.

Unerupted and malpositioned upper canines occurred in one individual at Curbridge, three females at Stanton Harcourt, one of these with both upper canines affected, and one male at Queensford Mill, who also had a reduced adjacent incisor and the lower canine and last molar on the same side not developed. Generally people with unerupted canines seem to have retained the deciduous canine, and the adult teeth, though partially visible in the maxillae, did not protrude in unexpected directions and cause trouble. One female at Stanton Harcourt had retained the second lower left deciduous molar, the premolar showing no signs of having developed.

Very few postcranial bones manifested congenital variants. The femora of a young man from Cassington (14) had the angle of the femoral neck with the axis of the femur widened. On the radiograph, the bone texture was normal, so the widened angle would appear to be a congenital variant. The left arm of an elderly person from Queensford Mill (33) showed complete fusion of the lower end of the humerus with the radius and ulna. Radiographs showed absence of a joint space and revealed no evidence of infective disease. Bone trabeculae and the cortex passed without interruption across the joint and the appearances are therefore those of a congenital bony syntosis.

There was a possible case of club foot in a young adult male from Queensford Mill (7). The articular surfaces of the right calcaneus and talus showed signs of degeneration. The talus appeared to have moved forward on the calcaneus and there was some hypoplasia of the anterior portion of the calcaneus. The osteo-arthritic changes in the talo-calcaneal joint are the dominant lesion and this could be the late result of congenital talipes equino varus (club foot). Brothwell (1967) discusses an earlier and more severe case from a neolithic longbarrow at Nether Swell, Gloucestershire.

Two cases of growth abnormalities were noted – both from Cassington. Flattening of the femoral head in an adult male (31) may be due to an old slipped epiphysis, while in E11.8.597, a woman of 40–45 years, it may be the result of either a congenital dislocation or possibly Perthes disease. Perthes disease, where the femoral head becomes fragmented, describes a condition in which a localized death of bone and cartilage cells occurs in the primary or secondary centres of ossification. It is thought to result from a defective blood supply to the affected area and may in many cases be the result of minor injury. It is often painful and if untreated osteo-arthritis is an inevitable sequel (Davies 1969).

Observations on pathology

Dental health is considered to have been poor in the Romano-British population, and this is comfirmed by Table 2, which shows the incidence of caries, abscess and ante-mortem tooth loss in the total number of teeth and tooth sockets seen, for different age groups, in the different cemeteries and in all cemeteries combined. While there are some striking differences in the figures for different cemeteries, the small sample size from which most of these figures are derived reduces their importance. It is clear that in most cases there is an increased deterioration in dental health with increasing age. This deterioration was often accompanied by serious periodontal disease. Some individuals had totally edentulous jaws. In some cases teeth were worn to the roots, or very unevenly worn where opposing teeth were missing. Caries had also reduced some teeth to roots.

In the rest of the skeleton the commonest findings were healed injuries and degenerative changes.

Cuts other than those associated with decapitation occurred in one individual, Queensford Mill 59, a female of between 30 and 35 years, who had three cuts on the skull which did not appear to be recent. One small cut about 15 mm long is on the right parietal; another, about 80 mm in length, extends from the left side of the frontal to the left parietal region, lying obliquely to the sagittal line; and the third, roughly parallel to the sagittal and about 100 mm long, extends from the left parietal to the occipital. The skull has an inca bone and a lambdoid wormian, but the skeleton is otherwise unremarkable. The appearance and site of the injuries are not dissimilar to those occurring in a decapitated skull from Cassington, a man (4) whose injuries are described below.

Table 3 shows the total number of reasonably complete limb bones from adults in all cemeteries, divided into pairs and odd lefts or rights. Fractures are not common. These are all the fractures seen on visual inspection, but old well-healed fractures may not have been recognized.

Only two, possibly three, women with healed fractures were noted. Queensford Mill 22 has an old greenstick fracture of the left radius which had healed with angulation of the distal

Table 2 Incidence of caries, abscess and ante-mortem tooth loss in teeth and tooth sockets seen, arranged according to age groups.

	Age in Years	Caries		Abscess		Loss	
Cassington	20–30	17/194	9%	08/206	4%	07/220	3%
	30–40	09/164	6%	15/203	7%	11/212	5%
	40+	24/136	18%	39/215	18%	126/313	40%
Curbridge	20–30	00/43	0%	00/47	0%	00/48	0%
	30+	09/33	27%	08/46	17%	08/61	13%
	40+	08/40	20%	02/36	6%	25/84	30%
Queensford Mill	20–30	07/252	3%	00/286	0%	06/302	2%
	30–40	35/246	14%	18/298	6%	27/326	8%
	40+	33/179	18%	59/314	16%	168/470	36%
Radley	20–30	08/82	10%	07/109	6%	03/112	3%
	30–40	23/98	23%	12/139	9%	28/168	17%
	40+	16/58	28%	20/121	17%	142/266	53%
Stanton Harcourt	20–30	26/301	9%	14/352	3%	16/392	4%
	30–40	24/91	26%	19/118	16%	06/122	5%
	40+	20/75	27%	27/121	22%	81/204	40%
All Cemeteries	20–30	58/872	7%	29/1000	3%	32/1074	3%
	30–40	100/632	16%	72/804	9%	80/889	9%
	40+	101/488	21%	147/807	18%	542/1337	41%

Table 3 Total numbers of intact adult limb bones and numbers of fractures recognized. P = pairs; S = singles.

	Cassington		Radley		Curbridge		Stanton Harcourt		Queensford Mill		Total		Fractures
	P	S	P	S	P	S	P	S	P	S	P	S	
Clavicle	29	7	4	1	3	2	25	2	50	2	111	14	4 cases
Scapula	25	4	1	2	3	2	25	0	50	1	104	9	1?
Humerus	31	8	23	4	5	2	26	2	48	4	133	20	0
Radius	29	7	19	6	4	2	28	0	50	1	130	16	3
Ulna	24	9	22	4	5	2	27	0	51	0	129	15	2
Femur	38	6	25	3	4	3	26	1	51	1	144	14	1
Tibia	31	6	23	6	3	3	27	2	50	1	134	18	2
Fibula	21	1	19	2	3	2	25	2	50	0	118	7	3
Ribs													4 cases

end of the radius so that the wrist would have been slightly deformed. Cassington 39 has a well-healed spiral fracture of the left mid-femoral shaft. The appearance of Radley 21 suggests a healed fracture of the left scapula but this was not confirmed by the radiograph.

Seven cases of healed fractures of clavicle and ribs occur among the male skeletons, suggesting recovery from severe falls or impact blows to the chest and back. Fractures to the lower arm, particularly the left, suggest attempts to parry a blow as in fighting (although there is little evidence from cut wounds of battle fighting). These lower arm fractures usually heal well (but see Cassington E11.8.587) with little deformity, as unless both bones are fractured, the uninjured bone acts as a splint for the injured.

Healed spiral fractures of the tibia and fibula are of the kind associated with a rotatory force—a boot or shoe gets caught in the stirrup, plough or rut in circumstances when the unshod foot would pull away or suffer lesions itself. One man, Queensford Mill 35, also had fractured his left clavicle and, more recently, his ribs. Some infective changes were present on the clavicle.

The discrepancy in the incidence of fractures between the sexes might indicate that male occupations or diversions were more likely to result in this type of injury. It is curious that most of the fractures occur on the left side. Splinting was known in ancient times but traction of fractures was not used until the 13th Century AD so that all the fractures of the lower limb, although well-healed, show some degree of angulation and overlap of the fragments causing shortening of the bone.

Bony spurs have developed at the site of a muscle attachment on the left femur of Cassington 5, a young adult male, and Radley 7, a much older male. These could be related to injury at the muscle insertion and are sometimes associated with horse-riding.

An older male from Cassington, 27, shows a quite marked cortical thickening of the anterior shaft of the right tibia. This is the type of thickening that is associated with sub-periosteal new bone formation and could be related to repetitive minor trauma.

Osteo-arthritis is a slowly progressive condition which eventually leads to destruction of a joint. Insult to the joint from infection or injury, or increased stress from congenital anomalies, may predispose to or initiate this condition. As a result of further wear and tear on the joint surfaces further deterioration occurs, although the more flagrant manifestations of the disease may not be apparent for many years.

Severe osteo-arthritis of the hip joint with osteophytic lipping of the acetabulum and femoral head were noted in two males from Cassington, 19 and 43 (Fig. 4, p. 158; two adults from Radley, 29 and 11; and two males from Stanton Harcourt, 29 and 67. In the last case, the osteo-arthritis of the right hip is almost certainly associated with increased stress on the joint following a malunited fracture of the left tibia and fibula. Usually the right hip is more severely affected than the left.

Injuries to the knee, in each case the right, were probably the predisposing factors leading to severe arthritis observed in two adult females, Queensford Mill 19 and Radley 22, and another old adult, Radley 32. In the case from Queensford Mill there is a small hollow in the articular surface of the medial condyle of the right femur. It could be due to osteochondritis dessecans. This is a disorder in which a small portion of bone and cartilage from the joint surface becomes detached and forms a loose body within the joint space. The condition is thought to result from defective blood supply to the affected area and may be brought about by a minor injury. Osteochondritis dessecans is seen most frequently in adolescents and young adults and usually occurs in the larger joints, especially the knee joint. It gives rise to pain and an excess of fluid in the joint space.

Recurrent dislocation of the patella may have led to the osteo-arthritis of the right knee of Radley 22. The anterior aspect of the lateral condyle is mainly affected with anterior fringe osteophytes suggesting chondromalacia patellae as a predisposing cause. This is a disorder in which degenerative changes occur in the articular cartilage covering the posterior surface of the patella (Davies 1969). The sacrum of this woman has spina bifida occulta of the first sacral vertebra.

Spondylotic changes on the vertebrae were very common throughout the sample and there were few adult bodies in any cemetery which did not show some evidence of this condition (Table 4). Spondylosis is a result of degenerative changes in the intervertebral discs and causes abnormal movement of the vertebral bodies and increased strain on the small posterior synovial joints. Small bony outgrowths (osteophytes) and spurs appear on the margins of the vertebral bodies and extend into the adjacent ligaments and may eventually bridge the intervertebral spaces and provide some stability. At the same time osteo-arthritic

Table 4 Total numbers of adult vertebral columns, the number of those affected by osteo-arthritis being shown in brackets.

(a) 'Complete' columns (missing less than 5 vertebrae)

Age	Cassington	Radley	Curbridge	Stanton H.	Queensford Mill	Total
20–30	5 (0)	–	–	8 (2)	4 (0)	17 (2)
30–40	2 (2)	1 (1)	–	5 (4)	6 (2)	14 (9)
40+	3 (3)	1 (1)	–	5 (5)	11 (10)	20 (19)
Adult	2 (1)	–	–	–	3 (1)	5 (2)

(b) Partially complete columns (about half the vertebrae or more present)

Age	Cassington	Radley	Curbridge	Stanton H.	Queensford Mill	Total
20–30	2 (0)	–	2 (0)	1 (1)	4 (0)	9 (1)
30–40	–	–	–	–	2 (0)	2 (0)
40+	1 (1)	–	–	1 (1)	2 (2)	4 (4)
Adult	5 (5)	–	–	1 (1)	1 (1)	7 (7)

Also 16 sacra from Radley.

changes occur in the posterior facetal joints. In modern populations minor spondylotic changes are very common over the age of 40 but the grosser manifestations do not usually occur until the late 50s. It is thought that minor congenital anomalies may predispose to spondylosis. In the cervical spine heredity certainly plays a part in its genesis, as a familial incidence has been demonstrated. The adult male from Cassington 41 is an example of its association with a congenital anomaly. The bodies of cervical vertebrae C1 and C2 are partially fused and the laminae are completely fused.

It is clear from a consideration of these individuals, and from smaller groups of vertebrae surviving from others, that vertebral osteo-arthritis was unusual in persons of less than 30 years of age, as it occurred in this age group only at Stanton Harcourt where evidence of slight growth on some of the lower thoracic and lumbar vertebrae was noted in five individuals.

In the 30 to 40 year-old age group generally the same areas were affected, but more vertebrae were involved. At Stanton Harcourt in addition four people in this group had some degeneration and growth on the cervical vertebrae.

In those persons regarded as over 40 years of age, only one, a female from Queensford Mill (67), appears to have remained unaffected by osteo-arthritis in the vertebrae. The degree of degeneration in this age group is variable, probably reflecting the range of ages over several decades; many have slight degeneration in all parts of the column, though in general the lower thoracic and lumbar vertebrae show more moderate to severe signs and in a few individuals fusion occurs. Many cases of fusion were shown on radiography to be congenital. However, in a man from Queensford Mill (5) spondolytic growths had united the final cervical and first thoracic vertebrae and also two other upper thoracics. The body of a lower thoracic vertebra had collapsed. Two thoracic vertebrae, the third and fourth, were fused in a man from Cassington (65).

At Radley, in sixteen persons of varying ages from whom only the sacral part of the spine had been retained, one ageing female (22) seems to have had the final lumbar vertebra joined to the sacrum by bony growth, and in one man (11) the final lumbar vertebra had also been kept, as it was joined to the sacrum by osteophytic spurs and bridges.

One individual from Curbridge (13) had eburnation on the articular facets of some vertebral fragments, and an elderly man from Stanton Harcourt (16) showed moderate evidence of spondylosis on all the vertebrae, the lower part of the column being more severely affected, accompanied by some collapse of the lumbar vertebral bodies.

Fig. 2 The cranium of Radley 17 showing the probable osteosarcoma of the left parietal bone. The wormian bone in the unusual position just below asterion can also be seen.

Fig. 3. Pott's disease or spinal tuberculosis in a woman from Queensford Mill (no. 157).

Thus the general picture is one of increasing deterioration with advancing age, the lower part of the back normally being first affected. People from Stanton Harcourt seem to have suffered more and at an earlier age than those from Queensford Mill but this is only an impression based on a small number of people, although it may be related to the high frequency of congenital fusion of vertebrae.

Other cases of degenerative disease were noted in an elderly woman from Cassington (22) and an elderly man from Queensford Mill (30). The woman showed collapse of the body of the fifth lumbar vertebra which was probably due to osteoporosis. This is a condition in which the supporting connective tissue of bone is defective and a generalized osteoporosis is common in elderly subjects, especially women.

Paget's disease of bone is rare under the age of 40 but the incidence rises to 5% in the 6th decade and it is slightly more common in men than in women. The disease causes softening and thickening of the bone with disorganization of the trabecular pattern which takes on a spongy appearance. Clinical symptoms are not common but in its advanced form pain and deformity of the bone may be a feature of the disease. Evidence for Paget's disease is to be found in the case of the elderly man from Queensford Mill (30). Radiographically the cortex of the right radius is seen to be thickened and the trabecular pattern is coarse and disorganized. (He also has a healed fracture of the medial end of the left clavicle).

Malignant bone tumours are not commonly found in early populations so the spectacular parietal bone tumour from Radley (17) is of particular interest (Fig. 2). It ranks with the equally important, though somewhat later, osteosarcoma of the knee from the Anglo-Saxon cemetery at Standlake (Brothwell 1967). Radiographs of the Radley skull show fine spicules of bone arising from and forming a boss on the right parietal bone. There appears to be a destructive process in the skull vault but this is patchy and partly obscured by sclerosis. The inner surface and the vascular channels are normal. The changes are most probably due to sclerosing proliferative osteogenic sarcoma. This tumour is usually highly malignant, grows rapidly and early secondary blood-borne deposits in the lungs and other organs are almost inevitable in untreated cases. Differentiation from meningioma can be difficult, if not impossible. Brothwell (1961) originally described the pathology as a sarcoma but on reconsidering the evidence (Brothwell 1967) preferred to interpret the changes to the skull vault as being caused by a meningioma or angioma.

A laminar periosteal reaction at the lower end of the forearm bones of Cassington 2 arouses the suspicion of a hypertrophic pulmonary osteo-arthropathy. The changes in the lower limbs are less convincing. The bones are otherwise remarkably healthy and are presumably of a young adult. The condition is usually associated with chronic inflammatory lung diseases, congenital heart disease or intrathoracic and pleural tumours. The bones would be less robust in congenital heart disease so that a chronic infective condition is more likely.

Very little evidence for infective bone disease was noted as is usually the case with earlier British populations. One possible case of Pott's disease or spinal tuberculosis was diagnosed in an adult woman from Queensford Mill (157) (Fig. 3). The vertebrae T9–L3 are affected and there is acute angulation in the dorso-lumbar portion of the spine, with collapse and destruction of the eleventh and twelfth thoracic vertebral bodies. Anterior buttressing is present with well consolidated new bone and some sclerosis. The condition is long-standing and is almost certainly due to healed tuberculosis.

Rheumatoid arthritis may have been present among the people of Cassington and also Queensford Mill. It is an inflammatory disorder of connective tissue which usually commences in early adult life and shows a much higher incidence in females than in males. Common sites for its onset are the small joints of the hands and feet, which become painful, stiff and swollen. The left hip of an adult male from Cassington (43) shows flattening of the femoral head with some cystic changes and lateral drift of the head within the acetabulum. There is gross osteophytic lipping of the acetabulum and osteophytosis of the inferior margin of the femoral head with some buttressing and new bone formation in the inferior margin of the femoral neck. The appearances are those of osteo-arthritis but this could be imposed on old rheumatoid disease (Fig. 4).

An elderly adult from Queensford Mill (33) shows osteo-arthritic changes to the right shoulder, congenital fusion of the left elbow and erosion of the head of the third metacarpal. This could be rheumatoid arthritis or gout, as the articular surface is intact.

An older adult male from Cassington (42) had survived fractures to the ribs and to his left ulna but radiographs of the ulna show that healing did not proceed normally and a chronic

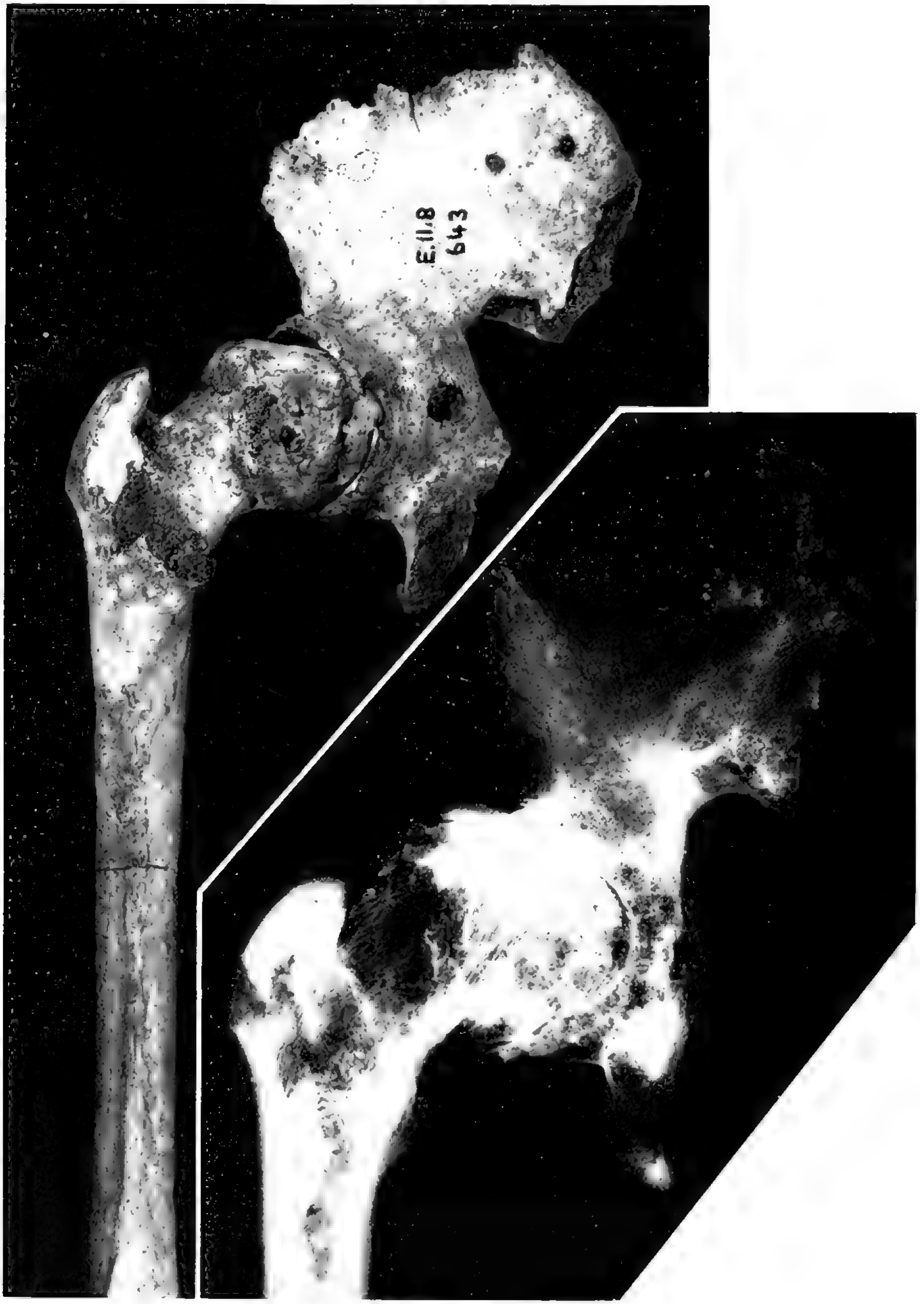

Fig. 4. Severe osteo-arthritis of the left hip in a man from Cassington (no. 43). Radiograph below.

infective process may have been involved in the cortical thickening and periosteal irregularity of the bone.

The evidence for nutritional diseases is extremely tenuous. A single femur from Radley (3) showed changes that could be due to healed rickets. There is marked bowing of the femur. Radiographs show the bone texture to be undisturbed although there is post-mortem pitting of the outer cortex. Some buttressing and remodelling had occurred on the inner border of the curve. This is unlikely to be due to physiological bowing, as the bone is usually remodelled by adult life, so a tentative diagnosis of healed rickets is suggested.

As noted elsewhere the skeletons from Radley are otherwise remarkable for the evidence they show for survival to an old age.

In assessing a population it is useful to consider the diseases that are not found. In these upper Thames valley Romano-British cemeteries no evidence of syphilis or leprosy was found although a case of leprosy has been documented from the probably contemporaneous, though Christian, cemetery at Poundbury, Dorset (Reader 1974).

There was little bone infection present, neither osteomyelitis nor periosteitis being recorded. There was, already noted, one probable case of tuberculosis of the spine from Queensford Mill, and the significance of this case may prove to be considerable in the light of future work in the area. In the meantime it may well stand as the earliest case of tuberculosis so far recorded for Britain.

Table 5 Frequency of orbital osteoporosis in late Romano-British populations

Site	No.	Extent of orbital osteoporosis		
		None	Slight	Moderate
Radley	17	12	4 (4, 11, 14/16C, 18A)	1 (120)
Cassington	32	28	4 (2, 6, 37, E11.8/587)	
Stanton Harcourt	24	22	2 (79, 104)	
Queensford Mill	49	41	8 (10, 16, 18, 31, 45, 48, 70, 178)	
Poundbury (adults)	166	125	9	32

Other diseases of poverty and overcrowding such as rickets and scurvy are also not recorded with certainty from these cemeteries. The one possible case of healed rickets from Radley (above) rests on such slender evidence that a strong diagnosis cannot be hazarded. However, mild cases of rickets have been recognized from Poundbury (Molleson, in prep.) and we may be seeing here and at Radley the first signs of deterioration in living conditions in Britain, in consequence of starvation, famine or overcrowding. It is worth recalling in this context that several of the women at Queensford Mill and one from Cassington (15) were of short stature.

No bone evidence of thallasaemia or sickle cell anaemia was recorded, although malaria was probably endemic in Britain at the time (Howe 1972). The severity of orbital and parietal osteoporosis was not great: this in marked contrast to the evidence from studies on the Romano-British population at Poundbury (Table 5). If the development of cranial osteoporosis can be taken as a response to hyperdevelopment of bone marrow consequent on chronic iron deficiency anaemia (Angel 1966; Caffey 1937) then the mildness of these conditions in the upper Thames valley populations can be taken as an indication of the generally good dietary health of the people.

Decapitated and prone burials

Distribution

Of the five cemeteries considered, four are remarkable for both the absence of child burials

Table 6 Decapitated and prone individuals from Romano-British cemeteries in the upper Thames region.

Site, No.	Sex	Age	Decapitated	Prone	Position of head, cuts, other comments
Abingdon					
3	♂	35–40	X		Head between legs, several cervical vertebrae attached to skull.
Bloxham					
3	♂	Elderly		X	
4	♀	18–25		X	
11				X	
18				?	
E11.8.376	♂	Adult	X		Skull between knees, on left side, facing left foot.
Cassington					
597	♀	40–45	X		Head between knees.
2	♀	Elderly	X	X	Head on back of legs just below knees. Atlas and axis with head. Axis shows cut.
602	♂	Adult	X		Head between legs. Dog over feet.
4	♂	30–35	X	?	Skull on back of knees, atlas and axis with it. Cut on axis.
6	♂	Elderly	X		Head between feet, atlas and axis with skull. C3 missing. C4 shows cut.
7	♂	35+	X		Head between knees, first three cervical vertebrae with skull.
12	♀	17–22	X	X	Skull resting on back of knees, face down, with first four cervical vertebrae and top portion of C5, showing cuts.
19	♂	45+		?	
21	–	7–8		X	
22	♀	40+	X	X	Head between knees face up, chin towards pelvis. Atlas and axis seen on neck end.
28	♀	40–45	X		Head between tibiae on left side.
32	♂?	–	X	X	Head between knees on right side, facing right knee.
35	♀	Adult	?		Short grave at head end.
39	♀	Adult		X	
40	♀	Adult	X		Head between tibiae facing up.
44	♂	20–25	X	X	Head between feet. C2 and 3 missing, cut on C4.
45	♂	Adult		X	
46	–	Adolescent	?		Grave too short for head.
47		Adult?	X	X	Skull between tibiae.
48	♂	Adult		X	Left forearm across back, right across waist.
62	♂			X	
65	♂	Adult		X	
66	♂	Adult	X	X	Skull below knees, cut on C4, C1–3 missing.
67				X	
Cassington Smith's Pit II					
2	♂	25–35		X	
3	♂	30–45		X	

Table 6 *cont.*

Site, No.	Sex	Age	Decapitated	Prone	Position of head, cuts, other comments
Curbridge					
19	?	45+	X		Skull face down between lower legs, neck towards body.
22	?	40+	X		Skull on left side between lower legs, facing knee.
30	♂?	30+	X		Skull beside right leg.
Radley					
4B	♂	30–35	X		Head between knees. Cuts on third cervical vertebra.
6		16–20	X		Head between knees. Cuts on axis.
–				X	
Stanton Harcourt					
25	♀	20–25	X		
32	♀	45+		X	
35	♀	30+		X	
51	♂	25–30	X		
67	♂	25–30	X	X	Cut through ventral portion of anterior articular surface of C – slightly oblique.
Wroxton-St-Mary					
1	♀	Adult	X		Skull between thighs, face down, chin towards feet. C1 and C2 with skull.
2	♂	Adult		X	Left arm raised against edge of grave.

and the presence of decapitated burials, prone burials also occurring in three of them. Table 6 shows the circumstances of the decapitated and prone burials at these cemeteries and four others in the vicinity.

At Cassington Captain Musgrave's notebooks record sixteen decapitations, confirmed in several cases by the discovery of cut vertebrae with the skeleton; some of these are still extant, but cervical vertebrae are missing from eight of the decapitated bodies (2, 6, 7, 12, 22, 40, 44 and 66). In the case of 2, 6, and 12 these are recorded in the Oxford Collection Catalogue as having cuts on them; it seems not unlikely that somewhere there is a small hoard of these cervical vertebrae. There were fourteen recorded prone burials at Cassington and a further two possible ones; in seven cases decapitated people were buried prone (Fig. 1, p. 146).

At Radley two decapitations and one prone burial were recorded, all buried quite close to each other. While the decapitated burials 10 and 14 may be identified with the bodies 4B and 6, both of which have cuts on cervical vertebrae, it is not possible to identify the person buried prone.

No prone burials were noted at Curbridge but it is at this cemetery that relationship between the three who were decapitated may be postulated, since they also shared the uncommon feature of an open metopic suture. In all, this variant occurred in four of ten individuals in this cemetery. As the group is small the question of kinship must be treated with caution.

At Stanton Harcourt there were three instances of decapitation, one of which was also a prone burial, and two other prone burials, all fairly close to each other.

Two individuals show cuts which may be associated with decapitation on bones other than vertebrae; Cassington 4, a decapitated man, had two cuts on the left parietal, on a line running approximately from the junction of the sphenoid with the parietal to lambda, but not extending the full length of this line. There is some similarity between these injuries and those inflicted on a woman from Queensford Mill (59) who was not decapitated. There are also three cuts on the right side of the mandible, one on the ascending ramus, cutting into the anterior margin below the coronoid process, and possibly also the cause of the loss of the third molar crown; one long cut extending almost from the sagittal line just below the mental foramen to just below the second molar, and one slicing a small portion off the inferior margin of the horizontal ramus. Stanton Harcourt 67, also a decapitated man, had a sliver of bone cut off the inferior margin of the right horizontal ramus of the mandible, very similar to the case at Cassington, and in addition a small portion of the right gonion of the mandible had been removed.

The only cemetery in the immediate vicinity of those described above in which decapitation is recorded is the one partially excavated at the Ashville Trading Estate, Abingdon (Parrington 1978 : 23, 25, 36–78; Edwards 1978 : 92). Here eleven graves discovered in foundation trenches were investigated, two only being fully excavated, so that the skeletal material recovered was restricted. Edwards, in his report on the human remains, identified three females and six males, of ages varying from late adolescence to considerably over 40 years, and one child of between 6 and 8 years. One male of between 35 and 40 years of age was found with the head placed between the legs and several cervical vertebrae still attached to the skull.

Bloxham, only twenty miles north of this group and just within the upper Thames basin, is similar in several respects. Most of the burials were rescued during ironstone working in the 1930s, some bodies being recovered complete, while some were partially recovered and some recorded from the testimony of the workmen. A total of 30 graves is believed to have been found, 24 recorded by Knight (1938 : 41–56) and a further six by Musgrave (ms. notes). Buxton (1938 : 46–47) reported on the skeletons retrieved; altogether four females and nine males were recorded, varying in age from 'young' to 'elderly'. Three, possibly four, were buried prone: of these, one was male, one female and two of undetermined sex. Musgrave recorded one adult male with skull between the knees, facing the left foot. No child graves are mentioned but the occupants of half the graves are not described, and in a lengthy salvage operation of this sort they may have been missed. The decapitated male should be in the Oxford Collection (E.11.8.376) but was not found; four others are recorded in the Oxford Collection Catalogue (E.11.8.581–584), of which only the last three were found; these may be from Knight's excavations. Bloxham IV was a female of 18–23 years, Bloxham VIII a male over 40 years, with evidence of osteo-arthritis in the vertebral column and shoulders, and, according to the catalogue, a 'remarkable pathological condition' of the right foot, which is now missing. The last from Bloxham, unnumbered, was a young person, possibly female, notable for a wormian bone just below the right asterion, very similar to those seen at Radley. It is curious that Buxton did not mention the 'remarkable pathological condition' of VIII in his report, but he has noted that Bloxham V had a Pott's fracture of the right tibia, so possibly there has been some confusion in the numbering.

At Wroxton-St-Mary, near Bloxham, part of a cemetery was excavated in 1980. At least four burials had been disturbed prior to the excavation which yielded a further four, including a woman with her head between her thighs and a man buried prone (Chambers, in preparation).

At Cassington Smith's Pit II, three adult burials were recorded south of the bypass in 1950, probably connected with the cemetery excavated in the 1930s. Two of these, both males, were buried prone.

The evidence from the above cemeteries shows that decapitation and prone burial were not uncommon in the upper Thames area in late Romano-British times, and the coincidence of the two not only in the same cemeteries but also occasionally in the same individual suggests that the two practices are connected. Study of the individuals concerned provides no explanation on osteological grounds for these forms of burial; both sexes and adults of all

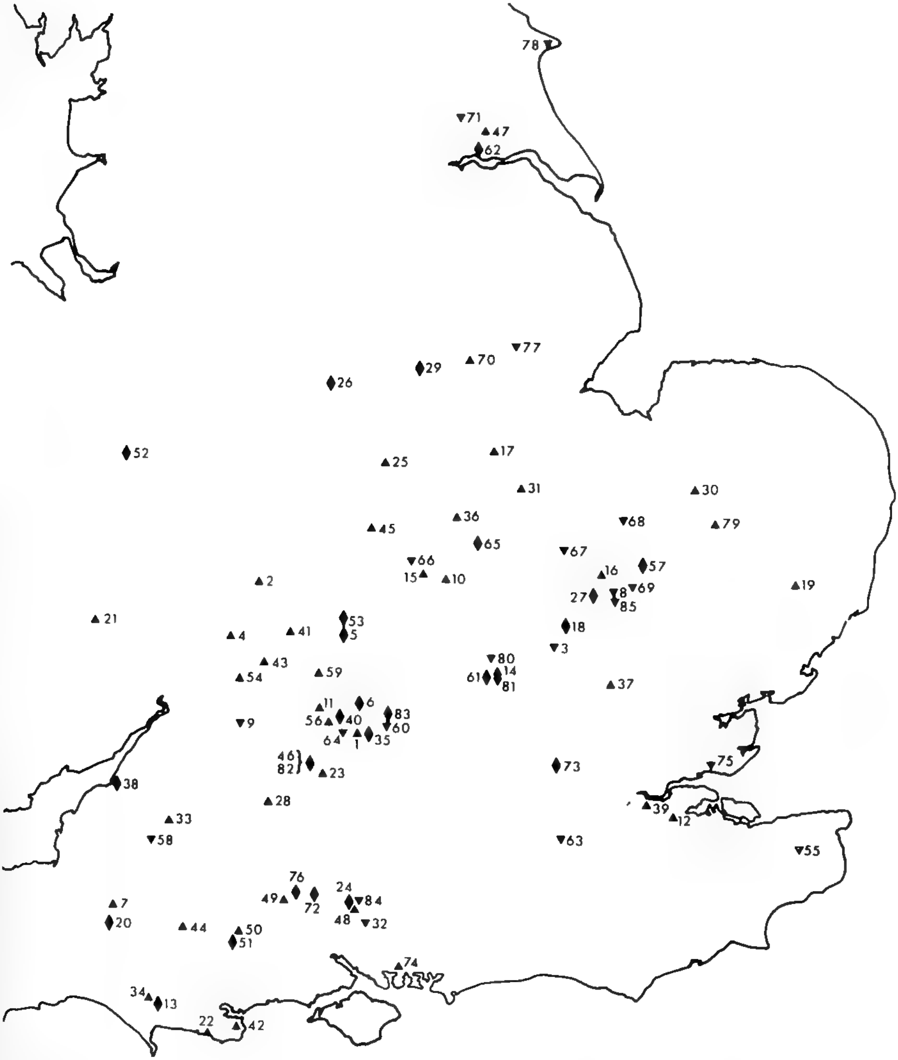

Fig. 5 Cemeteries of the Romano-British and Anglo-Saxon periods containing decapitated and prone burials. ▲ decapitated burials, ▼ prone burials.

ages have been treated thus. Two adolescents, from Cassington and Radley, were decapitated, while the only child over a year in age from Cassington was buried prone, with the arms flung out in an attitude of supplication. Those who had been decapitated at Curbridge may have been related. The virtual absence of children from these cemeteries suggests that they were perhaps not the cemeteries of a normal civilian population, or were used by a particular section of the community.

Both decapitated and prone burials are recorded at other Roman sites, most of them late, in England and both practices occur in Anglo-Saxon cemeteries. Some are recorded only as isolated burials, while others occur in small groups or large cemeteries. Appendix VI (p. 184) is a gazetteer of known instances with references. Regrettably few of these have been published in sufficient detail to make a useful comparison with the cemeteries already considered, but some show common features. In the following discussion the distinction between Romano-British and Anglo-Saxon sites is generally ignored, nor has any attempt been made to consider these examples within a more refined chronological scheme. The distribution of sites is shown on the map, Fig. 5, p. 163.

Nature of the cemeteries

Most of the cemeteries in which these burials occur appear to be normal civilian ones, containing people of both sexes and all ages, but there are some which are unusual. Winchester has a high proportion of infant and child inhumations; at Alcester 10 infants were buried in the same area as the decapitated girl; at Sawbridgeworth most of the burials were of females. At Helmingham they were allegedly all male, including the children, but at this site other mutilations were noted and it was suggested that the bodies had been buried after a skirmish or massacre, though the report of 'several hundred' bodies, apparently buried in order, might argue against this. Springhead seems to be a site of special character; the decapitation of infants is rare and the placing of pairs of infant burials in successive floors of a religious structure, one decapitated and one not, each in opposing corners, may be explained as sacrificial, similar to foundation sacrifices, which are often those of infants.

Several sites associated with earlier barrows or other earthworks are distinctive. At Walkington Wold, published in detail, there were remains of 12 people buried randomly around a Bronze Age barrow; 10 of them were decapitated, the skulls found separately from the bodies, the mandibles of several being detached from the skulls. All but one were male: some were simultaneous burials, but there was evidence of some graves cutting into others. Some had cuts other than those on the cervical vertebrae. The excavators favoured the explanation that the mound was an execution site, possibly the site of a gibbet, and the remains of those who were punished had been buried around the barrow. Wor Barrow is a very similar site: 17 secondary burials, almost entirely males, two with their heads buried by their femora, eight with heads missing, one buried prone. Rushton, where 24 secondary burials, all decapitated, occurred beside an earlier Romano-British barrow, might be regarded as an execution site, but the burial of males, females and children in two rows seems more akin to a normal civilian cemetery.

Possible execution sites occur also in the Anglo-Saxon period. At Dunstable there were 94 secondary burials, some simultaneous, in a Bronze Age barrow, mostly males and many with their arm bones in a position suggesting that their wrists were tied; three were prone and two headless. At Meon Hill and Roche Court Down there were respectively 10 and 18 secondary burials in ditches, almost entirely adult males. Some have their wrists tied, often behind the back, and there is a high proportion of decapitated and some prone burials. Cuddesdon is a curious site, unique in having 'several' burials, all prone, and arranged radially, feet to the centre, possibly originally associated with a barrow. Tied wrists occur in other cemeteries, including some in which neither decapitated nor prone burials appear. One such is Old Sarum, where tied wrists were noted in all 14 secondary burials, mostly men of mature years (Meaney 1964 : 275). Thetford, where 'about fifty' decapitated skeletons were found, is reminiscent of Rushton: it is unfortunate that no further information is available for either of these sites. Little Wilbraham seems to have a preponderance of male burials.

All the above sites, known to have peculiar characteristics, are perhaps not directly comparable with the others considered in this paper, many of which appear to be normal civilian cemeteries, though others are isolated burials or scantily recorded.

The decapitated burials

Both males and females have been beheaded and though adults are usually in the majority in cemeteries, decapitated children seem to be disproportionately few. Apart from those at Rushton, they are recorded at Sea Mills, Lankhills, Dunstable, Leicester, Great Casterton and possibly Alcester (a young girl). At Leicester the skull was between the femora, and at

Sea Mills upon the pelvis, both unusual positions. Children are more rarely found buried prone; this is recorded at Cassington and Lankhills.

The position of the detached head in the grave is normally towards the lower end. In 101 cases where the position is recorded, it was between the lower legs or feet in 38 cases, beside them in 28, near the feet or lower legs in 11, beside or between the femora in 10. The skull was found on the pelvis at Guilden Morden, Sea Mills, Brighthampton and Loveden Hill, and beside it at Lord's Bridge. At Roche Court Down several unusual positions occurred: on the chest, by the arms, and near the neck. The severed head was replaced in its correct anatomical position in two instances at Meon Hill, also at Portsdown, at Guilden Morden, and at Helmingham, though at the last site it may be the restoration to normal appearance of a body mutilated through misfortune. If heads deliberately severed in 'normal' circumstances were often buried in their correct anatomical position, the number of decapitations recognized would be reduced due to poor bone preservation in some soils.

Other portions of the body have occasionally been detached. At Kimmeridge the deliberate removal of the mandible from the severed head and from the second burial is postulated, while one of the burials at Dunstable had not only the head removed and placed between the thighs, but also the lower legs cut off and buried beside the upper arms. Another body at Dunstable with the left leg shortened by a malunited fracture had the foot of the right leg removed at the ankle as if to even up the length, the foot being buried with the body. At Wor Barrow the feet and lower part of the tibiae of an adult male had been cut off. At Tripontium the skeleton of a young woman who retained her head was found with the last thoracic, all lumbar vertebrae and sacrum, both legs below the knee and the left arm missing. At Helmingham a lower arm, and an arm and leg had been severed in two individuals. Finally at Aldwick le Street, Yorkshire, in the chance discovery of four burials during the digging of service trenches, one was found with the feet and left hand cut off (Dolby 1970 : 252–3). These bizarre examples are not, apparently, the result of disturbance to the graves.

Injuries to the skull are recorded at Cassington (described above), at Uffington, where two men had 'cleft skulls', at Brighthampton and Burwell, and at Roche Court Down where one has a cut across the left orbit. Guilden Morden B3 and Roche Court Down 15 had cuts across the right mastoid process, which was shorn off in the latter case. The right side of the mandible showed cuts in the individuals Cassington 4 and Stanton Harcourt 67 as described above, and also Lankhills 379, Portsdown, and five people from Roche Court Down. Wroxton St Mary 1 has a probable cut on the left side of the mandible. Lambourn had damage to the left scapula, Cogenhoe and Meon Hill 7 had cuts on the right clavicle. The vertebrae involved in the removal of the head are shown in Table 7. In some cases such as Lambourn, Manton Down, Radley 4B and Meon Hill 1, there is evidence of more than one stroke. Clarke (1979 : 193) avers that at Lankhills 'the precise severing of the heads between the third and fourth vertebrae . . . points to a well-defined ritual'; this on the basis of four skeletons on which Watt (1979 : 342–4) noticed lesions on the inferior aspect of the third cervical vertebrae or on the superior aspect of the fourth. Lankhills 451, however, had the first four vertebrae buried with the head, in good condition and with no noticeable damage, suggesting a very neat cut between the fourth and fifth (or below, with subsequent tidying of the stump!). Poundbury 1425 had the first five cervical vertebrae with the head. The sixth and seventh vertebrae are missing. The first thoracic vertebra has a horizontal cut on its superior aspect and a small slice has been removed from the right first rib. This is a remarkably low place at which to sever the neck.

It is clear from Table 7 that normally the upper part of the neck was severed, but the vertebrae involved vary. The occurrence of cuts in a similar position both at Lankhills and at Roche Court Down may perhaps be attributed to skill rather than to defined ritual, though cuts into other bones at these and other sites, and evidence of several blows, suggest a lack of precision in the operation on some occasions. It would appear, from damage to vertebral bodies and processes which does not extend to the dorsal surface, that the blow was generally delivered from the front; this is suggested also at Dunstable. Damage to the right side of the

Table 7 Cuts recorded on vertebrae, affecting single vertebrae or passing between two vertebrae.

Vertebrae involved	Site and skeleton number
C2	Cassington 2, 4; Radley 6; Cogenhoe; Kimmeridge; Roche Court Down 18
C2 & 3	Roche Court Down 6, 8, 10, 15
C3	Radley 4B; Stanton Harcourt 67; Lankhills 379, 427; Meon Hill 7; Mundford 6; Portsdown
C3 & 4	Girton; Roche Court Down 17; Todbere
C4	Cassington 6, 44, 66; Lankhills 441, 445
C4 & 5	Meon Hill 5, 6; Woodyates
C5	Cassington 12
C5 & 6	Meon Hill 9
C6	Guilden Morden A2, A8; Manton Down
C7	–
C5, 6 & 7	Meon Hill 1
T1 & R1	Poundbury 1425

vertebrae, skull and mandible suggest that in some cases blows were directed from the right, and a few cases suggest blows from the left. Tildesley (1932 : 583–599), writing of Roche Court Down, felt that the necks were severed from the back, while the body was upright, but there is no real evidence as to whether the person whose head was removed was lying on the ground, supine or on one side, or placed against an upright. There is also no clue to indicate whether beheading is the cause of death or a post-mortem mutilation.

Dating

The connection between decapitated and prone burial already noted in the Oxford group of cemeteries is apparent also in others, again occasionally in the same individual as at Lankhills, Margidunum and possibly Guilden Morden. Prone burials have also been found in cemeteries not known to contain decapitations, as at Baldock, Owslebury, Cirencester and several Anglo-Saxon sites. The distribution of both types of burial is concentrated in the midlands and the south. Most of them are late Romano-British, though some cannot be so precisely dated, and some, such as Cuxton, are considered to be early; there are also Anglo-Saxon examples, some as late as the seventh century. Though, as Clarke suggests, they appear to be more common on rural sites, several occur in cemeteries outside small towns, and some have been found at the major urban centres, but both the distribution and any apparent emphasis on rural communities may simply reflect the incidence of cemeteries and isolated burials which have been recorded. One late Iron Age burial of a young man from Old Down Farm, Andover, may foreshadow the practice of decapitation: there were a number of slashes and stabs on the back of the torso, and the cervical vertebrae had been cut through, though the head was buried in the correct anatomical position (S. Davies, in preparation). The burial did not appear peculiar in any other way.

There are at least 144 examples of decapitated burial from Romano-British contexts and at least 69 prone burials. From Anglo-Saxon cemeteries the minimum totals are 29 (excluding 50 decapitated burials from Thetford) and 33 respectively. χ^2 tests suggest that there probably is a significant difference between the proportions of decapitated and prone burials in Romano-British and Anglo-Saxon times, prone burials becoming relatively more important during the Anglo-Saxon period. However, if Thetford is included in the analyses there is no significant difference.

Discussion

Reasons for decapitation, other than execution and massacre, have been suggested by several authors. Calkin (1947), writing of Kimmeridge where the mandible was also separated, suggests the prevention of communication from the dead, otherwise respected and buried with care. Lethbridge (1936), in the report on Guilden Morden, and Dewar (1961), considering Charlton Mackrell, both support the idea that it was to prevent the dead from walking. Liversidge (1977 : 35) states that 'decapitation of a corpse is a well-known way of laying a ghost' and Keyser (1854 : 305, 307) says that the old Scandinavians, if the dead appeared as a spectre, opened the burial mound, cut off the head, and laid it between the legs. Clarke (1979) has observed at Lankhills a convincing connection with graves which were military, rich, or 'ritually unusual'. One (400) was a cenotaph, and one (447) a group of jumbled bones possibly buried in a bag, perhaps retrieved from an alien burial place. A young man (443) had two decapitated women buried above him, one simultaneously, the other, who was also prone, being added later. Another possible association between decapitated and prone burial occurs in adjacent graves 378 and 379 and it is clear from the cemetery plan that, except for 120 (the only decapitated child), both forms of burial are restricted to the eastern part of the area excavated. His contention that at Lankhills decapitations are sacrificial may hold, though amongst his reasons are the 'care with which the operation had been performed' and signs of coercion of living victims. The position of 451 in the grave may suggest twisted arms, but the cut mandible of 379, in conjunction with similar injuries observed elsewhere, is perhaps the result of a badly aimed cleaver rather than brutal persuasion. MacDonald (1979), in a lengthier consideration of the decapitations, discusses the possibility that they were 'expendable' members of the community: children, old women, criminals and prisoners of war. In view of the association with military burials, he favours the idea that the decapitated persons were sacrificed. They would have been substitutes for slain men or boys whose bodies were not recovered, and who were otherwise condemned to wander as spirits after death, prevented from entering into life in the next world.

It is suggested that since the soul was thought to reside in the head, the removal of it in a particular way might transfer its immortality to another person, and thus the burials at Springhead might be not only normal foundation burials but an attempt to bestow immortality upon the structure itself. In at least two instances at Lankhills the decapitated body was buried later than the person with whom it was associated, so that perhaps it constituted an offering to a semi-divine departed. Difficulty arises over the presence of hobnails with two of the decapitated burials. If deprived of their souls, either as substitutes or offerings, the dead would not require shoes in after life, though perhaps their bodies returned like automatons to the gods who owned them. Alternatively this was simply the consequence of confused thinking over an old custom. Of particular interest is the observation that earlier literary evidence describes the necessity of a living victim, so that first the throat was slit and then the head removed. The probability of the head being regarded as the seat of the soul relates the decapitated burials of the south to the cult of heads for which evidence occurs more commonly in the north and west, and which has been discussed at length by Ross (1967).

Prone burial is recorded in more individuals in the Romano-British period, but occurs in more cemeteries in the Anglo-Saxon period. It is less commonly discussed than decapitated burial, and the connection between the two has not been commented on before now. The number of prone burials now recorded, and their circumstances, no longer permits the acceptance of Rolleston's (1870 : 477) explanation of insobriety on the part of the coffin or bier bearers. Nor can they all be accounted for as a result of personal idiosyncracy, as is recorded of Mary McLeod, the seventeenth century bardess, who directed that she should be laid prone in her grave (Watson 1934 : xix). Hawkes & Wells (1975) have discussed the examples from Worthy Park, both females, and regard them as burials of criminals, possibly buried alive, possibly killed previously, perhaps by drowning. The burial of persons who may have been alive is noted also at Camerton and at Sewerby. Some prone burials, generally of females, may be explained as sacrificial, as at Sewerby, where an adult female lay prone above the coffined burial of another female with rich grave goods, and at Mitcham, where again a female lay prone above a simultaneous burial, probably also of a female. These burials, which have features in common with the decapitated burials at Lankhills, are the subject of a study by Hirst (forthcoming).

Some prone burials are described as careless, as at Baldock, Elloughton and Farthing Down where they were 'thrown in', at Owslebury 'carelessly laid out' and another at Mitcham 'carelessly thrown in'. Some are doubled up, or sprawling. On the other hand others, as at Worthy Park, are 'carefully laid out' or, at Little Wilbraham, 'deposited with much apparent care'. So although some may be the result of hasty and careless burial, not all can be explained in this way. Perhaps it is possible that, as with decapitation, prone burial may have occurred to prevent a ghost from walking; to confound the aspiring spirit and encourage it to enter deeper into the earth instead of rising to the surface.

In the absence of rich or military burials in most cemeteries, particularly of the late Romano-British period, associations of the type described at Lankhills have not often been observed. Perhaps Lankhills and the possible Anglo-Saxon sacrificial sites are special cases in the same way that sites such as Springhead and the 'execution' cemeteries such as Walkington Wold, Wor Barrow and Roche Court Down seem to be. At all these sites, however, the idea of the deprivation of the soul is a plausible reason for such treatment, whether as a sacrifice or as a punishment. Isolated burials, poorly recorded early excavations and inadequately published recent ones reduce the number of examples which can be usefully discussed. There remains a group of cemeteries, however, which contain some decapitated or prone burials, or both, and which have either the appearance of being normal civilian cemeteries, or are curious on account of the absence of child burials. It is possible that these were criminals buried in the community cemetery, as may be the case at Worthy Park, but to regard all in this light might lead to an unacceptably high proportion of criminals in the general population.

Both prone burial and decapitation could be merely a final form of indignity inflicted on the corpse of an individual in consequence of particular characteristics or offences during life. But it seems more probable that both were believed to have some effect on the subject in an after life. There seems to be no explanation, however, for the choice of individuals who were treated in this way. Further evidence suggesting reasons for both practices may emerge through full publication of more of the cemeteries in which they have been noted, or through further excavations with detailed osteological reports.

Did C. L. Dodgson, yarning on the Thames at Oxford while colleagues delved in pits and barrows, also preserve some vestige of the past in the Queen of Hearts' peremptory commands?

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Appendix I

Burials from Cassington

No.	Sex	Age	Height	Caries	Abscess	Loss	Vertebral osteo-arthritis	Lambdoid wormians	Longer right arm	Cranial index	Prone	Decapitated	Orientation	Oxford Coll. number: E.11.8:-	Other comments
	♂	30–35	5′6¾″ 1·69 m	01/25	01/28	00/28	×	0		76·7			SW	587	Healed fracture of left ulna.
	♂	Adult					×	–					SW	588	Now in New Mexico.
	♂	Adult						–					NW	589	Now in New Mexico.
	♀	35–40	5′3¼″ 1·60 m	00/11	01/27	01/28		3		81·6				593	
	♂	Adult	5′5″ 1·65 m					–						594	
	♂ ?	30–35		00/11	00/16	00/16		0		74·6				596	
	♀	40–45	5′2½″ 1·59 m	00/11	01/15	00/15	×	0				×		597	Osteo-arthritis in right hip. Perthes disease of the femoral head?
	♂	Adult						–						598	
	♂	45+	5′8″ 1·72 m	00/16	01/26	06/32		0		73·3				599	Healed fractures of both clavicles.
1	♂	40–45		03/25	00/27	05/32		0					SW	600	
1B	?	30–35		00/13	00/15	00/15		–						600a	
1A	?	25–30		02/14	01/15	01/16		–						600b	
2	♀	Aged	5′1¼″ 1·56 m	–	02/04	09/14		–			×	×	NE	601	Bronchial carcinoma?
3	♀	25–30	5′6″ 1·68 m	04/25	04/28	03/28		2		78·5			NW	602	Fifth lumbar vertebra is sacralized.
	♂	Adult						–				×		(602)	Buried with dog. Now in New Mexico.
4	♂	30–35	5′10½″ 1·79 m	02/23	03/28	05/32		11		80·4	?	×	NE	603	One coronal wormian bone. Sword? cuts on skull and mandible.
5	♂ ?	20–25	5′6½″ 1·66 m	00/29	00/29	00/29		0		74·6			NW	604	Exostosis on femoral shaft.
6	♂	Aged	5′7¼″ 1·71 m	–	00/01	23/24		4		73·0		×	NW	605	
7	♂	35+	5′4¼″ 1·63 m	00/03	03/12	06/16		3		74·9		×	SE	606	

8	♂	30–35		00/28	00/31	01/32		0		76·9			NW	607	
10	♀?	Aged		01/03	01/14	08/13		1		81·4				608	
11	♂	Adult						–					SW	609	
12	♀	17–22	5′4¼″ 1·63 m	01/32	00/32	00/32		0		78·9	×	×	SE	610	
13	♂?	Aged		01/01	04/06	08/14	×	0		76·3			SW	611	C2 and C3 fused congenitally.
14	♂	20–25	5′5¼″ 1·66 m	02/31	00/32	00/32		0	×	79·6			SW	612	First sacral vertebra is separate.
15	♀	30–40	4′9″ 1·45 m	05/24	06/26	03/29		0		74·3			W	613	Osteo-arthritis on radius.
16	♂?	20–25		02/16	00/18	00/24		–					NE	614	Parts of two skulls and skeletons – confusion in numbering.
X	♂	40–45		00/02	00/12	00/12		–						616	
17	♀	Aged		–	00/04	07/11		0						615	
18	?	under 1						–					NW	617	Buried very close to 19. ? Simultaneous burial.
19	♂	45+	5′5¼″ 1·66 m	00/03	00/06	10/16	×	1+		70·9	?		SE	619	Osteo-arthritis in right hip.
20	♀	Adult	5′2½″ 1·59 m				×	–					NW	620	
21	?	7–8						–			×			621	
22	♀	40+	5′4½″ 1·63 m	07/20	03/21	12/32	×	0		77·8	×	×	SW	622	Metopic. Osteoporosis of the 5th lumbar vertebra.
23	♂	Adult	5′8″ 1·72 m				×	–						623	Osteo-arthritis in right ankle.
24	♀	Adult	5′4″ 1·60 m					–	×					624	First sacral vertebra not completely joined.
25	♀	Adult						–						625	
26	♀	45+	5′1″ 1·55 m	02/11	02/11	13/25	×	6	×	77·8			E	626	
27	♂	45+	5′6½″ 1·69 m	04/12	14/25	12/30	×	1	×	74·3			SW	627	Cortical thickening of right tibia and fibula.
28	♀	40–45	5′0¾″ 1·54 m	03/10	00/11	03/14		0	×	75·1		×	NE	628	
29	♀	Adult	4′11¾″ 1·52 m					–					SW	629	
30	♀	25–30	5′1¾″ 1·57 m	02/29	03/31	03/32		1		82·3			W	630	
30	?	neonatal						–						630	Infant buried with adult.
31	♂	Adult	5′7½″ 1·71 m				×	–					SW	631	Osteo-arthritis in both hips. Flattened femoral head.
32	♂?	Adult						–			×	×	NE		
33		Infant						–							
34	♂	Adult						–					NE		
35	♀	Adult	5′5¾″ 1·67 m					–	×			?	W	635	

Burials from Cassington—*cont.*

No.	Sex	Age	Height	Caries	Abscess	Loss	Vertebral osteo-arthritis	Lambdoid wormians	Longer right arm	Cranial index	Prone	Decapitated	Orientation	Oxford Coll. number: E.11.8:-	Other comments
36	♀	20–25	5′4½″ 1·64 m	05/30	00/32	00/32		0		81·3			NW	636	
37	♂	35–40	5′4½″ 1·63 m	01/29	04/32	01/32	×	11		74·9			NE	637	Metopic.
39	♀	Adult						–			×		E	639	Healed fracture of left femur.
40	♀	Adult	5′7½″ 1·71 m				×	–				×	E	640	
41	♂	Adult	5′5½″ 1·66 m				×	–					W	641	Lesion on left tibia. Congenital fusion of C1 & C2.
42	♂	45+	5′8¼″ 1·73 m	00/07	02/10	01/11	×	8+	×	73·0			NE	642	Metopic. Healed fractures of three ribs and left ulna.
43	♂	Adult	5′7½″ 1·71 m				×	–					SW	643	Osteo-arthritis in left hip, imposed on old rheumatoid?
44	♂	20–25	5′6½″ 1·69 m	01/04	00/07	00/09		4+	×		×	×	NE	644	
45	♂	Adult						–			×		NW		
46	?	Adolescent						–				×	N		
47	?							–			×	×	N		
48	♂	Adult						–			×		N	648	
49	♀							–					E		
51	♀	Adult	5′6½″ 1·69 m				×	–					NE	651	
52	?	Adult						–						652	
53	?	Adult						–						653	
61	♂	Adult						–					W		
62	♂	Adult						–			×		W		
64	♂	45+		03/14	04/22	03/14		2		78·2			W	664	
65	♂	Adult	5′7½″ 1·72 m				×	–			×		N	665	Osteo-arthritis on shoulders and sacrum. Fused T3 & T4: spondylosis.
66	♂	Adult	5′7¾″ 1·72 m					–	×		×	×		666	Partial sacral spina bifida occulta.
67	?							–			×				

68	♂	Adult	–	
69	♂	Adult	–	E
70	♂	Adult	–	SW
71	♂	Adult	–	SW
72	♂	Adult	–	SE

Notes. 1. This table includes information derived from the Oxford Collection Catalogue and the excavator's notes: those skeletons which have no Oxford Collection number we believe to be no longer extant.

2. In four instances of 34 possible there is some disagreement over the sex of individuals:

No.	This paper	Oxf. Coll. Catalogue	Excavator's notes
10	♀?	♂	–
13	♂	♀	–
27	♂?	♀	♂
29	♀	♂	♂

Appendix II

Burials from Curbridge

No.	Sex	Age	Height	Caries	Abscess	Loss	Lambdoid wormians	Metopism	Decapitated	Orientation	Other comments
3	–	20–25		00/23	00/24	00/25				N	
4	♀	40+	5′1″ 1·55 m	03/16	00/09	00/19				N	
5	♂?	20–25	5′8¾″ 1·75 m	00/20	00/23	00/23	2+			N	Lying on side.
7	♀	Adult	4′10½″ 1·49 m	01/05						N	Slight osteo-arthritis on thoracic vertebrae.
8	♂	30+	5′5″ 1·65 m	01/04	02/11	01/15				E	
11	♀	40+		03/13	00/16	06/23				E	Inca bone. Slight osteo-arthritis on thoracic vertebrae.
12	♂?	Adult								N?	
13	?	40+		01/08	01/09	01/09	1+	×		N	Osteo-arthritis on cervical vertebrae. Fractured rib.
14	?	16–20								E	
15	♂?	45+		00/01	01/02	08/12				E	
19	?	45+				03/08		×	×	E	
22	?	40+				00/05				N	
23	♂	40+		01/02		07/08		×	×	N	
25	♀?	Adult								N	Osteo-arthritis on cervical vertebrae.
27	♀	30+	5′0¾″ 1·55 m	05/22	04/24	05/32				N	
28		7 mo. i.u.								N	Buried beside 27, probably simultaneous burial.
32		7 mo. i.u.								N	
30	♂?	30+		03/07	02/11	02/14	1	×	×	N	Osteo-arthritis on cervical vertebrae.

Note. Nothing remained from graves 2, 16 and 26. The numbers are not consecutive because 'missing' numbers belong to other features on the site.

Appendix III

Burials from Queensford Mill

No.	Sex	Age	Height	Caries	Abscess	Loss	Lambdoid wormians	Other comments
1	♂	30–40		03/17	04/25	08/32		
2	♂	30–35	5′5½″ 1·67 m	02/28	01/31	00/31	1	
3	?	*c*3						
4	♀?	17–20		00/28	00/25	00/28	0	
5	♂	45+	5′11¾″ 1·82 m		04/09	07/16	0	Osteo-arthritis on all vertebrae. Two pairs fused: C7 & T1, 2 upper thoracics.
6	♂	30–35	5′7¼″ 1·72 m	03/14	01/16	00/16	0	Slight osteo-arthritis on two lumbar vertebrae.
7	♂	20–25	5′8½″ 1·74 m	00/25	00/25	00/29	0	Right arm longer. Benign osteoma on frontal; club foot.
9	♀	Aged			02/11	07/16		
10	♀	45+	short	00/01	01/05	10/14	0	
11	♀	45+?				03/04		
12	♂	Adult	5′6″ 1·67 m				0	Separate neural arch on fifth lumbar vertebra. Sacral spina bifida occulta.
13	?	*c*7		00/12	00/19	00/04		
14	♀	25–30	5′4¼″ 1·64 m	00/22	00/23	00/23	0	
15	♀	45+		02/07	02/14	06/20	0	
16	?	13–14		00/16		00/16		
17	♂	30–35	5′5¼″ 1·66 m	02/28	01/29	01/32	0	Bipartite inca bone.
18	?	*c*7		01/16	00/20	00/04		
19	♀	Adult	5′7″ 1·70 m					Lesion on R femur, distal end.
20	♂	45+		00/01	05/09	21/28	0	
21	♀	35–40	4′11¾″ 1·52 m	03/08	00/12	00/12	0	
22	♀	30–35	5′3″ 1·60 m	03/11	00/12	03/17		Slight osteo-arthritis on lumbar vertebra, sacrum and left wrist. Greenstick fracture of left radius.
24	?	3–5		01/17	00/20			
25	?	*c*12		00/22	00/24	00/24	0	

Burials from Queensford Mill—*cont.*

No.	Sex	Age	Height	Caries	Abscess	Loss	Lambdoid wormians	Other comments
26	♀	40+		04/27	01/27	05/32	0	Slight osteo-arthritis on cervical vertebrae.
29	♂	45+	5′8½″ 1·74 m		06/19	11/31	6	Slight osteo-arthritis on thoracic and lumbar vertebrae. Separate neural arch on final lumbar vertebra.
30	♂	45+		03/12	08/24	10/32	1	Slight osteo-arthritis on all vertebrae and thumbs. Fractured clavicle. ? Paget's disease.
31	?	5–6						
32	♂	35–40	5′6½″ 1·69 m	06/27	03/28	05/32	0	Right arm longer. Slight osteo-arthritis on many vertebrae and wrists.
33	?	45+		03/07	01/13	03/16		Osteo-arthritis on most vertebrae and at joints. Congenital fusion of elbow?
34	♀	20–25		01/01	00/06	00/06		
35	♂	25–30		01/16	00/24	00/24	0	Separate neural arch on fourth lumbar vertebra. Metopic. Fractured ribs, clavicle, left tibia and fibula.
36	?	*c*12		00/16	00/21	00/19	1	
37	♀	young adult	short					Inca bone.
38	?	*c*2		00/17	00/20			
39	♀	20–25		00/30	00/32	00/32	0	
40	?	5–7						
43	?	*c*10		01/14	00/17	00/06		
45	♂	40+	5′3¾″ 1·62 m	02/04	05/15	14/28	0	Slight osteo-arthritis on lower cervical vertebrae.
46	♂	40+	5′7½″ 1·71 m	02/12	04/23	03/25		1 sagittal wormian. Metopic. Slight osteo-arthritis on lumbar vertebrae.
47	♀	40+	5′1¼″ 1·56 m	00/05	01/11	03/14	1	Inca bone. Slight osteo-arthritis on cervical and thoracic vertebrae.
48	?	*c*9		00/24	00/24	00/12		
49	♀	30–35	5′5½″ 1·66 m	01/17	01/24	00/24		
50	♀	17–20	5′5¼″ 1·66 m	00/11	00/14	00/14		
51	?	*c*1½		00/07	00/20			
52	?	*c*3		00/14	00/20		2	1 sagittal wormian.
53	♀	25–30	5′5½″ 1·66 m	01/17	00/15	00/19	1	1 sagittal wormian.
55	♂	25–30	5′9½″ 1·76 m	02/13	00/13	01/14		

56	♀	20–25	4′10½″ 1·49 m	00/30	00/31	00/31	10	2 coronal wormians.
56a	?	7–8 mo. i.u.?						
57	♀	20–25	5′0¾″ 1·55 m	00/04	00/13	01/14	0	
58	?	45+		00/04	00/04	11/15		
59	♀?	30–35	5′3¾″ 1·62 m	04/21	01/26	01/27	1	Inca bones. ? Cuts on skull.
63	♀	30–35	5′1¾″ 1·57 m	02/13	00/15	01/16		Cleft neural arch on eleventh thoracic vertebra.
64	♀?	17–20		00/25	00/08	00/28		
65	♂	25–30	5′9¼″ 1·76 m	00/31	00/31	00/32	1	Cleft neural arch on atlas.
66	♂	30+	5′6″ 1·68 m				1	Slight osteo-arthritis on mid-thoracic vertebrae.
67	♀	45+	4′11″ 1·50 m	04/24	07/32	07/32	5	
68	♀	Adult	5′4″ 1·62 m					
70	♀	20–25	4′10¼″ 1·48 m	00/01	00/07	00/08		
72	♂	Aged	5′2¼″ 1·58 m			06/06	0	Slight osteo-arthritis on some cervical and some lumbar vertebrae, left hip.
73	♀	30–35		01/20	04/30	00/30	0	
74	?	*c*1¾		00/20	00/20			
78	♀	45+		02/06	02/16	15/31		Osteo-arthritis on cervical vertebrae, but C3 and C4 fused congenitally.
88	♀	20–25	4′10¼″ 1·48 m	00/29	00/30	02/32	0	
105	?	2–4						
107	?	7–8		02/16	00/24	00/12		
106	♂	45+	5′7″ 1·71 m	02/09	05/14	13/23	1	2 coronal wormians. Osteo-arthritis on cervical and lumbar vertebrae.
150	♂	45+	5′8″ 1·73 m	01/16	01/20	03/23	0	Left fibula fractured.
151	♀	40–45	5′1″ 1·55 m	05/24	01/27	01/31	0	
152	♂	30–35	5′7¾″ 1·72 m	04/12	02/20	08/27	5+	Metopic. Slight osteo-arthritis on lower thoracic and first lumbar vertebrae. Infective arthritis of right big toe.
153	♂	45+	5′3¾″ 1·62 m	03/20	03/24	09/32	1	Right arm longer. Hole in sternum. Osteo-arthritis on several vertebrae, ankles.
155	♀?	30–35	5′4½″ 1·64 m	01/30	00/30	00/30	0	
157	♀	25+	5′0″ 1·53 m				0	Metopic. ? Healed tuberculosis of spine.

Burials from Queensford Mill—*cont.*

No.	Sex	Age	Height	Caries	Abscess	Loss	Lambdoid wormians	Other comments
172	♀	Adult	4′11¾″ 1·52 m					
174	?	Adult						
175	♂	20–25	5′5½″ 1·66 m	02/28	00/30	02/32	0	
176	♀	20–25	4′11½″ 1·51 m	00/05	00/06	00/06	1+	
177	♀	25–30	5′1½″ 1·56 m					
178	?	15–18		00/22	00/28	00/28		
179	?	13–14		00/28	00/28	00/28	6	Cleft neural arch on fifth lumbar vertebra. Sacral spina bifida occulta.

Appendix IV

Burials from Radley

No.	Sex	Age	Height	Caries	Abscess	Loss	Bones present		Lambdoid wormians	Asterionic wormian	Longer right arm	Cranial index	Decapitated	Other comments
							Skull	Long bones						
2	♀	Adult	5′7¾″ 1·72 m					×						
2	♀	Adult						×						
3/E	♂?	18–23	5′3¼″ 1·61 m					×						L femur shaft curved – rickets?
4/B	♂	30–35	5′5½″ 1·67 m	02/20	00/31	00/31	×	×	0	0		72·8	×	L arm longer. Osteo-arthritis on lumbar vertebrae.
C	♀	20–25	5′2½″ 1·59 m	00/29	00/32	00/32	×	×	6	0		72·8		
6/D	♀	20–25	5′6″ 1·68 m	01/15	04/25	03/28	×	×						Parts jaws only.
6	♂	16–20						×			×		×	Sacralized fifth or sixth lumbar vertebra.
7/15	♂	40+	5′6¼″ 1·68 m	00/00	00/00	30/30	×	×						Osteo-arthritis on R radius and ulna Exostoses on femur.
8	♂	40+	5′6″ 1·68 m	00/00	02/08	22/30	×	×	3	0	×	75·9		Osteomata on frontal bone.
9A	♀	35+	5′4¼″ 1·63 m	03/05	02/09	07/16	×	×	2	×	?	74·8		
9B	♂	35+	5′6¾″ 1·70 m	00/00	02/03	04/07	×	×						Exostosis on R tibia and fibula.
9/23	♂	40+	5′6½″ 1·69 m	04/09	03/13	19/32	×	×	0	×	×	76·3		Osteoma on frontal.
10/24	♀	30+	5′2″ 1·58 m	07/22	05/27	04/32	×	×	1	×	?	70·2		Osteo-arthritis on sacrum, proximal ends of tibiae.
11	♂	40+	5′6½″ 1·69 m	01/11	05/19	08/27	×	×	7		×			Metopic. Osteo-arthritis on all bones, especially hips and sacrum.
13	?	30–35		00/10	01/15	02/17	×	×						

Burials from Radley—*cont.*

No.	Sex	Age	Height	Caries	Abscess	Loss	Bones present Skull	Bones present Long bones	Lambdoid wormians	Asterionic wormian	Longer right arm	Cranial index	Decapitated	Other comments
14/16A	♂	40+	5′9″ 1·76 m				×	×	2	0				Osteo-arthritis in L scapula and humerus, sacrum.
14/16B	♀	17–22		03/21	02/32	00/32	×	×	1?	0	×	77·5		
14/16C	♀?	40+	4′10¾″ 1·49 m	02/04	00/11	05/16	×	×		0				Severe growth on L humerus, slight on L femur.
15A	♂	Adult						×						Osteo-arthritis on humerus.
15B	♂	Adult						×						
17	♂?	Adult					×		1	×		75·9		Large tumour on R parietal.
18A	♀	40+		00/01	01/08	07/16	×		1	0		77·7		1 sagittal wormian bone.
18B	♀?	35–40		02/06	00/13	11/24	×		0	0		77·7		
18C	?	30+		03/07	00/11	05/16								Mandible only.
18X	♂?	Adult						×						
18Y	♂?	Adult						×						
19	♂?	30+	5′7¼″ 1·71 m	00/04	00/10	06/16	×	×						
20	♂	30–35	5′6½″ 1·69 m	09/29	06/32	00/32	×	×	0	0	×	73·0		Slight osteo-arthritis in L hip.
18N/21	♀	40+	5′5″ 1·65 m	04/17	01/26	06/30	×	×	0	0	×	74·9		Six lumbar vertebrae. Osteo-arthritis on some vertebrae. Healed fracture of L scapula.
22	♀	40+	5′3¼″ 1·61 m	01/05	03/16	16/32	×	×	0	0	×	77·0		Osteo-arthritis on sacrum. Diseased R knee.
25	♀	17–22	5′1¼″ 1·55 m	04/17	01/20	00/20	×	×	2	0	×	77·8		
28	♂?	Adult	5′8½″ 1·74 m					×						Slight osteo-arthritis on humerus.
29	♂?	Adult						×						Slight osteo-arthritis on radius. Severe deformity of femora.
32/33	♀	Adult					×							

32/33	♂	Adult					×		
32/33X	?	40+				10/12			Mandible only.
32/33Y	?	40+				08/10			Mandible only.
32/33Z	?	40+		01/06	01/08	00/08			Mandible only.
32/33A	♂ ?	Adult	5′11″ 1·81 m					×	Diseased knee.
32/33B	♀	Adult						×	Slight osteo-arthritis in L hip.

Notes. 1. In compiling the above table, some bones in differently numbered boxes have been allocated to the same body because they appear to belong to each other, though some element of doubt must remain. Hence: 7/15, 9/23, 14/16A, 14/16B, 14/16C, 18N/21.

2. Skeletons 3/E, 4/B, 6/D and 10/24 bore dual identifications. The skulls, mandibles and post-cranial remains in the multiple groups 18 and 32/33 could not be satisfactorily correlated.

3. It is clear from the excavation report that there were two instances of decapitation and one prone burial. All the graves lay approximately N–S. For purposes of Table 5 the following have been omitted to avoid the possibility of duplication: 18X and Y, 32/33A, B, X, Y and Z: 32/33 have been considered as ♀ and ♂, both over 40 years.

Appendix V

Burials from Stanton Harcourt

Grave No.	No.	Sex	Age	Height	Caries	Abscess	Loss	Lambdoid wormians	Prone	Decapitated	Coffin nails or stain	Orientation	Other comments
2	4	♀	30–35	5′6″ 1·68 m	03/19	03/30	00/30	1			×	S	Osteo-arthritis on vertebrae. 6 lumbar vertebrae. C2 & 3 fused congenitally.
5	7		14–18									N	
8	10	♀	17–22	5′3″ 1·60 m	01/26	00/28	00/27	2			×	S	
11	13	♀	20–25		03/22	00/21	01/31					N	
14	16	♂	40+	5′6″ 1·68 m	00/03	04/07	24/32	2			×	N	Osteo-arthritis on vertebrae and arms. Broken ribs and radius.
17	19	♂	20–25		01/04	00/03	00/04					N?	
20	22	♀	20–25		03/16	03/18	05/27	5+			×	N	Metopic.
23	25	♀	20–25	5′1½″ 1·56 m	01/25	00/23	00/31	1		×	×	N	
27	29	♂	40+	5′6″ 1·68 m	02/28	04/29	00/29	0				N	Osteo-arthritis on six lumbar vertebrae, R hip. C3 & 4 fused congenitally.
30	32	♀	45+	5′7¼″ 1·71 m	05/13	05/19	12/32	0	×			N	Osteo-arthritis on vertebrae, both hips. Considerable mandibular torus. T5 & 6 fused congenitally.
33	35	♀	30+	5′3¼″ 1·61 m	05/10	05/24	06/30	0	×			S	Slight osteo-arthritis on vertebrae.
36	38	♂	30–40	5′6¾″ 1·70 m	10/27	04/30	02/32	3			×	N	Metopic. Osteo-arthritis on vertebrae and some joints. Hole in sternum.
43	45	♀	18–23	5′4¼″ 1·64 m	00/30	00/32	00/32	0				N	

46	48	♂	40+	5′8¼″ 1·74 m	00/03	05/11	05/16	2+			×	N	Osteo-arthritis on vertebrae. Fractured L clavicle. C2 & 3 fused congenitally.
49	51	♂	25–30	5′7¾″ 1·72 m	01/30	00/32	00/32	2		×	×	S	Hole in sternum.
52	54	♀	25–30	5′5¾″ 1·67 m	04/18	06/30	01/29	6			×	N	
60	62	♀	20–25	4′10″ 1·48 m	03/32	00/32	00/32	3+				N	Metopic.
60	64	?	neonatal									N	Buried with 62.
65	67	♂	25–30	5′8″ 1·73 m	05/21	01/27	01/28		×	×	×	N	Osteo-arthritis on vertebrae and R hip. Fractured L tibia & fibula.
68	70	♂	25–30	5′8″ 1·73 m	02/28	02/30	03/32	0			×	N	Osteo-arthritis on vertebrae. ? Cyst on vertebra.
71	73	♀	25–30	5′2″ 1·58 m	02/21	00/32	00/32	1			×	N	Slight osteo-arthritis on vertebrae.
74	76	♀	40+		04/06	00/08	16/24	0				N	Osteo-arthritis on vertebrae.
77	79	♂	25–30	5′6¼″ 1·68 m	00/29	00/29	00/29	1				S	
82	84	♀	Adult									N	Slight osteo-arthritis on vertebrae.
85	87	♂	25–30		01/22	00/16	00/22					N	
88	90	♀	30–35	4′11″ 1·50 m	06/22	05/28	02/28					N	Upper third molars impacted.
91	93	♂?	Adult									N	Osteo-arthritis on vertebrae. Overlies 98 in same grave.
94	96	?	Adult									N?	
91	98	♂?	40+		02/05	03/08	04/12					N?	Osteo-arthritis on vertebrae and elbows: Underlies 93 in same grave.
99	101	♂	30–35	5′10¾″ 1·80 m	05/23	07/30	02/30				×	S	Osteo-arthritis on vertebrae and L hip. C2 & 3 fused congenitally.
102	104	♂	40+		02/02	01/07	09/16	1+			×	N	Osteo-arthritis on vertebrae and R humerus.
106	108		*c*6 mo.									S	
113	115	♀?	Adult								×	S	
56	117	?	35+		00/05	00/08	05/13	0					Disturbed and reburied.
56	117	♂?	25–30		00/03	02/27	05/32	4					Disturbed and reburied.
118	120	?	*c*1½								×	N	

Appendix VI

Gazetteer of cemeteries in Great Britain containing decapitated and prone burials

The following gazetteer has been prepared from a survey of the literature. The sites, which are arranged alphabetically, are divided chronologically into two broad groups, Romano-British and Anglo-Saxon; there is one site of doubtful period.

Abbreviations used in the gazetteer

(a) Journals, &c.
A = Archaeologia
AC = Archaeologia Cantiana
AJ = Archaeological Journal
B = Britannia
BAR = British Archaeological Reports
CB = Crania Britannica
CBARR = Council for British Archaeology Research Report
G = Glevensis
JBAA = Journal British Archaeological Association
JRS = Journal of Roman Studies
MA = Mediaeval Archaeology
N&QS&D = Notes and Queries for Somerset and Dorset
O = Oxoniensia
PCAS = Proceedings of the Cambridge Antiquarians Society
PDNHAS = Proceedings of the Dorset Natural History and Archaeological Society
PHFC = Papers and Proceedings of the Hampshire Field Club
PSA = Proceedings of the Society of Antiquaries
RCAHM = Royal Commission on the Ancient and Historical Monuments
VCH = Victoria County History
VEHSRP = Vale of Evesham Historical Society Research Papers
WAM = Wiltshire Archaeological Magazine

(b) Other abbreviations
A–S = Anglo-Saxon
B = burial
C = century
Cr = cremation
D = decapitated burial
Ex = excavated
F = female
M = male
P = prone burial
R–B = Romano-British
Ref. = reference

The entries list the names of the site; county; National Grid reference; number of burials – B; number of cremations – Cr; number of decapitations – D; number of prone burials – P; dating – R–B or A–S; year(s) of excavation – Ex; and references – Ref. References not listed in full, other than to journals, &c., abbreviated as above, will be found on p. 169. Each site is preceded by a number by which it can be located on Fig. 5, p. 163).

Gazetteer of Romano-British and Anglo-Saxon cemeteries containing decapitated and prone burials

A. Romano-British cemeteries

1. Abingdon, Oxon. SU 483974. B11. D1; head between knees, adult M. P0. Probably late R–B. Ex. 1974. Ref. *B* (1975) **6** : 279; Parrington, M. (1978), *CBARR* **28** : 23–25, 36–37, 92.
2. Alcester, Warwicks. SP 089572. B11: 1F, 10 infants. D1: head between legs, young F. P0. Late C4 or later. Ex. 1975. Ref. *B* (1976) **7** : 331.
3. Baldock, Herts. TL 247339. B8: 2 adults, 6 juveniles. D0. P1: adult. R–B. Ex. 1968. Ref. *JRS* (1969) **59** : 222.
4. Beckford, Worcs. SO 982361. B10. Cr1. D5: heads between knees or feet, some also had hobnails, one possibly in a coffin. P0. R–B. Ex. 1972. Ref. *B* (1973) **4** : 287; *G* (1973) **7** : 6–7; *VEHSRP* (1975) **5** : 1–12.
5. Bloxham, Oxon. SP 4236. B30. D1: adult M. P3 or 4. R–B. Ex. 1930s. Ref. Knight, W. E. J. (1938).

6a. Cassington, Oxon. SP 449103. B100+, Cr 2. D16: 7 buried prone. P14 or 16: 7 also decapitated. R–B. Ex. 1930s. Ref. *JRS* (1937) **27** : 237; this report; *O* (1936) **1** : 201; *O* (1937) **2** : 201; *O* (1938) **3** : 165.

6b. Cassington, Smith's Pit II, Oxon. SP 450282. B3. D0. P2: adult Ms. Possibly same as bypass cemetery. Ex. 1950. *O* (1950) **15** : 104–110.

7. Charlton Mackrell, Somerset. ST 532294. B15. D2: skull placed at feet. P0. R–B. Ex. 1956, 57. Ref. Hayward, L. C. (1958), *N&QS&D* **27** : 180–181; Dewar, H. S. L. (1958), *N&QS&D* **27** : 206–207.

8. Cherry Hinton, Cambs. TL 484555. B3. D0. P1: F under 20 years. Probably R–B, possibly Iron Age. Ex. 1907. Ref. Walker, F. G. (1908), *PCAS* **12** : 267–273.

9. Cirencester, Glos. SP 0201. B354. D0. P5. R–B. Ex. 1970-74. Ref. *B* (1975) **6** : 271.

10. Cogenhoe, Northants. SP 828607. B1. D1: elderly M. P0. R–B. Ex. 1975. Ref. *Northants Arch.* (1976) **11** : 191.

11. Curbridge, Oxon. SP 337089. B21: some with hobnails. D3. P0. C2–C4. Ex. 1975. Ref. Chambers, R. A. (1976, 1978).

12. Cuxton, Kent. TQ 712665. B1, but possibly part of inhumation and cremation cemetery. D1: head between knees, young F. P0. Late C1? Ex. 1962. Ref. Tester, P. J. (1963), *AC* **78** : 181–182.

13. Dorchester, Dorset. SY 697906. B68+: most in wooden coffins. Cr2, D1: head between knees. P2. R–B. Ex. 1838–39, 1971. Ref. *RCAHM Dorset* **11** (1970) : 573; *B* (1972) **3** : 345.

14. Dunstable, Beds. TL 017215. B101. D12: head between or beside legs, includes one decapitated infant 3–6 months old, one F with head removed and placed between thighs, lower legs removed and placed beside upper arms. Late R–B. Ex. 1970s. Ref. Matthews, L. (1979), *Curr. Archaeol.* **69** : 310–312.

15. Duston, Northants. SP 732603. B17. D3: all adult, 1M, 1F; one with head between legs. P0. R–B. Ex. 1974, 1976. Ref. *B* (1976) **7** : 334; *Northants Dev. Corp. Arch. Unit* (forthcoming). NCD site R101.

16. Girton, Cambs. TL 423609. B large cemetery, inhumations and cremations. D1: head and first 3 cervical vertebrae between feet. P0. Mainly Anglo-Saxon, decapitated burial regarded as Roman. Ex. 1881, 1886. Ref. Hollingsworth, E. J. & O'Reilly, M. M. (1925), *The Anglo-Saxon Cemetery at Girton College Cambridge;* Liversidge, J. (1977); Meaney, A. (1964) : 65–66.

17. Great Casterton, Rutland. TF 0009. B several. D3: adult or sub-adult, one child. P0. Possibly Roman or Saxon. Ex. 1966. Ref. *JRS* (1967) **57** : 183, 185.

18. Guilden Morden, Cambs. TL 286402. B120: M, F, adults, children, Cr60+. D7+ : 1F+1? with head at feet; 1F with head in lap; 1 with head between legs; 1M buried prone was decapitated but had head in normal position. P2: Ms, one in charred coffin with head missing and lower arms and legs charred, other with head cut off. R–B. Ex. 1924, 1935, 1968. Ref. Fox, R. & Lethbridge, T. C. (1926), *PCAS* **27** : 49–63; Lethbridge, T. C. (1936); *JRS* (1969) **59** : 223.

19. Helmingham, Suffolk. TM 1857. B24 + several hundred, all M or children buried in enclosure, others also mutilated: severed arms, leg removed. D1: head in correct position relative to body, propped on a flint, one vertebra buried apart. P0. R–B. Ex. 1860s. Ref. Cardew, G. (1865), *JBAA* **21** : 267–273; *VCH Suffolk* **1** (1911) : 308.

20. Ilchester, Somerset. ST 520224. B60. D 'burial with displaced head occurred'. P 'prone burials occurred'. Late C4 or C5 AD, mainly adults, mostly coffined, mostly with boots. Ex. 1975. Ref. *B* (1976) **7** : 357–358.

21. Kenchester, Herts. SO 4442. B2. D1. P0. R–B. Ex. 1977. Ref. *B* (1978) **9** : 438.

22. Kimmeridge, Dorset. SY 906792. B2. D1: head by shins, elderly F in cist with spindle whorl, mandible apparently detached independently; second burial of elderly F on cist lid also had detached mandible. P0. Late C3? Ex. 1947. Ref. Calkin, J. B. (1947).

23. Lambourn, Berks. SU 358817. B3. D2: heads at feet. P0. C4. Ex. 1960. Ref. *Berkshire Archaeological Journal* (1967–68) **63** : 70.

24. Lankhills, Hants. SU 479303. B374. D7: heads by legs or feet, one child. 3M, 2F, 1 other adult. P14: 5M, 1F (also decapitated), 1 infant. Late C4. Ex. 1970s. Ref. Clarke, G. (1979).

25. Leicester, Leics. SK 580044. B3+ : 1F, 2 infants. D1: head between thighs, infant. Late R–B. Ex. 1953, 1975. Ref. *B* (1976) **7** : 327.

26. Littlechester, Derbys. SK 362375. B46: adults and children. Cr? D3: 1M, 1F? P7: 3M, 4F. R–B. Ex. 1979. Ref. Director, Trent Valley Archaeol. Res. Comm. (pers. comm).

27. Lord's Bridge, Cambs. TL 394544. B2. D2?: one with head separated from body; F about 23 years, also prone disjointed skeleton laid out in correct order, head by pelvis. P1: disjointed F in stone coffin with hobnails, also decapitated. First decapitated skeleton may be secondary, possibly A–S. Ex. 1907. Ref. Walker, F. G. (1908), *PCAS* **12** : 273–284.

28. Manton Down, Wilts. SU 1471. B1. D1: head between feet, young F, in chalk-cut cist, neck severed at 6th cervical vertebra, first cut slanting. Early C4. Ex. 1891. Ref. *WAM* (1892) **26** : 412.
29. Margidunum, Notts. SK 701413. B15+: M, F, adults, children. D1: head beside feet, also buried prone, youth, possibly M. P1: youth, also decapitated. Late R–B. Ex. 1968. Ref. Todd, M. (1969), *Trans. Thoroton Soc. Nott.* **73** : 75.
30. Mundford, Norfolk. TL 793941. B7. D2: heads beside feet, young adult M and elderly F. P0. C4? Ex. 1963. Ref. *Norfolk Res. Comm. Bull.* (1963) **15** : 10; *JRS* (1964) **54** : 168.
31. Orton Longueville, Hunts. TL 167952. B8: adults. D1: skull in foot of grave, old F. P0. Associated with early C2 farmstead. Ex. 1974. Ref. *B* (1975) **6** : 252.
32. Owslebury, Hants. SU 525246. B51. Cr19. D0. P1: carelessly laid out. C2–C4. Ex. 1961–72. Ref. Collis, J. (1977), *CBARR* **22** : 26–34.
33. Perrymead, Somerset. ST 7563. B1. D1: 'headless skeleton' in stone coffin. P0. R–B. Ex. 1952. Ref. *JRS* (1953) **43** : 123.
34. Poundbury Camp, Dorset. SY 685911. B1400+. D2F: skull by feet (disturbed by later grave?); in ditch at Poundbury Camp, head at feet. P0. Late R–B. Ex. 1970–80. Ref. *PDNHAS* (1970) **92** : 138; (1971) **92** : 281.
35. Radley, Berks. SU 514983. B35: adults. D2: heads between knees. P1. C4. Ex. 1945. Ref. *JRS* (1946) **36** : 144; Atkinson, R. J. C. (1952).
36. Rushton, Northants. SP 860838. B24. D24: M, F, children, secondary burials in two rows around a barrow. Date uncertain. Ex. 1964. Ref. *JRS* (1965) **55** : 210.
37. Sawbridgeworth, Herts. TL 473137. B24: 22F, 1 infant, 1 child, some with hobnails. D1: head above shins. P0. C3–C4. Ex. 1936. Ref. Andrews, L. C. (1936), *Trans. E. Herts. Arch. Soc.* **9** : 364–366; *JRS* (1937) **27** : 239.
38. Sea Mills, Glos. ST 558137. B3. Cr9. D1: skull placed on pelvis, child. P2: adults, one with boots. Cr: early; B: C2 or later. Ex. 1972. Ref. *Arch. Excav.* (1972) : 53; *B* (1973) **4** : 309–311.
39. Springhead, Kent. TQ 6172. B4. D2. P0. 2 pairs of infant burials each associated with a different floor level, and each including one decapitated infant. One burial in each corner of Temple IV, all appear to be crouched. Ex. 1950s. Ref. Penn, W. S. (1960), *AC* **74** : 113–140.
40. Stanton Harcourt, Oxon. SP 415050. B36. D3: heads between knees or at feet, one buried prone. P3 : 1 adult M also decapitated, 2 adult F, R–B. Ex. 1978. Ref. McGavin, N. (1981), *O* **45** : 112–123.
41. Stretton on the Fosse, Warwicks. SP 218383. B14+: some with boots, some in coffins, D?. P0. Late R–B. Ex. 1971. Ref. *W. Midlands Arch. News Sheet* (1972) **14** : 22; *CBA* (1977) **22** : 53–64.
42. Studland Church, Dorset. SZ 0382. B1. D1: head by left foot, F in cist with spindle whorl. P0. R–B. Ex. 1952. Ref. *JRS* (1953) **43** : 125.
43. Temple Guiting, Glos. SP 1226. B16+: some with boots, some in coffins. D2 at least: 1 head by feet, 1 head between knees. P0. R–B. Ex. 1870s, 1880. Ref. Royce, D. (1882-3), *Trans. Bristol Glos. Arch. Soc.* **7** : 76–77.
44. Todbere, Dorset. ST 8020. B1. D1: skull with first 3 vertebrae, beside shins, M, in lead coffin with hobnails and spindle whorl. P0. R–B. Ex.? Ref. Mansell Pleydell, J. C. (1892), *PDNHAS* **14** : 24.
45. Tripontium, Warwicks. SP 535795. B50+ scattered: M, F, adult, children, including a headless body and 1 young F buried without lower vertebrae, left arm or lower legs – some evidence of strangulation. D1 or 2: head across ankles, young F. P0. R–B. Ex. since 1930. Ref. Cameron, H. & Lucas, J. (1967, 1973), *Trans. Bgham Arch. Soc.* **83** : 130–179; **85** : 93–144.
46. Uffington, Berks. SU 300865. B46: M, F, adults, children. D3?: 1M head below knees, also buried prone, 1M & 1F headless. P5: 1M also decapitated. Burials in barrow, few disorderly. Ex. 1858. Ref. *CB* (1865) pl. 51 : 1–6; *WAM* (1927) **43** : 437.
47. Walkington Wold, Yorks. SE 962357. B12: 11M, 1F. D10: the only F burial has head buried a little beyond the feet. P0. Secondary burials around a barrow, 3 simultaneous in 1 grave above a fourth. Associated with 'Germanic' objects. Ex. 1967, 1968. Ref. Bartlett, J. E. & Mackay, J. W. (1973), *E. Riding Archaeol.* **1** : 1–93.
48. Winchester, Hants. SU 481299. B80: 12 adults, 68 children or infants. Cr92. D1: adult. P0. Late C1 or C2. Ex. 1973-77. Ref. *B* (1978) **9** : 465.
49. Winterbourne Down, Wilts. SU 203324. B14: 5 adults, 3 infants in coffins, hobnails and cleats in 5 graves. Cr36. D3: adults. P0. Cemetery within banked enclosure, C4. Ex. 1962. Ref. *WAM* (1963) **58** : 470.
50. Woodyates, Dorset. SU 032199. B5: burials with a square enclosure. D: 1 or 2, 1 head and four vertebrae by right tibia, a possible decapitation with boots. P0. Late R–B. Ex. 1888–91. Ref. Pitt Rivers, F. L. (1892), *Excavations at Bokerly and Wansdyke* **3** : 211.
51. Wor Barrow, Dorset. SU 012172. B17: secondary burials in barrow, 16 adult M, 1 adolescent. D2: skulls by left femora, also 8 with heads absent. P1, beside 2 decapitations. R–B. Ex. 1893–96. Ref. Pitt Rivers, F. L. (1898), *Excavations in Cranborne Chase* **4** : 58–78.

52. Wroxeter, Salop. SJ 5608. B1. D1: head by shins, also prone. P1: also decapitated. Late or post-Roman. Ex. 1923–27. Ref. Atkinson, D. (1942), *Excavations at the Roman Town of Wroxeter*: 112–113, pl. 30B.
53. Wroxton St Mary, Oxon. SP 415418. B8+. D1: head between thighs, adult F. P1, adult M. R–B. Ex. 1980. Ref. Chambers, R. A. (forthcoming).
54. Wycombe, Glos. SP 025197. B few? D1: head at feet, M. P0. C4. Ex. ? Ref. Clarke, G. (1979).

B. Anglo-Saxon cemeteries

55. Beakesbourne, Kent. TR 200555, B40+. D0. P1. A–S. Ex. 1950s. Ref. Meaney, A. (1964) : 109.
56. Brighthampton, Oxon. SP 383033. B67+: some with cleft skulls. Cr11+ D1: skull in lap. P0. A–S. Ex. 1857. Ref. Akermann, J. Y. (1857), *A* **37** : 391–398.
57. Burwell, Cambs. TL 590660. B113. D1: skull beside feet, cuts into face, adult M. P1. A–S. Ex. 1884, 1924–26. Ref. Lethbridge, T. C. (1924–28), *PCAS* (1924-5) **27** : 72–79; (1925–6) **28** : 116–123; (1926–7) **29** : 84–94; (1927–8) **30** : 97–109.
58. Camerton, Somerset. ST 686566. B115. D0. P1: adult F. A–S. Ex. 1926–32. Ref. Meaney, A. (1964) : 218.
59. Chadlington, Oxon. SP 330210. B16: M, F, adults, children. D3: adult M. P0. A–S. Ex. 1930s. Ref. Leeds, E. T. (1940), *O* **5** : 23–30.
60. Cuddesdon, Oxon. SP 600031. B several: arranged radially feet to centre of circle, legs crossed. D0. P all. A–S. Ex. 1847. Ref. *AJ* (1847) **4** : 157–159; Dickinson, T. (1974), *BAR* **1** : 1–24.
61. Dunstable, Beds. TL 006210. B94: mostly adult Ms, some simultaneous burials, many with hands tied. D2? headless. P3. A–S. Ex. 1926–29. Ref. Dunning, G. C. & Wheeler, R. E. M., *AJ* (1931) **88** : 193–217.
62. Elloughton, Yorks. SE 941278. B some: careless burials, M, F, 1 child, in a sack? D1? headless. P some. A–S. Ex. 1940. Ref. Meaney, A. (1964) : 287.
63. Farthing Down, Surrey, TQ 299583. B27. D0. P2: 1M?, 1F. A–S. Ex. 1760, 1871, 1939, 1948–50. Ref. Meaney, A. (1964); *Arch. News Letter* (1950) **2** : 170.
64. Frilford, Berks. SU 437964. B numerous. D0. P1: M. A–S. Ex. 1868. Ref. Rolleston, G. (1870) : 437, 477.
65. Great Addington, Northants. SP 957744. B many. D3? three or four stones heaped up in place of heads of headless bodies. P some. A–S. Ex. pre-1847. Ref. Meaney, A. (1964) : 186.
66. Holdenby, Northants. SP 695671. B29+. D0. P1: F, above an older burial. A–S. Ex. 1862, 1864, 1899, 1909. Ref. Meaney, A. (1964) : 190.
67. Houghton, Hunts. TL 285721. B1. D0. P1: face down and doubled up. A–S. Ex. pre-1868. Ref. Meaney, A. (1964) : 106.
68. Little Downham, Cambs. TL 523838. B many. D0. P1: M. A–S. Ex. 1928, 1933. Ref. Meaney, A. (1964) : 64.
69. Little Wilbraham, Cambs. TL 560577. B200+. Cr135+. D0. P2: adults, 1M. A–S. Ex. 1847–51, 1923, 1926. Ref. *AJ* (1851) **8** : 172–175; Neville, R. C. (1852), *Saxon Obsequies* : 15.
70. Loveden Hill, Lincs. SK 908458. B12. Cr300+. D1: head on stomach. P0. A–S. Ex. 1921–26, 1955–70s. Ref. Meaney, A. (1964) : 158.
71. Market Weighton, Yorks. SE 8741. B2. D0. P1: F. A–S. Ex. 1906. Ref. Meaney, A. (1964) : 295.
72. Meon Hill, Hants. SU 344352. B10: secondary burials at a hill fort, 4 probably with hands tied. D6: M, 2 with heads between knees, 1 between thighs, 2 in normal position, 1 also prone. P2: Ms, one also decapitated, A–S. Ex. 1932. Ref. Liddell, D. M. (1934), *PHFC* **12** : 127–162.
73. Mitcham, Surrey. TQ 270861. B230+: several have extra skull in graves, excavations poorly recorded. D1: M, skull at feet. P4: three F, one above another supine F, simultaneous burial. A–S. Ex. early C19, 1888–1922. Ref. Bidder, H. F. & Morris, J. (1959), *Surrey Arch. Coll.* **56** : 51–131.
74. Portsdown, Hants. SU 666064. B14+. D1: shoulder placed close against east end of grave with head on top, young adult. P0. A–S. Ex. 1816, 1966. Ref. Bradley, R. & Lewis, E. (1968) *PHFC* **25** : 27–50.
75. Prittlewell, Essex. TQ 878873. B several. D0. P1. A–S. Ex. 1931. Ref. Meaney, A. (1964) : 87.
76. Roche Court Down, Wilts. SU 251357. B17: probably entirely male cemetery, 4 at least probably had hands tied. D9 or 10: Ms, 1F? P2: young adult M, one possibly also decapitated. A–S. Ex. 1930. Ref. Stone, J. F. S. (1930–32), *WAM* **45** : 568–599.
77. Ruskington, Lincs. TF 076514. B25. Cr2. D0. P3: child c. 9 years, 2F: adolescent, adult, A–S. Ex. 1975. Ref. Atkin, M. (pers. comm.).
78. Sewerby, Yorks. TA 205691. B49+: M, F, adults, children. D0. P1: F above coffined burial of F. A–S. Ex. 1959. Ref. *MA* (1960) **4** : 137.

79. Thetford, Norfolk. TL 860820. B about 50, associated with an earthwork. D all decapitated. P0. A–S. Ex. 1957. Ref. *Bull. Br. Archaeol. Assoc.* (1957) **93** : 2.
80. Toddington, Beds. TL 030292. B13. D0. P1: M. A–S. Ex. 1861, 1874, 1876, 1883. Ref. *PSA* (1884) **10** : 36–38; Meaney, A. (1964) : 40.
81. Totternhoe, Marina Drive, Beds. TL 008214. B38+ many. D0. P1. A–S. Ex. pre-1957, 1957–8. Ref. Meaney, A. (1964) : 41.
82. Uffington, Berks. SU 300865. B6: carelessly buried skeletons. D3: 2M, 1 young person, head beneath knees. P0. A–S. Ex. 1858. Ref. *CB* (1865) pl. 51: 1–6; *VCH Berkshire* (1906–) : 247.
83. Wheatley, Oxon. SP 602046. B16+. D1: skull between knees. P1. A–S. Ex. 1883. Ref. Leeds, E. T. (1916), *PSA* **29** : 48–64.
84. Worthy Park, Hants. SU 500327. B94. Cr37+. D0. P2: one F, late 20s disorderly, one adolescent F, laid out, possibly tied. A–S. Ex. 1961–63. Ref. *MA* (1962–3) **6–7** : 307, (1964) **8** : 233; Hawkes, S. C. & Wells, C. (1975).

C. Doubtful period

85. Wandlebury, Cambs. TL 495533. B5+: one individual had sword cut in chin, no artefacts. D0. P1: with arms outstretched, above another supine burial. Presumed to be Iron Age. Ex. 1976. Ref. Taylor, A. & Denston, B. (1977), *PCAS* **67** : 1.

The Jurassic irregular echinoid *Nucleolites clunicularis* (Smith)

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Synopsis

The often-cited echinoid species *Nucleolites clunicularis*, from the Middle Jurassic of western Europe, has been interpreted in a broad sense in the literature, and in consequence its systematic position has become obscured. It is shown here that the species should be ascribed to William Smith. His holotype exists and is redescribed. Its age is Oxfordian (Corallian).

Introduction

Much of the curator's work consists in the painstaking accumulation of information about specimens, their cataloguing and their preservation and retrieval from storage when required. This work is largely a matter of careful routine, but occasionally a detective story emerges, such as the one recorded here, which is of additional importance to the systematist. *Nucleolites clunicularis* of authors is a common fossil at certain horizons in England, in sediments ranging from Bajocian to Oxfordian age, and appears frequently in faunal lists particularly those of the Cornbrash. It is sometimes ascribed to authors such as Lhwyd, Fleming or Conybeare and includes diverse forms which can be referred to several distinct species. However, which of these diverse forms is in fact the true *N. clunicularis*?

The taxonomic position of *Nucleolites clunicularis*

Edward Lhwyd (1699 : 48) described an echinoid figured by Lister (1678 : tab. 7, fig. 26), giving it the name *Echinites clunicularis*. This species does not appear to have been described or mentioned again by a pre-Linnaean author, except in the later illustrated edition of Lhwyd's book published in 1760. The first post-Linnaean use of the name was in William Smith's *Stratigraphical System of Organized Fossils* (1817*a*) and in the third part of his *Strata identified by Organized Fossils* (1817*b*). As an appendix to the first of these (1817*a* : un-numbered pages at end) Smith wrote some 'Observations on Echini', on the second page of which appears the following:

> The Stratigraphical Table exhibits many instances of repetition of the same species in more than one stratum, and a little attention evinces the accuracy of an observation previously made, that "*similar strata contain similar fossils*;" Clypeus, No. 2 (clunicularis Llwyd), is a common instance. This species is repeated in five different strata, all of them calcareous, for the fossils in the Clay over the upper Oolite lie within a small depth of the rock, and are generally filled with stony matter.
>
> Yet although the same species is repeated in these different strata, a considerable difference in appearance may be traced between specimens from the Pisolite and others from the Cornbrash and Oolites. These last are thinner at the edge, with a more undulated base and flatter sides, particularly that side containing the groove.

It is evident from the above quotation that Smith considered the specimens from above the Cornbrash to be more typical of the species. In the 'Stratigraphical Table of Echini'

Bull. Br. Mus. nat. Hist. (Geol.) 35 (3) : 189–194

Issued 29 October 1981

(1817*a* : second col. plate) he described Clypeus No. 2 as follows:

> Oblong, subquadrangular; base concave in the middle; mouth small, five-angled; upper side convex, with a large deep furrow on one side from the apex to the margin; rays ten biporous lines in five pairs, depressed on the base: apertures opposite, excentric from the broad or furrowed end. Shell unequally covered with small granula, most numerous on the base.

He records it from the 'Under Oolite, Upper Oolite, Clay over the Upper Oolite, Cornbrash, and Coral Rag and Pisolite'. The only mention of Clypeus species 2 in the general text of this work is on page 110 on which is recorded

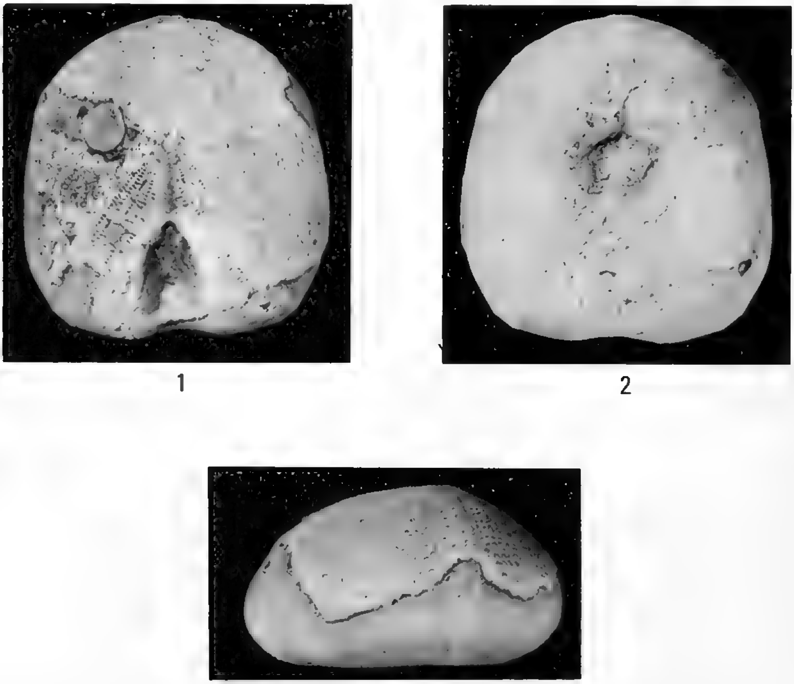
Clypeus. *Coral Rag and Pisolite*
Churchill

but this section of his work is concerned with the 'Under Oolite'.

In the second work (1817*b*), Smith figured on the plate illustrating 'Coral Rag and Pisolite' fossils a *Clypeus* to which no specific name was given (pl. facing p. 20, fig. 6). This is the only example of *Nucleolites* which Smith illustrated and, furthermore, it is evidently the form that he considered to be '*Clypeus*' *clunicularis*, for he stated (1817*b* : 20):

> This latter specimen, as shown in my "Stratigraphical Table of Echini" is one of the characteristic distinctions of the Pisolite part of the rock.

He records the species from Meggot's Mill, Coleshill, Longleat Park and Hinton Waldrish. The figured specimen is in the British Museum (Natural History), reg. no. E495; it is the only



Figs 1-3 *Nucleolites clunicularis* (Smith). E495, lectotype herein selected, ×2. The specimen was coated with ammonium chloride to enhance the detail. 1, apical surface. 2, oral surface. 3, lateral view.

surviving specimen of this species in William Smith's collection and is labelled as being from Meggot's Mill.

Although we have followed a rather tortuous route, we now have a valid species described and figured by Smith to which he gave the name *Clypeus clunicularis*. Although he refers to Lhwyd's description, the specimens referred to by Smith from the Coral Rag and Pisolite form the syntype series of which the figured specimen survives and is here formally selected as the **lectotype**.

Subsequently, Conybeare (1822 : 188), when describing the Coral Rag, referred to *Clypeus clunicularis*, citing fig. 6 of Smith's plate. Fleming (1828 : 479) also cited Smith's fig. 6 and Conybeare's citation in his listing of *Clypeus clunicularis*. Fleming gave the name *Clypeus lobatus* to the specimen figured by Lister (1678 : tab. 7, fig. 26), to which Lhwyd had given the name *Echinites clunicularis*. Unfortunately, Thomas Wright (1859 : 334) revised the description of '*Echinobrissus*' *clunicularis* at a time when some workers adopted names published before Linnaeus' *Systema Naturae* and others did not. Wright attributed the species to Lhwyd, but correctly pointed out that it is impossible to decide from the illustrations cited by Lhwyd whether the Inferior Oolite or the Coral Rag form is represented by the drawings. Wright then restricted his '*Echinobrissus clunicularis* Llhwyd' to the forms found in the sediments ranging from the Inferior Oolite to the Cornbrash, excluding the typical Coral Rag form altogether. He relegated into synonymy valid specific names already given by French authors to the Bajocian and Bathonian forms which are available for use and are used by continental authors. In the preparation of faunal lists, most English authors have followed Wright's interpretation of *Nucleolites clunicularis*. In this instance, however, common usage cannot be invoked as an excuse for setting aside all designations of *Nucleolites clunicularis* previous to that of Wright (1859 : 332–337). Moreover, Wright's figured specimens (1859 : pl. XXIV, figs la–k) have not been located in any collection. It would greatly facilitate future revision of the Jurassic species of *Nucleolites* to return to the correct definition of *N. clunicularis* given by Smith (1817).

Systematic Description

Superorder **ATELOSTOMATA** Zittel, 1879

Order **CASSIDULOIDA** Claus, 1880

Family **NUCLEOLITIDAE** Agassiz & Desor, 1847

Genus ***NUCLEOLITES*** Lamarck, 1801

Nucleolites clunicularis (Smith, 1817)

MATERIAL. E495, the lectotype (herein selected), in the William Smith collection of the Department of Palaeontology, British Museum (Natural History). Figs 1–4.

PRESERVATION. The specimen is very worn, and has lost slightly more than half of the original test. The remaining test is present above the ambitus and has the apical system preserved, together with petaloid ambulacra I, II, and III, the adoral ends of which are missing. A small portion of the adapical end of the ambulacral petal IV is present, and about half of ambulacral petal V, with portions missing from the middle of its length and at the adoral end. The periproct is mostly covered by matrix. The remainder of the specimen is an internal cast.

DIAGNOSIS. Test almost as broad as long. The outline is rounded anteriorly, the lateral margins almost straight, and marked with a shallow sulcus at the posterior end. An elongated V-shaped deep groove leads from the periproct to the sulcus. Apical system tetrabasal, anterior of centre, with test preserved between it and the periproct rim. Test moderately inflated above the ambitus, with the highest point towards the anterior end. Petaloid ambulacra about equal, narrow and open. Ornament on the test consists of closely packed, asymmetrically developed primary tubercles surrounded by small milliary tubercles. Oral surface gently rounded. Mouth pentagonal and situated vertically below the apical system.

DIMENSIONS. Length of test 24·4 mm, width 23·1 mm, maximum height 13·5 mm. The approximate lengths of the ambulacral petals are: I > 13·3 mm, II > 11·7 mm, III > 11·7 mm, IV > 11·7 mm, V > 12·5 mm.

APICAL SYSTEM. This is small, worn and incomplete. Fig. 4.

(a) *Ocular plates.* Remains of the ocular plates IV and V show the ocular pore in a roughly triangular plate. Depressions marking the positions of the ocular pores are also present in plates I, II, and III.

(b) *Genital plates.* Genital plates 1, 3, and 4 are present with elongate genital pores. Each pore is about 0·8 mm long. The precise shape of each plate is obscured by erosion of the test. There are the remains of a dividing bar across the short width of each of pores 1 and 3 but no such bar is present in pore 4. Genital plate 2, the madreporite, is large, extends to the centre of the apical system, and is more or less circular in outline. It has many pores opening onto its surface. Genital plate 5 is missing, and in its place, extending posteriorly to meet the interambulacrum 5, are four small plates. One of these is five-sided, ornamented by one larger tubercle surrounded by several smaller tubercles, and is situated adjacent to the madreporite. The second is posterior to the first and is an irregularly-shaped plate bearing several small tubercles. Laterally adjacent to both is a third plate with an irregular outline and bearing several small tubercles. The fourth plate is small and is situated anterior and adjacent to the third, but is too worn to describe accurately.

PERISTOME. None of the original test is present on the oral surface, only the internal cast. The peristome is pentagonal, 4·6 mm across the widest part, and 3·6 mm from the anteriormost point to the base of the pentagon. The peristome is in a shallow depression in the test and is eccentric anteriorly. It is 11·6 mm from the posterior ambitus to the pentagon base, and 8·8 mm from the anterior part of the ambitus to the pentagon apex.

PERIPROCT. This is present at the bottom of a deep furrow which broadens posteriorly into interambulacrum 5. The furrow is 5 mm wide at the mid-point of the test where some original test remains. The furrow is a long V-shape, extending from the ambitus to just posterior of the apical system. The walls are steep, and are about 2·75 mm high at the deepest part. In cross-section the furrow is U-shaped. Traces of the periproct can be seen at the adoral end and at the adapical end. At the adoral end the margin of the periproct is a broad V-shape. The central portion is buried beneath matrix. At the adapical end the peristome closes in a shallow V.

APICAL SURFACE. (a) *Ambulacra.* None of the ambulacra are complete. Paired ambulacral petals I and V, seen as internal casts and with some original test, are slightly longer than paired ambulacral petals II and IV and unpaired ambulacral petal III. They are all flush with the surface of the test; all are long and thin, and all have a maximum width of 3 mm. The paired ambulacral petals have their anterior pore rows in an almost straight line from the gentle curve near the apical system. The posterior pore rows are gently curved posteriorly. Ambulacral petal III has pore rows which are more or less straight to the anterior margin.

All the petals have similar types of pore-pairs and ornament. The pores of each pore-pair are not equal. The adradial pores are elongate and almost tear-drop shaped, surrounded by a smooth, shallow, raised rim. The perradial pores are circular and also have a smooth raised rim; they are slightly adoral to the adradial pores, so that the pore-pairs are oblique. Between the adradial and perradial pores is a small swelling, but because of wear of the test its exact nature cannot be determined. Between each pore-pair is a low ridge bearing three or four small tubercles. The interpore zone has ornament which consists of large tubercles surrounded by smaller tubercles. The large tubercles alternate in position so that each one is adjacent to one which is either perradial or adradial in position to itself, both along the

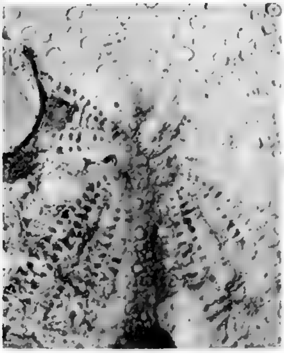


Fig. 4 *Nucleolites clunicularis* (Smith). E495, lectotype, detail of part of the apical surface to show the apical system, × 5. The specimen was coated with ammonium chloride.

length and across the width of the petal. Where a large tubercle is adjacent to an interpore ridge, the ridge bears only three small tubercles. Other ridges have four small tubercles. The large tubercles have broad, low, crenulated bosses, but no mamelons are preserved intact; the weathered remnants show them to have been relatively large. Each boss has a fairly deeply indented scrobicule which is more or less circular in outline. The bosses are centrally placed on the scrobicules near the apical end of ambulacral petals II, III and IV but towards the ambitus they are placed adorally eccentric on the scrobicule. Each tubercle is surrounded by a ring of smaller tubercles. The bosses of the large tubercles retain their central position throughout the length of ambulacral petals I and V.

(b) *Interambulacra.* The ornament of the interambulacra consists of tubercles similar to those of the ambulacra. Near the apical region the bosses on interambulacra 1–4 are placed centrally on the scrobicules, but they become increasingly eccentric towards the ambitus, anteriorly on interambulacra 2 and 3, and anterolaterally on interambulacra 1 and 4. The ornament of interambulacrum 5 is similar to that of the other interambulacra, but the tubercle bosses are centrally placed within the scrobicules over the whole of the surface. Tubercles within the furrow and on the furrow walls have been almost completely weathered away. Only faint remains can be seen. Those on the 'shoulders' of the furrow have similar preservation to the tubercles on the rest of the test. At the adapical end of the furrow the test is rather deeply undercut. Above the undercutting, interambulacrum 5 continues towards the apical system in a narrow, slightly depressed, almost parallel-sided strip of test. The ornament is similar to that of the rest of the test.

NOTE ON THE ORNAMENT. The tubercles of the interambulacra are remarkably uniform in size over the test, except near to the apical system where they are slightly smaller. Those further from the apical system measure 0·5 mm–0·75 mm in diameter, and those near the apical system about 0·3 mm. The ambulacral tubercles show similar uniformity of size, and are slightly smaller than those of the interambulacra. They are 0·5 mm in diameter further from the apical system, and about 0·25 mm nearer to it. The tubercles are quite closely packed and have a regular order, alternating along the length of the ambulacra, whilst those of the interambulacra alternate both in horizontal rows and in a dorso-ventral direction at the interradial position.

ORAL SURFACE. None of the test remains on the oral surface nor on the lateral parts of the specimen. The lower part of the specimen is represented by a badly worn internal cast. The ambulacra are present as raised portions of the cast, with the pore pairs seen as closely packed horizontal bars, or holes, arranged in two rows for each ambulacrum. The bars join a naked area along the middle of the ambulacrum.

Stratigraphy and locality of the lectotype

Smith recorded the geological horizon and geographical locality of the lectotype as the Coral

Rag of Meggot's Mill, Coleshill. The specimen itself has the remains of writing on it which reads 'Rag. Hill'. This indicates that it comes from the Coral Rag of Coleshill.

Coleshill is about 4·5 km north of Shrivenham, Berkshire, and about 3·5 km west of Great Coxwell. Just to the south-west of the village, at National Grid reference SU 235934, is a disused mill, marked on the 1 : 10 560 (6 inches : 1 mile) Ordnance Survey map as 'Coleshill Mill'. It is quite likely that this is the original locality. The mill is situated on the upper Oxfordian ('Corallian').

Smith (1817*b* : 19) writes 'The Coral Rag consists chiefly of lumps of coralline Limestone, which in the quarry are very rough, irregular, and dirty; . . . The Pisolite Freestone beneath is softer.' He clearly states (1817*b* : 20) that *Clypeus* 'is one of the characteristic distinctions of the Pisolite part of the rock.' His stratigraphic terms may be compared with modern terms in the following table:

Chronostratigraphy		Lithostratigraphy	
	Stage	*Modern terminology*	*Smith's terminology*
Upper Jurassic (part)	Oxfordian, including 'Corallian'	Coral Rag	Coral Rag and Pisolite
Middle Jurassic	Callovian	Upper Cornbrash	Cornbrash
	Bathonian	Lower Cornbrash	
		Bradford Clay	Clay over Upper Oolite
		Great Oolite	Upper Oolite
	Bajocian	Inferior Oolite	Under Oolite

Acknowledgement

We would like to thank Paul Lund of the Photographic Unit of the British Museum (Natural History) for taking the photographs.

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Phanerotinus cristatus (Phillips) and the nature of euomphalacean gastropods

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Synopsis

New specimens of *Phanerotinus cristatus* (Phillips) found in the Lower Carboniferous of Cumbria have contributed to a re-appraisal of the morphological characters and function of this unique gastropod, which confirms that it belongs to the Euomphalacea. Various morphological features and the relationships of this superfamily are evaluated. A revised classification of the superfamily, eliminating some post-Palaeozoic genera, is proposed.

Introduction

Several factors have led to this paper on *Phanerotinus cristatus.* A certain uneasiness concerning the published interpretation of this unusual gastropod prompted one of us (N.J.M.) to re-examine the original material in order to establish how such an animal may have functioned. The comparative rarity of the species, which may have been limited to Britain and of which only three further specimens have been recognized in the 150 years since it was first collected, underlines its position as an object of interest. The historical background and involvement of a number of the important figures in nineteenth-century British palaeontology with the collection and description of the original specimens, in the Gilbertson collection, also provided a further motive, but it has now been decided to discuss this aspect elsewhere.

William Gilbertson (1789–1845), a pharmaceutical chemist in Preston, Lancashire, diligently amassed a unique collection of Palaeozoic fossils, mainly from the Carboniferous Limestone outcrops in the Clitheroe district of the neighbouring county of Yorkshire. Owing to the use of this collection by many of the earlier descriptive palaeontologists such as John Phillips (1836) and J. de C. Sowerby (1827–1844), see Cleevely (1974), Gilbertson could be regarded as the most significant and influential of the earlier collectors resident in the north of England. He may well have considered offering the collection to the British Museum while it was still in use by Sowerby, for correspondence in the Sowerby archive requests the return of borrowed specimens; soon after, in 1841, it was acquired by Dr J. E. Gray for the Dept. of Zoology, where it remained until transferred to the Dept. of Geology in 1881.

The early descriptions of the large, ornate, but rather rare genus *Phanerotinus* J. de C. Sowerby, 1844, from the Lower Carboniferous of Britain, were based on a single specimen in the Gilbertson collection. Yet these descriptions covered all the more important and distinctive characters of this unusual fossil gastropod: its large size, the regularly open-coiled shell and the very long sawtooth-like projections on its outer margin. Unfortunately, the natural breakage of the specimen had occurred along the relatively smooth base and a clear idea of the arrangement of these distinctive projections was difficult to obtain. In fact, both Phillips (1836) and Sowerby (1844) were led to suggest that there were two rows of such spines. However, the acquisition of a further specimen, from the Tennant collection in 1881, eventually contributed to a careful study by Knight (1941 : 239) which established that only a single row existed. He explained that flattening and consequent breakage during fossilization had led to the false impression that there were two rows of projections.

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The fortunate discovery of two further specimens in the collections of the Institute of Geological Sciences has assisted in the re-appraisal of the genus. Closer examination of the Tennant specimen utilized by Knight has revealed that a small area of the dorsal surface of the shell is preserved and this clearly shows a re-entrant sinus at the top of the adapical margin. Sectioning of this same unique specimen has enabled us to discover further ornament detail. We have been able to reinterpret the nature of *Phanerotinus*, and confirm its status within the family Euomphalacea.

Taxonomic description

Superfamily **EUOMPHALACEA** de Koninck, 1881

Family **EUOMPHALIDAE** de Koninck, 1881

Genus ***PHANEROTINUS*** J. de C. Sowerby, 1843

TYPE SPECIES. *Euomphalus cristatus* Phillips (1836), by subsequent designation of de Koninck (1881 : 107).

REMARKS. Other species included in this genus by earlier authors, e.g. J. de C. Sowerby (1844) and Fischer (1885 : 852), belong elsewhere.

The genus *Elkoceras* Lintz & Lohr, 1958, misinterpreted as a cephalopod in its original description, is included as a synonym of *Phanerotinus* in the addendum of the Treatise (Knight *et al.* 1960 : I331). In the original description of the only species, the periphery (termed venter in cephalopod terms) is rounded (Lintz & Lohr 1958 : 980). If this is a correct interpretation of slightly crushed material then *Elkoceras* differs from *Phanerotinus*. In a later correction, Lintz (1962 : 612) accepts that *Elkoceras* belongs to the Euomphalidae, including it as a synonym of '*Straparollus (Euomphalus)*'. Based on the figure and description of Lintz & Lohr (1958) we prefer to retain the genus in the Euomphalidae provisionally as a separate genus of uncertain affinities.

Phanerotinus cristatus (Phillips)

Figs 1–4

1836 *Euomphalus cristatus* Phillips : 225, 249; pl. 13, fig. 5.
1843 *Euomphalus cristatus* Phillips; Morris : 144, 155.
1843 *Phanerotinus cristatus* (Phillips) J. de C. Sowerby : pl. 624, fig. 1.
1844 *Phanerotinus cristatus* (Phillips) J. de C. Sowerby : 30.
1854 *Phanerotinus cristatus* Sow.; Morris : 267.
1881 *Phanerotinus cristatus* (Phillips); de Koninck : 107.
1915 *Phanerotinus cristatus* (Phillips); Cossman, **10** : 177.
1941 *Phanerotinus cristatus* (Phillips); Knight : 239–40, fig. 19; pl. 70, figs 1–2.
1960 *Phanerotinus cristatus* (Phillips); Knight *et al.* **I** : 194, fig. 109.6.

MATERIAL. Holotype: BM(NH) reg. no. G184 and counterpart from the William Gilbertson collection, presumed to be the holotype by Knight (1941 : 239). An entry in an MS entitled *A Catalogue of Mountain Limestone Fossils in the collection of Wm. Gilbertson . . .*, assumed to be by Gilbertson and of which the Palaeontology Library, BM(NH) holds a photographic copy, states on p. 14 against no. 269: 'E. cristatus, this unique specimen . . .'. This establishes that Knight's conclusion was correct and that G184 is the only known specimen in the Gilbertson collection.

2. BM(NH) reg. no. G72, purchased from the Executors of J. Tennant in September 1881; referred to by Knight (1941 : 239).

3, 4. Institute of Geological Science reg. nos. LZB 29 and LZB 34; collected by R. Dixon in November 1978.

At a late stage (June 1981) P. Doughty of the Ulster Museum, Belfast, informs us that they have two specimens of *Phanerotinus cristatus* in their collections. These were collected from

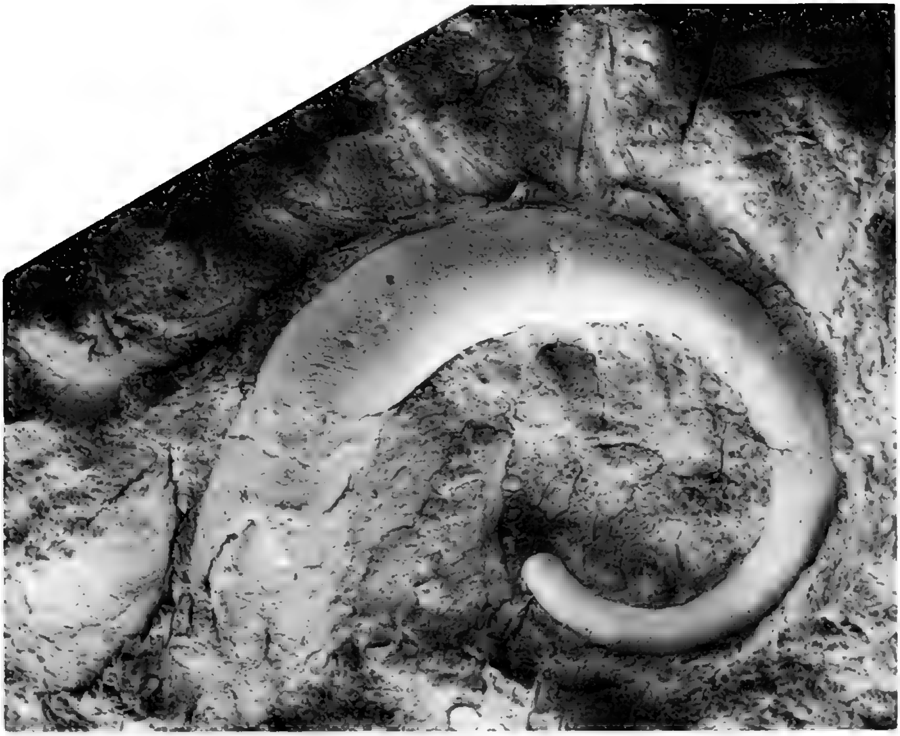

Fig. 1 *Phanerotinus cristatus* (Phillips), holotype. Basal view of steinkern which shows rounded end of body whorl septa, traces of growth lines and the peripheral spines. BM(NH) G184, × 0·9; Carboniferous Limestone, ? Bolland, or Whitewell, Yorkshire; William Gilbertson collection, purchased 1841.

Athlone by Robert Young (1821–1917), a railway engineer, and presented to the Belfast Natural History and Philosophical Society. In K5119 a third of an outer whorl is preserved in matrix (diameter of shell 18–20 cm, plus spines 30 cm), and in K1665 there is half of a whorl with a diameter of 17 cm, but no spines. In thin sections from the matrix of K5119 John Wilson of the Ulster Museum has recently found large specimens of the foraminifer *Ammarchaediscus (Rectodiscus)* sp. These are normally indicative of a late Arundian age.

The specimen listed by Carrington (1865 : 49) from Wetton, Derbyshire as *Phanerotinus cristatus* is now in the Sheffield City Museum; upon examination it proved to be a fragment of the brachiopod *Pugnax*.

Stubblefield *in* Mitchell & Stubblefield (1941) identified possible examples of *Phanerotinus cristatus* in a fauna from the *Productus humerosus* Beds (= C_2) at Breedon-on-the-Hill, Leicestershire, but although this material should be in the IGS collections we have been unable to examine the specimens.

OCCURRENCE AND LOCALITY. J. de C. Sowerby recorded that the figured specimen (G184) was from 'Whittle' in Yorkshire, while Phillips had earlier given the locality as Bolland. It is now realized that Phillips used the locality Bolland in a much more restricted sense than Gilbertson. In the spring of 1835, Phillips had carried out an extensive geological survey of that district, whereas Gilbertson simply used the name for the broader district in which he

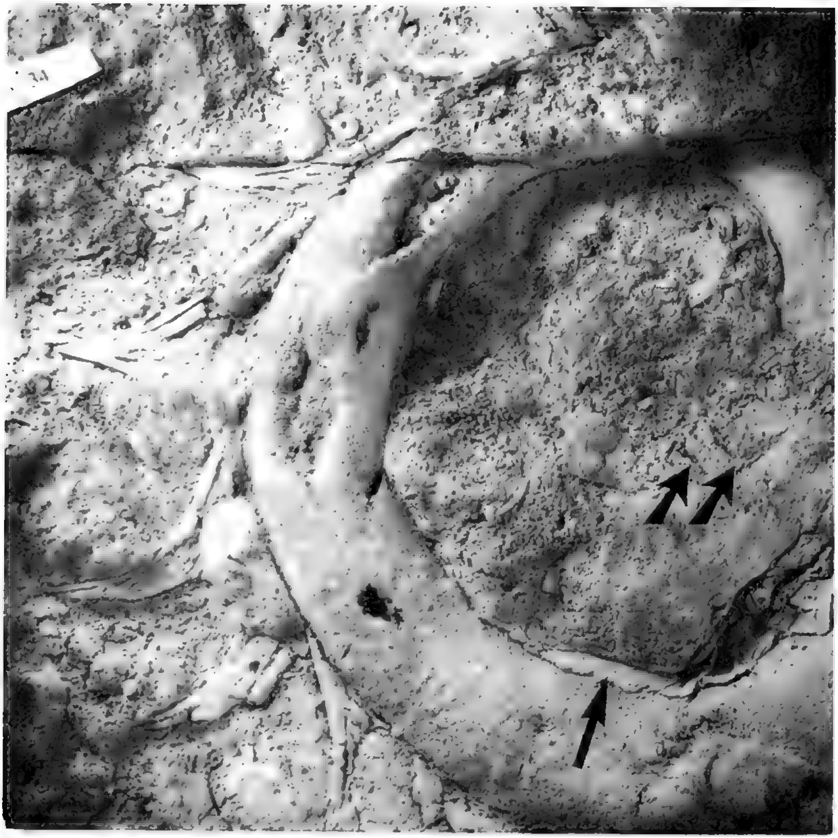

Fig. 2 *Phanerotinus cristatus* (Phillips). Basal view; the septa are visible as faint concave lines in the remnants of the early whorls at centre right; the inner carina is visible at lower right. IGS LZB 34, ×0·8. ? Red Hill Oolite, Carboniferous Limestone, ? Arundian; Plumpton Quarries, near Ulverston, Cumbria (SD 3072 7848); found in wall by R. Dixon, November 1978.

collected. In discussing Bolland, Phillips (1836 : 20) mentioned both Whitewell and the Whitewell Inn and this is presumably the locality to which Sowerby referred. Phillips also commented that the limestone might be considered to form two oval exposures in the area, one centred on Slaidburn and the other on Chipping with Whitewell close to its boundary. Arbour (or Thornley) Quarry, near Chipping, Yorkshire has been suggested as the probable site for many of Gilbertson's specimens, but it is felt that they would all have come from quarries in the Clitheroe district (personal communication M. Mitchell, N. Riley, R. Grayson and C. H. C. Brunton), although this obviously does not apply to his activities on the Isle of Man.

The locality of Tennant's specimen (G72) has not been recorded, but in the catalogue of his collection Tennant (1858 : 64) records a specimen of *Phanerotinus cristatus* as coming from Ireland. However, the matrix of G72 would appear to be very similar to that of G184.

The two IGS specimens were found loose at different places in the extensive workings at Plumpton, near Ulverston, Cumbria. It has been suggested from a comparison of their lithologies that both specimens came from the Red Hill Oolite (which is a pelleted limestone,

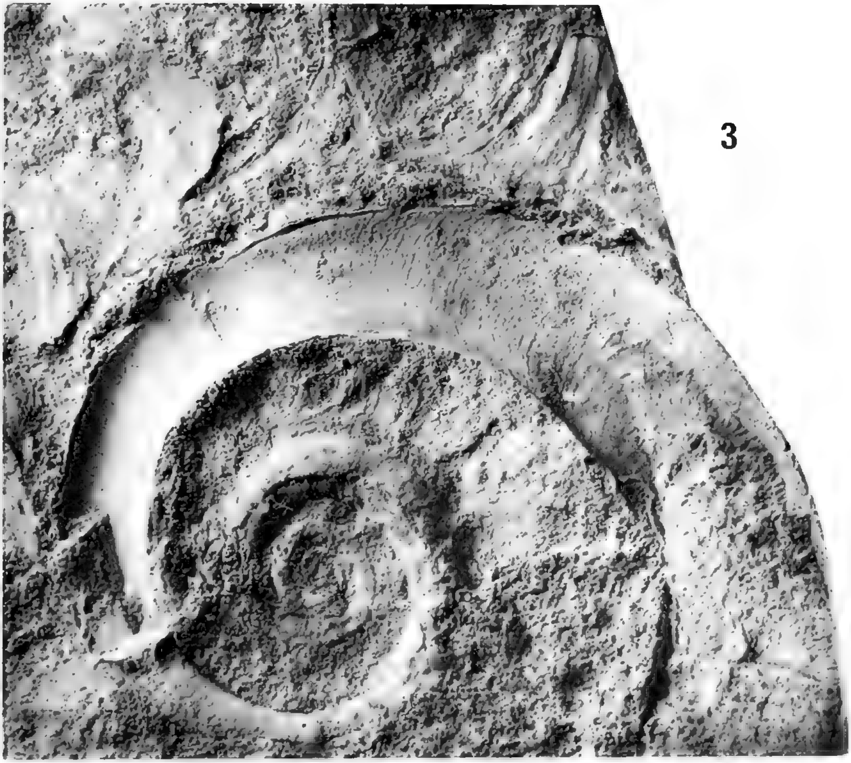

Fig. 3 *Phanerotinus cristatus* (Phillips). Latex mould of specimen shown in Fig. 4, showing impression of early whorls and a mould of the body whorl preserving the dorsal emargination and faint traces of its spines. BM(NH) G72, × 1·5.

not an oolite) of early Arundian age (personal communication M. Mitchell). Rose & Dunham (1978 : 29, 161) mention that fossils are not common in the Red Hill Oolite, but small simple corals, e.g. *Koninckophyllum* cf. *praecursor* and *Palaeosmilia murchisoni,* can generally be found together with specimens of the tabulate coral *Michelinia megastoma*; they also state that the fauna is typical of the C_2S_1 Zone. However, we are not entirely confident that the preservation of the originally larger shell (LZB 29) is identical to that of the other (LZB 34), which we understand was collected from a wall! The rock matrix of LZB 34 contains many crinoidal ossicles which do not occur in any of the other specimens.

DESCRIPTION. Large-size discoidal gastropods, with coiling interpreted as dextral, but with the majority of whorls showing a characteristic wide open coiling. (Although the early whorls are preserved it is not possible to discern their character accurately.) The early whorls are partitioned off by a transverse septum, or septa, with concave side forward. Four to five whorls are present in the more complete specimens.

Whorl cross-section subcircular but slightly asymmetrical, being rather wider than high and with the dorsal angulation closer to the inner margin. The upper and basal lips are sub-radial. The aperture is noticeably prosocline. A hollow spine-like extension of the outer apertural lip occurs in the lower third of the whorl circumference and produces a corona of large thorn-like extensions; a much smaller and shorter spine occurs at the same level on the inner lip of specimen G72 while in IGS LZB 34 the inner side of the whorl is relatively smooth for much of its length but has an irregular carina.

Fig. 4 *Phanerotinus cristatus* (Phillips). The dorsal emargination is preserved in an external mould of the early whorls. The growth lines on the base of the whorl and the peripheral spines of several whorls are also shown. Note that the spines are close to the inner margin of the succeeding whorl. BM(NH) G72, × 1·1. Carboniferous Limestone, locality not recorded; James Tennant collection, purchased from his executors 1881.

The upper lip has a small V-shaped dorsal emargination, which bears short hollow spines directed towards the aperture; the prominent fine and evenly-spaced growth lines are opisthocyrt on either side of this 'selenizone', crossing the dorsal spine and extending progressively forward over the top of the peripheral spines, but turning sharply backwards on their lower surface. The spines are more frequent on the inner whorls than the later ones, but are much smaller. The presence of the spines markedly increases the diameter of the shell, which comparison of the following measurements, taken wherever preservation permitted, confirms.

	G 186	G 72	LZB 34	LZB 29
Diameter of steinkern	105 mm	97 mm	150 mm	152 mm
Diameter with spines	195 mm	160 mm	245 mm	—
Height of steinkern	—	22 mm	—	—
Width of steinkern	—	—	—	38 mm

DISCUSSION. The limited number of available specimens of this remarkable gastropod and their poor preservation have prevented a satisfactory interpretation of its biology. Yet, despite these drawbacks, earlier authors have assigned *Phanerotinus cristatus* to the Euomphalidae.

Its general shell morphology indicates such a relationship, for the presence of the upper whorl angulation and the regular series of opisthocyrt growth lines are characteristic of that family. The discovery of a slight V-shaped dorsal emargination coinciding with the angulation provides further confirmation of this classification; in common with all living Pleurotomariacea and Fissurellacea this feature would tend to divide the aperture. Such a slit accommodates the exhalant current and the dispersal of faeces from the closely situated anus, while dividing the mantle cavity into areas occupied by the right and left gills. The close similarity in shell morphology between many Euomphalacea and Pleurotomariacea leads to the conclusion that the majority of these gastropods also had a central dorsal anus and exhalant current, with symmetrically-paired gills on either side. Knight's (1941 : 239) description of the protective sheaths as open groove-like canals extending from the outer lip is correct, but his suggestion that these were excurrent is surely mistaken. The implications of his interpretation would be that the post-torsional right gill was hypertrophied; no such mollusc has ever been described. We hold the opposite view that this current could only have been inhalant, and we feel that such an interpretation is consistent with the bizarre nature of the shell of *Phanerotinus*.

As there is no apparent change in the shell geometry during its ontogeny, *Phanerotinus* must be regarded as open-coiled throughout most of its life. However, this conclusion is based on the poorly-preserved examples listed above, which give no clear evidence of the early whorls. Yochelson (1971 : 237) gives several factors as being responsible for open coiling, but indicates that these are not of a different nature from the logarithmic factors involved in normal coiling. In the case of *Phanerotinus*, it is the increase in the factor D (Raup 1966, Vermeij 1971 : 16), i.e. the distance of each whorl from the axis, which is solely responsible. This increase is due to slightly varied rates of shell deposition on either side of the whorl. The inner side of the shell grows comparatively faster than in most other gastropods and this results in bringing it further away from the axis.

Consideration of the probable advantage of open coiling, together with the presence of spines, indicates:

1. A sedentary/sessile mode of life and filter feeding. Open coiling would be quite unsuitable for regular locomotion and so would rule out an active benthonic existence, a point made by Yochelson (1971 : 240) when he described *Nevadaspira*.
2. The lengthy thorn-like spine on the outer whorl margin extends the area of the aperture and thus improves the efficiency of the mantle current and provides optimum conditions for filter feeding.
3. The extension of the relatively smooth, flat bottom of the shell provided by these spines would increase the area in contact with the bottom; on soft sediments this might prevent sinking by spreading the load. We also believe that the spines would contribute to stability of the shell by preventing it from being overturned and ensuring that it maintained its position on the sea floor.
4. The spines could have afforded protection to the gastropod from predators such as fish, but we believe that this is less likely.

Phanerotinus resembles the open-coiled Ordovician genus *Ecculiomphalus* Portlock (Knight 1941 : pl. 71, figs 3a–c) and also *Lytospira* Koken, but lacks the deep V-shaped sinus which these genera usually have. We have examined the type material of *Ecculiomphalus*; in this genus there is a continuous peripheral flange, in contrast to the peripheral spines of *Phanerotinus* (Fig. 5); it should be pointed out that the figure in the *Treatise* (Knight *et al.* 1960 : fig. 107.5a–b) actually shows *Eccyliopterus*. Superficially, the general ornament of *Phanerotinus* resembles that of the north European Silurian genus *Poleumita* Clarke & Ruedemann, but this genus does not have peripheral spines. The similar open coiling occurring in the Devonian and Carboniferous genus *Serpulospira* Cossmann would seem to be convergence, for its virtually smooth ornament suggests to us that the two genera are not closely related. We suspect that in *Phanerotinus* we are dealing with a rather rare taxon, or at least one that only occurred in a restricted environment and whose closer relatives remain to be discovered.

Characteristics and relationships of the Euomphalacea

Shell Structure

Knowledge of the shell structure of the Euomphalacea is based upon evidence found in a very small proportion of the taxa normally placed in this superfamily. Knight (1934) described the essentially two-layered nature of the shell as a prismatic outer layer (of unspecified mineralogy) and an inner layer which he thought might have been nacre. He later revised this opinion, for in co-operation wih the other *Treatise* authors (1960 : I189) he described the Euomphalacea as having 'shell wall relatively thick, with external prismatic layer of calcite which may be pigmented and internal layer of aragonite which is lamellar and not nacreous'. His use of 'lamellar' apparently refers to the growth of laminae of the inner layer.

Yochelson, White & Gordon (1967), in their x-ray diffraction analysis of the mollusca from the Pennsylvanian Kendrick Shale, showed that *Amphiscapha* had a calcite outer layer and an aragonitic inner layer. It is possible that this material may have been recrystallized to a certain extent, with unstable aragonite changing to calcite, as minor amounts of calcite were found in the associated bivalves '*Yoldia*' and '*Parallelodon*' which would have originally been aragonitic. We have, however, been able to confirm their findings in two new examples. The twofold shell structure is clearly visible in polished and etched sections of *Amphiscapha subrugosa* (Meek & Worthen), BM(NH) PG5089, from the Cisco Formation collected at Fort Graham, Texas, although both layers have suffered from some recrystallization. The ghosts of original shell structures are commonly preserved in the associated molluscan fauna. These have been described by McClintock (1967), Batten (1972) and Morris (1979), and have also been observed by us in both Crassatellacean bivalves and Subulitacean gastropods. In at least one example, *Pseudoconocardium lanterna* (Branson), x-ray powder diffraction analysis has shown that they are now preserved as calcite (A. Hall personal communication). The ghost structures include nacre and crossed-lamellar structure, both of which must have originally been aragonitic as they are always formed of aragonite today.

In *Amphiscapha*, the outer calcite layer is preserved as a deep grey pellucid layer, while the inner recrystallized and originally aragonitic layer is preserved as a buff or orange-buff opaque layer, in which radiating cross lamellae are clearly visible on the etched sections of better-preserved specimens.

The outer calcitic layer has, clearly preserved, growth laminae and small-scale radiating prisms that fan out (Fig. 11, p. 209) at the anal emargination and the outer carina. Its calcitic layer is not composed of large-scale hexagonal prisms as in pterioid bivalves (Taylor *et al.* 1969), but is more like the outer layer of *Chama pellucida* (Kennedy, Taylor & Morris 1970), although the large blocky units they describe have not been observed. Within the Gastropoda, in addition to occurring in the Patellacea, Neritacea and Platyceratacea, calcitic outer layers have been recorded for certain buccinaceans and muricaceans.

The inner layer has well-preserved growth laminae with radiating crossed lamellae normal to the outer shell interface in transverse section and approximately aligned with the whorl in tangential section. These are typical gastropod crossed lamellae and there is every reason to believe that the structure was originally aragonite. We have not been able to discover the shell structure of the septa, or any additional inner layer that might be confluent with them.

A specimen of *Euomphalus* sp., BM(NH) PG5088 from the Upper Pennsylvanian Buckhorn Asphalt of South Oklahoma, also shows a similar outer layer of calcite. The inner layer of this species was presumably aragonitic for it was not preserved in the same way and has largely been destroyed. The occurrence of well-preserved nacre and crossed lamellar structures, in associated specimens of cephalopods and neritaceans respectively, may reflect that the single euomphalid specimen is poorly preserved.

The presence of an outer calcitic layer in both *Amphiscapha* and *Euomphalus* suggests, but does not prove, that this structure was widespread in the Euomphalidae. At present, we adhere to the normally-accepted view of molluscan shell structures, which interprets the aragonitic nacreoprismatic shell as the primitive type of calcareous shell of the conchiferan Mollusca (Taylor 1973). This type commonly occurs in cephalopods, archaeogastropods and different groups of bivalves and at least one rostroconch. It would seem that the calcitic outer layer of the Euomphalidae is a character developed separately from other gastropods.

Opercula of the Euomphalacea

It is reasonable to assume that the presence of an operculum is primitive, that virtually every known Palaeozoic gastropod had an operculum, and that almost all these animals retained them throughout life (Yochelson & Linsley 1972). Remarkably few opercula are preserved, because it is only rarely that their organic material served as a matrix for calcification; fossilization normally occurs only when the operculum has been calcified as in some members of the Trochacea and among the Neritacea. Linsley & Yochelson (1973 : 17) argued for a non-calcified operculum in those members of the Euomphalacea that have adherent shell fragments.

The operculum, found in place, of the Australian Devonian, seemingly left-handed, *Euomphalus northi* (Etheridge) described by Yochelson & Linsley (1972) is multispiral or finely concentric on its outer surface and was apparently originally calcified (Fig. 5). Its growth increments at the periphery may be traced inwards. These follow the outer edge and then turn to form the smooth inner surface, which resembles a flattened ring-doughnut with

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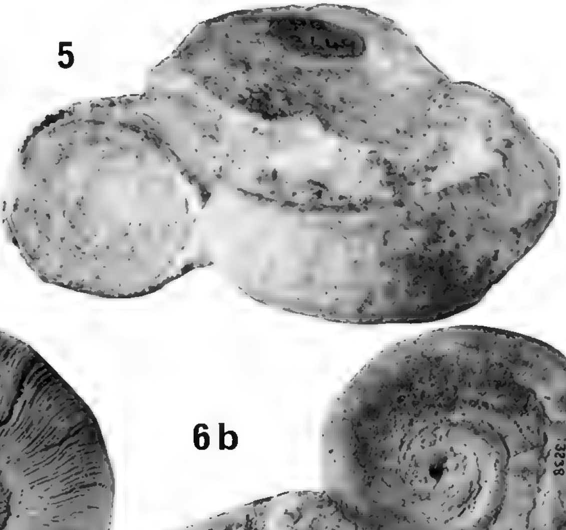

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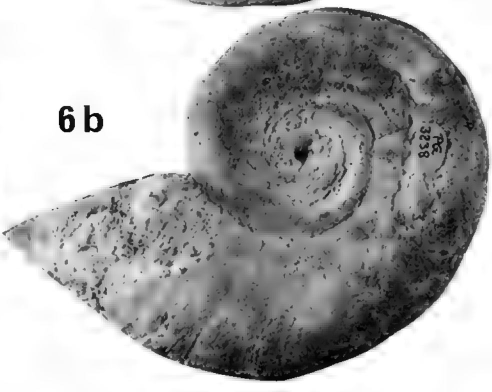

6b

Figs 5, 6 *Euomphalus northi* (Etheridge, jr). This species is considered to be coiled sinistrally because the angulation which is present is assumed to be on the dorsal surface. Fig. 5, oblique apertural view with operculum in place; BM(NH) PG3649, × 1·6. Fig. 6, BM(NH) PG3838, ×0·9; a, dorsal view; b, basal view, showing the typical relatively smoother surface. Both specimens from the Lilydale Limestone, Lower Devonian. Yeringian; Cave Hill Quarries, Lilydale, Victoria, Australia; C. T. Trechmann collection, bequeathed 1964.

a flat disc-shaped surface filling the central hole and forming a slight depression. Its general form is comparable with that of the opercula of Trochidae and Pleurotomariidae, but this may only be the result of its similarity in fitting a circular aperture. The outer surface resembles that of some species of *Oriostoma* (Lindström 1884), but the inner surfaces of opercula belonging to the Oriostomatidae do not have the same radial symmetry.

The multispiral or concentric operculum of *E. northi* is in sharp contrast to the paucispiral operculum found in *Maclurites*, which leads us to suspect that they are not closely related. This evidence cannot, however, be taken as proof because the calcified paucispiral operculum of the Turbinidae (Trochacea) has apparently evolved from the multispiral uncalcified operculum possessed by their close relatives the Trochidae and Pleurotomariidae.

The growth increments in the euomphalid operculum are separated by narrow concentric slits when viewed from the outer surface; examination of the broken outer edge shows that some of these follow each increment to its inner surface. This suggests that each apparent calcereous layer was separated by a slightly narrower organic layer. The purpose of the central depressed area on the inner surface of the operculum is not clear. Two possible explanations are that the area either marks the position of attachment of the foot, or that it represents the juvenile stage when the operculum was much thinner.

The opercula of other genera of Euomphalacea are now known, e.g. *Polhemia* and *Oreospira* (Knight *et al.* 1960 : I189), *Ceratopea* (Yochelson & Wise 1972) and *Helicotoma* (Yochelson 1966*a*). These are quite unlike that of *Euomphalus* and lead us to keep these genera in a separate family.

Septation

Yochelson (1966*b*, 1971 : 238–9) and Linsley & Yochelson (1973 : 21) have discussed the occurrence and preservation of septation in the Euomphalacea and in doing so emphasized the inadequacy of existing knowledge. The steinkerns of three specimens of *Phanerotinus* show a very marked rounded end, indicating the presence of the septum at the end of the living chamber. In IGS LZB 34, there are indications of at least five septa in a whorl length of 5 cm in the earlier whorls (Fig. 2). Unfortunately, the specimens are not sufficiently well preserved to permit the frequency of septa to be related to the frequency of spines.

We suggest that septation allowed the gastropod to vacate early-formed, narrow whorl space and occasionally to lose its earlier whorls without undue disturbance. Early whorls are frequently absent in a number of euomphalid specimens. This view is offered as an alternative to those of Yochelson (1971), who postulated that the septa were formed to strengthen the shell, or as a consequence of the physiological requirement to remove and utilize calcium carbonate caused by the sessile habit, or were the result of shortening the body apparently as an adaptation to a sessile mode of life (Linsley & Yochelson 1973 : 21).

Open coiling

Within the Euomphalacea the open-coiled form is relatively common, but is far outnumbered by conjoined coiled forms, both in numbers of species and of individuals. However, both types occur early in the history of the family, e.g. during the Lower Ordovician, and we cannot deduce from the euomphalaceans alone which is the more primitive form. It is the normally accepted view that a closely or conjoined coiled shell is a primitive feature of the Gastropoda.

Yochelson (1971 : 236) defined gastropods which lack conjoined whorls as 'open-coiled' and used the term 'uncoiled' for taxa resembling *Vermetus* which have profound deviations in shape caused by changes in life habit. This definition of 'uncoiled' would seem to require clarification and its use should best be confined to taxa lacking regular spiral form. Peel (1975 : 214) discussed open-coiled gastropods and divided them into four, what he described as 'loose morphological', categories, though he apparently attached no real significance to any one of them: he did not specify into which category he placed *Phanerotinus*. Both authors followed Linsley (1968) in recognizing that variation in shape within open-coiled species stretched beyond the normal limits accepted for gastropods.

In common with Yochelson (1971) and Peel (1975), we interpret the widely phaneromphalous, discoidal and open-coiled nature of most Euomphalaceans as a reflection of a relatively sessile habit and agree with them that this is probably an adaptation for filter feeding. Such a conclusion is based on a comparison with the filter-feeding Vermetidae, of which widely disjunct coiling is also a feature. They are usually considered to be related to the tightly coiled but tall Turritellidae, which are also filter feeders. However, Linsley & Yochelson's living examples the Xenophoridae, although mainly sessile, are not open-coiled and are thought to be algal grazers. The Upper Palaeozoic Omphalotrochidae have relinquished the discoidal phaneromphalous form, but whether or not these were also filter feeders is more uncertain.

Orientation of the Euomphalacea

Both the Ophiletidae and Euomphalidae include open-coiled forms that are most satisfactorily interpreted as filter feeders. Acceptance of this may imply that the discoidal and conjoined taxa of both groups were also filter feeders, or at least largely sessile. If the Ophiletidae are correctly interpreted as right-handed and normally torted, then the position of the anal emargination which lies at the periphery, either at the mid-whorl or dorsally, suggests that the animal was orientated quite differently from any of the Euomphalidae. In those Ophiletidae where the emargination is in the mid-whorl position, the dorsoventral axis of the mantle cavity and the lower part of the animal would be at right angles to the axis of coiling. Although this is the conventional orientation of prosobranchs, it would make locomotion extremely difficult for an animal with a horizontally held discoidal shell, and would thus indicate a sessile habit. The euomphalid orientation, where the dorsoventral axis is apparently parallel to the coiling axis, may have developed from the ophiletid orientation by turning through 90° to facilitate occasional locomotion.

Having recognized a dorsal anal emargination in the Euomphalidae (Figs 9–10, p. 208)

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Fig. 7 *Poleumita discors* (J. Sowerby); shows ornament of short spines on dorsal emargination (= sinus) and its prosocline growth lines. BM(NH) 73893, × 1; Wenlock Limestone, Silurian; Bethal Edge, near Much Wenlock, Shropshire; purchased from S. Allport, March 1873.

Fig. 8 *Euomphalus pentangulatus* J. de C. Sowerby; shows typical growth lines, its smooth shell and the dorsal angulation of euomphalaceans. BM(NH) 43619, × 1; Carboniferous Limestone, near Preston, Lancs.; originally belonging to Gilbertson collection but part of Sowerby collection, purchased January, 1861.

and by using its presence axiomatically, we can recognize a large number of right-handed taxa in the Euomphalacea and a much smaller number of left-handed taxa. The commonly accepted interpretation of euomphalid orientation, which we in fact follow, is further supported by the nature of the surface ornament. In the Silurian genus *Poleumita* (Fig. 7) the conventionally-interpreted upper surface is much more ornate than the virtually featureless lower surface. To a lesser extent, this situation prevails in the examples of *Phanerotinus* described above. The classification of the Euomphalacea below distinguishes left-handed taxa. However, left-handed forms occur in some taxa which are generally right-handed; e.g. within the genus *Euomphalus* itself, *Euomphalus northi* (Etheridge) from the Lower Devonian of Australia is a left-handed form (Fig. 5, p. 203).

Morphological similarities and relationships

The discoidal form of the Euomphalidae occurs in three other groups represented in the Ordovician, the Helicotomidae, the Trochonematacea and the Pseudophoracea. All three have a radially-situated prosocline aperture, but only the Helicotomidae have an anal emargination comparable to that of the Euomphalidae. *Helicotoma* is intermediate in orientation between *Ophiletina* and early euomphalids and is almost certainly correctly placed in the same superfamily. The trochiform shape and the lateral emargination of the Pseudophoracea suggest an inhalent current at the base of the periphery and the existence of only one gill. The similarity of form between the Trochonematidae and some early Palaeozoic Pleurotomariacea led Knight *et al.* (1960) to suggest that this group may also have had paired ctenidia, but the evidence here seems to be equivocal. The similar discoidal shape of the shell in all these groups may indicate a close common ancestry in pre-Ordovician times.

We are struck by the similarity of *Sinuopea* (Pleurotomariacea) and *Holopea* (Platyceratacea). The former has the primitive shell form of the Pleurotomariacea, turbiniform with a marked anal emargination in the form of a broad sinus in the outer lip, while *Holopea*, although lacking the sinus and anterior emargination, has the same overall turbiniform shape. Together with the many characters mentioned by Fretter & Graham (1962 : 612–3) as shared by the Pleurotomariacea and Trochacea, we feel that this is indicative of the primitive form likely to be shown by the ancestor of the Pleurotomariacea, Trochacea and Neritacea, which is inferred to have had paired ctenidia in addition to paired kidneys. It follows that the commonly-held view (Yonge & Thompson 1976 : 50) that left and right paired ctenidia are a primitive feature of the gastropods is accepted; symmetrically-paired gills occur in most other living Mollusca.

But we do not believe that an anal emargination of the shell and mantle is a feature of the earliest gastropods: in other words we do not consider that it is a synapomorphic character of the whole class. In our view it arises convergently in the Mollusca, particularly in some gastropods and Monoplacophora because of the advantage of placing the anus in the exhalent current. It is suggested here that the anal emargination has evolved separately in the Euomphalacea and possibly on more than one occasion. This would not be particularly unusual as, for example, this feature appears to have arisen at least twice in the Bellerophontacea, in which the animal is regarded as untorted and best classified with the Monoplacophora (Morris & Cocks, in prep). It is also considered that the slit may have arisen on more than one occasion in the group currently classified as Pleurotomariacea. Moreover, the posterior exhalent and anal sinus has clearly developed entirely independently in the neogastropod family Turridae.

The Euomphalacea are an early, but distinct, group of the Archaeogastopoda, which apparently did not survive beyond the earliest Mesozoic. What little is known of the shell structure of *Euomphalus* and *Amphiscapha* supports the view expressed by Sohl (1960) that Mesozoic genera ascribed to the Euomphalidae by both Wenz (1938) and Knight *et al.* (1960) are misplaced.

Two genera from the Albian, *Discohelix* and an astraeiform species tentatively regarded as

Jurassiphorus, are included with the genera *Vivianella*, *Paraviviana*, *Colpomphalus*, *Platybasis* and *Nummocalcar* in a group of nacreo-prismatic shells of typical aragonitic structure within the Trochina. *Weeksia* has an entirely crossed lamellar shell with a multi-whorled hyperstrophic protoconch and appears to be an Architectonicacean. There is some uncertainty about the Triassic genera *Woehrmannia*, *Anisostoma* and *Amphitomaria*, but the Jurassic *Coelodiscus* and the Upper Cretaceous *Condonella* are certainly not correctly included in the Euomphalacea and their true taxonomic position must remain doubtful.

Classification of the Euomphalacea

As a result of our studies of euomphalacean gastropods, we have provisionally re-arranged the genera belonging to this superfamily and incorporated others that we think were wrongly assigned elsewhere. (For taxa references, see Knight *et al.*, 1960).

Subclass **PROSOBRANCHIA** Milne-Edwards, 1848

Order **ARCHAEOGASTROPODA** Thiele, 1925

? Suborder **PLEUROTOMARIINA** Cox & Knight, 1960

The Euomphalacea are tentatively removed from the Macluritina, and placed in the Pleurotomariina, as they at least share the assumed primitive character of paired ctenidia. It is by no means certain that they share any character with the Macluritacea apart from the coiled shell.

Superfamily **EUOMPHALACEA** de Koninck, 1881

Mainly discoidal phaneromphalous shells with some later trochiform taxa; often with dorsal emargination suggestive of an exhalent current close to the anus and separating paired gills; emargination varying from peripheral to apical position on the aperture; shell septa commonly present; calcareous opercula preserved in several taxa. Shell composition of calcite and aragonite occurs in the Euomphalidae. A number of open-coiled taxa known.

Family **OPHILETIDAE** Knight, 1956

[*nom. transl.* herein, *ex* Ophiletinae Knight, 1956]

Dorsal emargination in the form of a broad and deep V-shaped sinus; shell with little ornament; horn- or wedge-shaped opercula present in *Ceratopea*. We recognize four informal groups:

1. Group with sinus in peripheral position. *Schizopea* Butts, 1926 (U. Camb. – L. Ord.), *Dirhachopea* Ulrich & Bridge, 1931 (U. Camb. – L. Ord.), *Ceratopea* Ulrich, 1911 (L. Ord.), ? *Pararaphistoma* Vostokova, 1955 (Ord.), *Ophileta* Vanuxen, 1842 (L. Ord.), *Ozarkispira* Walcott, 1924 (L. Ord.), *Calaurops* Whitfield, 1866 (L. Ord.).
2. Group with sinus at top of aperture when axis of coiling is positioned vertically. *Barnesella* Bridge & Cloud, 1947 (L. Ord.), *Lecanospira* Butts, 1926 (L. Ord.), *Lesueurilla* Koken, 1898 (Ord.).
3. Group with the same characters as 2 but open-coiled. *Lytospira* Koken, 1896 (L. Ord. – M. Sil.), *Ecculiomphalus* Portlock, 1844 (U. Ord.), *Mastigophora* La Rocque, 1949 (Dev.).
4. Group similar to 3 but with addition of a selenizone. *Ophilitina* Ulrich & Schofield, 1897 (M. Ord.), *Odontomaria* Roemer, 1876 (M. Dev.).

Family **HELICOTOMIDAE** Wenz, 1938

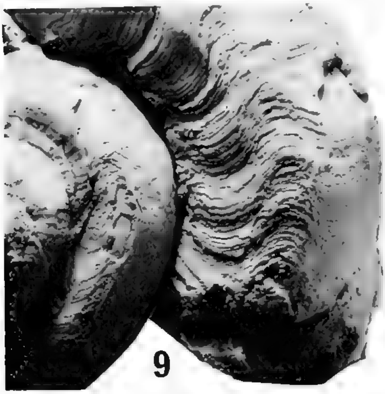
Dorsal emargination shallower than in the Ophiletidae, occurring at top of outer lip position and often carinate, with a notch or short slit, sometimes developing into a selenizone; spire slightly elevated. Calcareous operculum with few whorls in *Helicotoma*, but described as wedge-shaped in *Polhemia* and *Orospira*. *Eccyliopterus* is open coiled.

Lophonema Ulrich *in* Perdue & Miser, 1916 (L. Ord.), ? = *Polhemia* Cullison, 1944 (L. Ord.), ? = *Orospira* Butt, 1926 (L. Ord.); *Helicotoma* Salter, 1859 (L. – U. Ord.); *Eccyliopterus* Remelé, 1888 (Sil.).

Family **EUOMPHALIDAE** de Koninck, 1881

Round-whorled with emargination not deep and approximately in the central apical position of the whorl, but secondarily peripheral in later forms. Occasionally ornamented with spines, or scale-like projections; conjoined and open-coiled forms; left-handed taxa not uncommon. Shell of *Euomphalus* and *Amphiscapha* composed of an outer layer of calcite prisms and an inner layer of cross-lamellar aragonite. Calcified operculum present in one species of *Euomphalus*. We recognize three informal groups:

1. Group with conjoined or nearly joined whorls. Some Devonian species of *Euomphalus* and *Straparollus* bear adherent peripheral shell fragments; the name *Philoxene* Kayser (1889) has been used for one of these species (Linsley & Yochelson 1973 : 19). *Macluritella* Kirk, 1927 (L. Ord.), *Euomphalopsis* Ulrich & Bridge, 1931 (L. Ord.), *Poleumita* Clarke & Ruedemann, 1903 (Sil.), *Centrifugus* Bronn, 1834 (U. Sil.), *Sinutropis* Perner, 1903 (U. Sil.), *Euomphalus* J. Sow., 1814 (Sil. – M. Perm), *Straparollus* Montfort, 1810 (Carb.), *Philoxene* Kayser, 1889 (Dev.), *Leptomphalus* Yochelson, 1956 (Carb. – Perm.), *Omphalocirrus* Ryckholt, 1860 (Dev.) (left-handed), *Pleuronotus* Hall, 1879 (Dev.).
2. Group with open-whorled form, some bearing large spines; some others with adherent shell fragments. *Serpulospira* Cossmann, 1916 (Dev. – U. Carb.), ? *Nevadispira* Yochelson, 1971 (U. Dev.), *Phanerotinus* J. de C. Sowerby, 1843 (L. Carb.) *Sinistrospira* Jhoweri, 1969 (Dev.).? *Elkoceras* Lintz & Lohr, 1958 (L. Carb.).
3. Late Palaeozoic – ? Mesozoic group with dorsal emargination secondarily moved laterally towards dorsal edge of outer lip. *Amphiscapha* Knight, 1942 (U. Carb. – Perm.), *Cylicioscapha* Yochelson, 1956 (U. Carb. – Perm.), ? *Planotectus* Yochelson, 1946 (M. Perm), ? *Woehrmannia*, Böhm, 1895 (M. – U. Trias), ? *Amphitomaria* Koken, 1897 (M. Trias), ? *Anisostoma* Koken, 1889 (M. – U. Trias).



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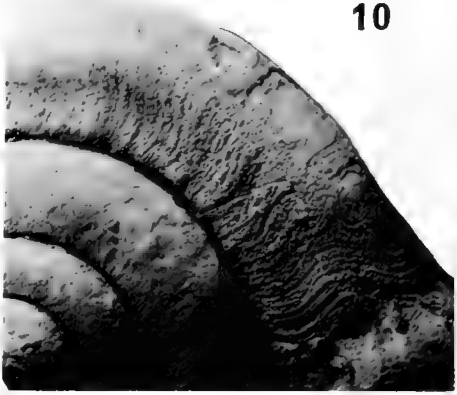

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Fig. 9 *Straparollus* sp.; shell shows growth lines and the selenizone at the dorsal emargination on the outer whorl. BM(NH) 64756, × 1; Carboniferous Limestone, Visé, Belgium; purchased from L. G. de Koninck, 1868.

Fig. 10 *Straparollus* aff. *acutus* (J. Sowerby); top surface showing dorsal sinus and growth lines. BM(NH) G41144, × 1·6; St Doolagh, Co. Dublin, Ireland; Carboniferous, Visean Zone D_2; Wheelton Hind collection, purchased 1921.

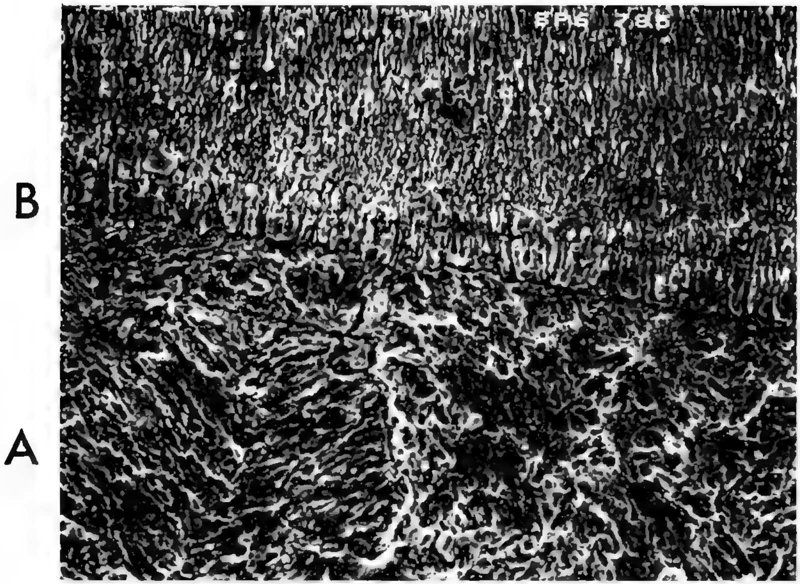

Fig. 11 Shell structure of *Amphiscapha subrugosa* (Meek & Worthen). Gold-coated polished and etched surface cut radially through outer whorl. Scanning election micrograph, approx. × 400. A, Inner shell layer composed of a single set of parallel-sided first order lamels with their short axes concentric with the shell surface. They are parallel to the aperture and formed of fine laths forming a herringbone pattern resembling polysynthetic twinning. These are interpreted as being originally aragonitic. B, Outer layer of radially-orientated fine prisms, interpreted as originally being calcitic. Upper Pennsylvanian, Texas, BM(NH) PG5089.

Family **OMPHALOTROCHIDAE** Knight, 1925

Trochiform euomphalaceans with anal emargination dorsal; central in *Discotropis*, but apparently in a broad shallow sinus on the whorl side in other genera. Operculum unknown.

? *Micromphalus* Knight, 1945 (M. Dev. – L. Carb.), *Orecopia* Knight, 1945 (Dev.), *Omphalotrochus* Meek, 1844 (U. Carb. – Perm.), *Discotropis* Yochelson, 1956 (U. Carb. – Perm.), *Babylonites* Yochelson, 1956 (Perm.), *Diploconula* Yochelson, 1956 (Perm.).

Summary of conclusions

Phanerotinus J. de C. Sowerby, 1844 has the typical characters shown by members of the Euomphalidae including what is interpreted as a dorsal anal emargination. The evidence indicates that the Euomphalidae may all have been filter feeders with two gills. As an adaptation for sessile living with a discoidal shell, the Euomphalidae are considered to have undergone 180° torsion in the normal anticlockwise direction and then rotated the mantle cavity with the lower part of the body clockwise through 90° within the shell aperture.

Some Euomphalidae are shown to have had a two-layered shell with an inner layer of crossed lamellar structure, thought to have been aragonitic originally, and an outer layer of fine prisms, thought to have been calcitic originally.

We are not convinced that there is a close relationship between the Euomphalacea and the

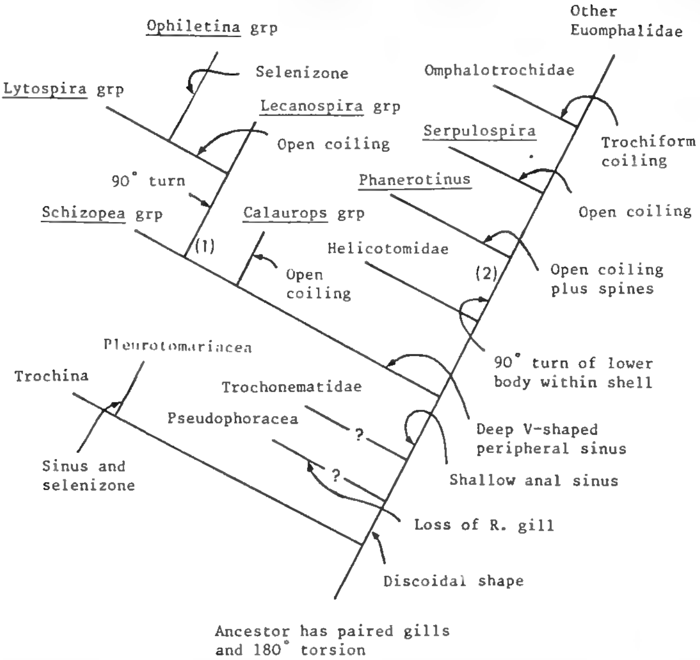

Fig. 12 Tentative outine of the phylogeny of the Euomphalacea with some synapomorphies. In this arrangement the 90° turn, additional to 180° torsion, takes place at points (1) and (2). The position of the Oriostomatacea is uncertain.

Macluritacea, but recognize that the Euomphalacea share some characters with the Pleurotomariacea although these may all be primitive gastropod characters. An initial radiation of the Euomphalacea seems to have taken place before the Ordovician and we suspect that other discoidal superfamilies, e.g. the Trochonematacea and the Pseudophoracea, may share close common ancestry with them; these views are summarized in an evolutionary diagram (Fig. 12).

A revised classification is proposed and this is essentially based on the nature of the aperture, which is considered to be related to the orientation of the mantle cavity within the shell.

Acknowledgements

We are particularly grateful to Dr Murray Mitchell, at the Leeds office of the Institute of Geological Sciences, for supplying the most recently discovered specimens of *Phanerotinus* and the accompanying stratigraphical details. The efforts of other collectors and curators, especially Clive Champion, T. H. Riley (Sheffield), Steve Tunnicliffe (IGS) and Dr W. D. I. Rolfe (Hunterian, Glasgow), in searching for other material is also appreciated.

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Agassiz, Darwin, Huxley, and the fossil record of teleost fishes

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Synopsis

Darwin cited teleost fishes as the best documented instance of the sudden appearance of a major group. This paper reviews the work of Darwin's contemporaries, particularly Louis Agassiz and T. H. Huxley, on the composition, characterization, and mode and time of appearance of the teleosts, and compares their opinions with views held today. It seems that modern ideas differ little from those of Darwin and his contemporaries. The problems which occupied them, and are still with us today, are principally problems of systematics, or discovering the natural system, problems that seem hardly to have been affected, and certainly not solved, by new discoveries of fossils and a century of progress in palaeontology.

Introduction

In the first edition of *The Origin of Species*, under the heading 'On the sudden appearance of whole groups of allied species', Darwin wrote (1859 : 305): 'The case most frequently insisted on by palaeontologists . . . is that of the teleostean fishes, low down in the Chalk period. This group includes the large majority of existing species. Lately, Professor Pictet has carried their existence one sub-stage further back; and some palaeontologists believe that certain much older fishes . . . are really teleostean. Assuming, however, that the whole of them did appear, as Agassiz believes, at the commencement of the chalk formation, the fact would certainly be highly remarkable but I cannot see that it would be an insuperable difficulty on my theory, unless it could likewise be shown that the species of this group appeared suddenly and simultaneously throughout the world at this same period.' Darwin goes on to note that 'hardly any fossil-fish are known from south of the equator' and proposes that teleosts might have developed within some enclosed basin, and dispersed rapidly thence when climatic or geographic change gave access to the open sea. In the sixth edition of *The Origin* (1872) Darwin amplified this passage by adding 'certain Jurassic and Triassic forms are now commonly admitted to be teleostean; and even some palaeozoic forms have thus been classified by one high authority'. This high authority was T. H. Huxley (1861), and 'now commonly admitted' amplifies the original reference to Pictet.

The aim of this paper is to discuss the fossil record of teleosts as it illuminates this passage from Darwin. Did teleosts first appear in the Cretaceous (Agassiz) or the Devonian (Huxley)? Is their time and mode of appearance a reflection of the imperfection of the geological record (the title of Darwin's chapter), or of the beliefs of palaeontologists (as his text suggests)? Could the teleosts, and their fossil record, be 'an insuperable difficulty' for Darwin's theory? There are three aspects to consider: the characterization of the teleosts, their composition and age, and their implications for Darwin's theory. These aspects are not independent, for the composition and age of the teleosts are largely dependent on the characterization of the group, and the implications of fossil teleosts – the general principles induced or deduced from their record – may vary with the age and composition of the group.

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Characterization of the teleosts

Agassiz' opinions on fossil teleosts stem from his *Recherches sur les Poissons Fossiles* (1833–44), and are summarized with exemplary clarity in a diagram (Fig. 1). His two orders Cycloidei and Ctenoidei include the bulk of the Teleostei (a group first named and defined by Müller, 1844). Agassiz' characterization of teleosts was based on scale structure, and the Cycloidei and Ctenoidei are those fishes with thin, flexible, unenamelled scales. Agassiz included some teleosts (in Müller's sense) in a third order, Ganoidei, characterized by enamelled scales. Agassiz' account of the structure of ganoid scales was deficient by modern standards. For example, he identified enamel in the scales of Recent catfishes, sturgeons and lungfishes, observations not confirmed by Müller (1844) or by later workers (e.g. Kerr 1952, 1955). As a result, Agassiz included in the Ganoidei the catfishes (Siluroïdes in Fig. 1), syngnathoids (Lophobranches) and tetraodontiforms (Gymnodontes, Sclérodermes), fishes

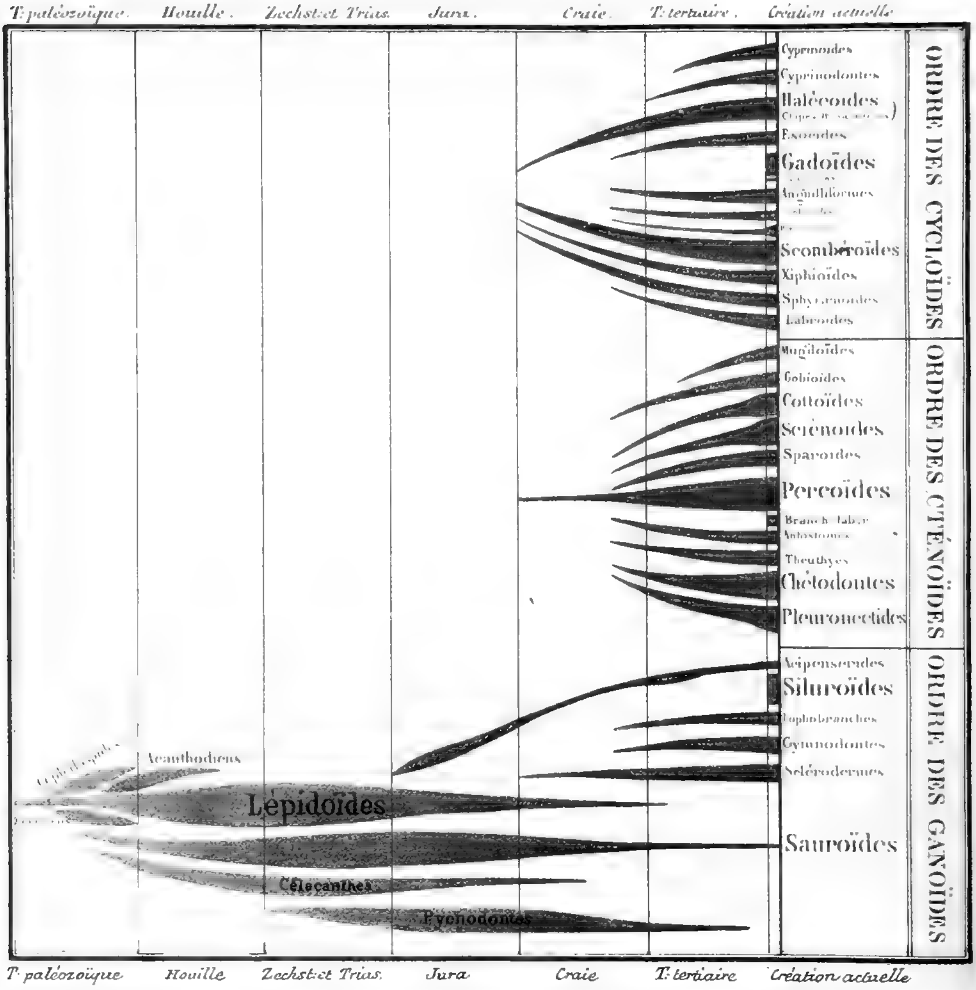

Fig. 1 Part of Agassiz' table, 'Généalogie de la Classe des Poissons' (1844, **1** : text-figure facing p. 170), modified by omitting the chondrichthyans.

which Müller showed to be teleosts by his criteria of soft anatomy (two valves in the conus arteriosus, no optic chiasma).

The problem of characterizing teleosts by osteological characters, applicable in fossils, was one which occupied pre-Darwinian palaeontologists (see Patterson, 1977, for a review). The solution which has best withstood the test of time is Heckel's (1850): teleosts are those fishes in which the caudal end of the notochord is roofed by uroneurals, or enclosed in a terminal half-centrum. This solution was not universally adopted by mid-nineteenth century palaeontologists because of their respect for Agassiz' scale characters. In fossils, Agassiz identified enamelled scales not by study of thin sections, but by 'l'oeil nu' (1844, **1** : 74). His Ganoidei included, as well as living teleosts like catfishes and tetraodontiforms, several Jurassic genera (including fishes now named *Leptolepis, Tharsis, Thrissops, Allothrissops, Anaethalion*) with thin, flexible scales. Müller (1846 : 520) examined scales of *Leptolepis* and confirmed the presence of enamel. It was more than a century before Heckel's caudal skeleton characters were revised and applied to fossil teleosts (Nybelin 1963), and it was as long before Agassiz' and Müller's authoritative statements about enamel on the scales of *Leptolepis,* etc., were shown to be wrong (Schultze 1966). Fishes with uroneurals may have cycloid scales, ganoid scales, or a mixture of the two (Schultze 1966, Nybelin 1966, Patterson 1968*a*). Müller's prediction that Agassiz' classification, because based on a single character, 'might prove rather an artificial than natural system' (Müller 1846 : 505) has been borne out. Yet Müller's definition of the teleosts (two valves in the conus) and Heckel's (uroneurals) also rely on single characters, as Agassiz (1858) pointed out. What, then, does 'natural' mean? Are single character classifications always suspect? The distinction between 'artificial' and 'natural' classifications goes back to antiquity (Russell 1916, Bather 1927, Simpson 1961), and the meaning of those terms has changed with underlying theory. Yet a common thread running through all discussions is that a natural classification is one conforming with a large number of characters, whereas an artificial classification is a key or identification system, relying on single characters. The difference between Agassiz' scale character (enamel) and Heckel's tail character (uroneurals) agrees with this distinction. For Agassiz' criterion, a grouping of all those fishes with enamelled scales, opposed to a group of all those with unenamelled scales, cuts across the groups formed by many other characters, and conforms with none. In phylogenetic terms, the first group (enamelled) would be paraphyletic, and the second (unenamelled) polyphyletic. Heckel's criterion, grouping all those fishes with uroneurals or a terminal half-centrum, agrees with Müller's (two valves) not because both criteria define the same group, but because Heckel's group includes Müller's as a subset (some fishes with uroneurals, such as *Albula* and *Megalops,* have two pairs of valves; Bertin 1958). But that cannot be the whole story, for Müller's group is also a subset of Agassiz' Cycloidei and Ctenoidei: all fishes with two valves in the conus have cycloid or ctenoid scales (some with cycloid scales, such as *Amia,* have three sets of valves). Why, then, are Agassiz' groups not natural? The answer involves further characters. For instance, additional osteological characters now thought to be characteristic of teleosts are epineural bones, a supraoccipital bone extending forwards into the otic region, and a myodome extending into the basioccipital (Patterson 1973). All these features occur in fishes with ganoid and with cycloid scales, but all occur only in fishes with uroneurals (i.e., as subsets of that group). When such conditions are met, probabilistic arguments (Wilson 1965, Patterson 1981) can be used to show that the congruence of the characters is unlikely to be due to chance, and the groups so formed may be regarded as natural, or, in phylogenetic terms, as monophyletic. Intuitive use of such arguments presumably influenced Agassiz, and by 1857 he had given up his classification of the teleosts.

Composition and age of the teleosts

Since Agassiz' and Darwin's time, the number of accepted fossil teleosts, and of teleost groups with fossil members, has grown enormously. This accretion has two sources: first, finds of new fossils, and second, inclusion of previously known fossils through changed characterization of the teleosts. In numerical terms (number of specimens, or of named species or higher taxa) the first of these must predominate; but in terms of general principles, or patterns, which occupied Agassiz and Darwin, the second is probably more important. For although the density of sampling and its geographic range have increased, the temporal pattern of the samples has altered little.

Agassiz' conclusion, that teleosts were unknown before the Cretaceous (Fig. 1) was not altered by inclusion in the teleosts of those groups (catfishes, etc.) which Müller showed were wrongly placed in the Ganoidei, for none of these had, or has, a fossil record extending beyond the Cretaceous. The opinions cited by Darwin (1859, 1872), whether teleosts first appeared in the Cretaceous, Jurassic, Triassic or Palaeozoic, concerned the characterization of the group, and whether various other fishes, known to Agassiz and included by him in the Ganoidei, were teleosts or not. According to Heckel (1850), who characterized teleosts by the presence of uroneurals, the Jurassic genera *Leptolepis, Thrissops, Tharsis* and *Anaethalion,* ganoids to Agassiz, were teleosts; teleosts therefore first appeared in the Lower Jurassic. According to Pictet (1854), who accepted Agassiz' identification of enamel on the scales of these Jurassic fishes, and the significance of that character, teleosts first appeared in the Cretaceous. But by 1858, Pictet had worked on newly-discovered teleosts from the Lower Cretaceous (Agassiz knew little or nothing from those strata), and found that their caudal skeleton was constituted in the same way as those of Jurassic leptolepids. Pictet believed that one of his Lower Cretaceous teleost genera had enamelled scales ('qui peut bien être un simple modification de la surface par la fossilisation') whereas the other lacked enamel. Therefore enamel could not be 'un caractère de premier ordre'. And Pictet agreed that the Jurassic fishes placed in the Teleostei by Heckel were true teleosts. I assume that Darwin (1859) cited Pictet's opinion from this 1858 paper.

In 1861 Huxley sought to extend the fossil record of teleosts into the Palaeozoic, by a detailed comparison of the dermal bones of the skull and shoulder girdle of the Devonian arthrodire *Coccosteus* and the Recent catfish *Clarias.* According to Woodward (1891 : vi), Huxley's error resulted 'from too narrow a conception of the limits within which certain minor skeletal characters may occur', or in more general terms (1891 : v) a 'tendency to interpret the past by a rigorous comparison with the present'. My own view is that Huxley's error lay in denying the generality of the osteological features used by Heckel and others to define the Teleostei and teleostean subgroups. For instance, Günther's (1859 : 1) definition of the Teleostei reads (in part) 'Fishes with ossified skeleton and completely separated vertebrae; the posterior end of the vertebral column either bony, or covered with bony plates'. In proposing *Coccosteus* (which lacks these features) as a teleost, Huxley denies that they are teleostean features, and denies that the catfish caudal skeleton (which Heckel found to be of the type termed 'steganochordal' by Huxley in 1859) is characteristic of that group. In short, Huxley seems to adopt a method which neglects the orderly hierarchy of homologous characters discovered by Müller, Heckel and others. Huxley's conclusion, that *Coccosteus* might be a teleost, found virtually no support: according to Woodward (1891 : vi), Newberry (1889) alone agreed.

In 1866, Pictet & Humbert published a monograph on the Cretaceous fishes of the Lebanon, a fauna known since the thirteenth century, but poorly represented in European collections; Agassiz (1833–44) listed only eight species. Darwin, writing to Lyell in 1866, called Pictet & Humbert's work 'a capital paper . . . It is capital in relation to modification of species; I would not wish for more confirmatory facts, though there is no direct allusion to the modification of species' (Darwin & Seward 1903, **2** : 160). Darwin was referring to the English abstract of Pictet & Humbert (1866*b*), and no doubt what pleased him most in this translation was statements like 'Salmones and Clupeae . . . [are] actually the descendants of the Jurassic teleosteans [*Leptolepis, Tharsis,* etc.] . . . and may be regarded as . . . the trunk of the genealogical tree'. And that the salmons and herrings (Clupeae) 'are also those that have the longest pedigrees'. 'Descendants' in the first quotation is 'continuateurs' (successors), a more Agassizian word, in the original, but 'pedigrees' in the second quote is 'aïeux' (ancestry) in the original. Pictet & Humbert go on to discuss Agassiz' group Halecoïdes (salmon, herring, etc.) in Owenian terms, as representing the archetype of teleosts, in addition to containing the only Jurassic forms. I suppose that the 'Jurassic' part of Darwin's (1872) addition to the *Origin* ('certain Jurassic and Triassic forms are now commonly admitted to be teleostean') comes from his reading of Pictet & Humbert. As for the source of the 'Triassic' part, one cannot be sure but there seem to be only two possibilities. The first is Lütken (1869, English translation 1871), who included the Triassic Belonorhynchidae (*Belonorhynchus* and *Saurichthys*) in the teleosts, and named them as the earliest members of the group. The second is Kner (1867), who suggested that *Furo* (= *Eugnathus*, Jurassic), *Ptycholepis* (M. Trias – Jurassic) and *Pholidophorus* (M. Trias – L. Cretaceous) might be teleosts.

Darwin cited Lütken's and/or Kner's opinions with approval, as if they helped his case. But these opinions were no more than expressions of belief: in none of the fishes named had teleostean characters (of the caudal skeleton or vertebral column, for example) been demonstrated. Subsequent work has found merit in only one of the suggestions, that *Pholidophorus* should be included in the Teleostei. The genus *Pholidophorus* has since been broken up into several genera (Brough 1939, Woodward 1941, Nybelin 1966, 1974, Patterson 1973, 1975, Griffith 1977), and certain better-known species have been found uniquely to share many osteological features with teleosts (Patterson 1977). My own current opinion is that the Teleostei are best characterized, as Heckel (1850) suggested, by the presence of uroneurals. By this criterion, the earliest teleosts are late Triassic pholidophorids. Other late Triassic fishes (pholidophorids, ichthyokentemids; Griffith 1977, Zambelli 1975, 1978, 1980, Nybelin 1974) are assigned to the Teleostei not because they have uroneurals (the caudal skeleton is unknown in detail), but because they show other teleostean features, such as two supramaxillae, or show close phenetic resemblance to fishes known to possess such features. As a possible middle Triassic teleost (pholidophorid), Griffith (1977) lists *Prohalecites* sp. *Prohalecites* Deecke, 1889 was erected for late Triassic species assigned to *Pholidophorus* by Bellotti (1857) and Kner (1866). Woodward (1895 : 489) referred to these as 'indeterminable immature Triassic fishes', but Alessandri (1910) argued that their size range (20–45 mm) was too great for them all to be immature, and that the specimens were sufficiently numerous and distinct to represent a good species. These remarks referred to specimens from Perledo, now thought to be of late rather than middle Triassic age, but *Prohalecites* also occurs at Besano (Brough 1939, BM(NH) specimens), which is middle Triassic. My own examination of these middle Triassic specimens has produced nothing conclusive: they are very small; they have, as Woodward said, a larval look; and they are none too well preserved. They look like pholidophorids, but I can see none of the characters that I would regard as decisive (structure of snout, epineurals, uroneurals, for example).

Thus today, as in Agassiz' and Darwin's time, the question 'which are the earliest teleosts?' can only be answered with an opinion. Opinions about the interpretation of particular fossils are less important than opinions about the characteristics of taxa like Teleostei. For a fish, fossil or Recent, can only be recognized as teleostean by recognizing teleostean characters, and the characters necessary to make a teleost are also a matter of opinion, not of fact. For instance, at one time (Patterson 1967, 1968*a*) I defined Teleostei by the presence of a single centrum supporting the first two hypurals, and of uroneurals extending forwards onto the pre-ural centra: this definition supported the consensus that leptolepids are teleosts and pholidophorids are not, so that teleosts first appear in the early Jurassic, as Heckel (1850) and Pictet (1858) said. I have changed my mind, and now (Patterson 1973, 1977) include in the Teleostei not only the pholidophorids, but pachycormids, aspidorhynchids, and any other fossil group which exhibits at least one character which is otherwise exclusively teleostean, implying that it is more closely related to teleosts than to any other Recent group. My change of mind was not owing to new finds of fossils, for the fishes we are arguing about (leptolepids, pholidophorids, *Prohalecites*, etc.) were all known in pre-Darwinian times. Instead, it was because I accepted Hennig's arguments (1966, 1969) about the meaning of relationship and the distinction between monophyletic and paraphyletic groups (or, as I would now put it, between natural, characterizable groups and unnatural, uncharacterizable groups). For to draw an arbitrary line separating teleosts from non-teleosts, as is done when leptolepids are included in Teleostei and pholidophorids are not, is to relegate pholidophorids to a paraphyletic group, characterizable only by absences of teleostean features, and absences are not characters.

So discussions about the earliest members of Teleostei, or any other taxon, concern the earliest occurrence of characters rated as diagnostic of that taxon. A familiar example is the question of the earliest mammals. Specialists agree (e.g. Lillegraven, Kielan-Jaworowska & Clemens 1979, Kermack, Mussett & Rigney 1981) that the earliest mammals are late Triassic or early Jurassic (cf. teleosts), but in phylogenetic diagrams (e.g. Carroll 1969 : fig. 1, Hopson & Crompton 1969 : fig. 1) the mammalian lineage is shown as distinct since the Carboniferous. The 'non-mammalian' members of this lineage, the mammal-like reptiles, or reptile-like mammals, are placed in uncharacterizable (paraphyletic) groups – Synapsida, Therapsida, etc. – and discussions of the origin of mammals concern a man-made problem, the appearance of one or more arbitrarily selected characters. Hennig (1969) gives a full discussion.

General principles

Agassiz (1833–44, 1859) derived two general principles from his study of fossil teleosts and other fishes, conclusions which came to be combined as one, the 'three-fold parallelism'. One conclusion was that there is a parallelism between ontogeny and the palaeontological history of a group, features which appear early in ontogeny appearing early in the fossil record, and features which appear late in ontogeny appearing late in the record. The second conclusion was that there is a parallelism between the fossil record and the natural system, characters of groups of high rank appearing earlier in the record than characters of subordinate groups (for example, 'the earliest fishes are rather the oldest representatives of the type of Vertebrata than of the class of Fishes, and that this class only assumes its proper characters after the introduction of the class of Reptiles upon the earth' –Agassiz 1859 : 166). Such principles, and diagrams like Fig. 1, seem ready-made for evolutionists, yet Darwin steered clear of the three-fold parallelism in *The Origin.* On the parallelism between ontogeny and the fossil record, he wrote (1859 : 338) 'I must follow Pictet and Huxley in thinking that the truth of this doctrine is very far from proved. Yet I fully expect to see it hereafter confirmed . . . For this doctrine of Agassiz accords well with the theory of natural selection'. And again (1859 : 449) 'Thus community of embryonic structure reveals community of descent . . . we can clearly see why ancient and extinct forms of life should resemble the embryos of their descendants, our existing species. Agassiz believes this to be a law of nature; but I am bound to confess that I only hope to see the law hereafter proved true'. I assume that the reference to Pictet in the first quotation is to his textbook (1853), whereas that to Huxley is to his 1855 paper criticizing 'the Progression theory' which, he wrote, 'resolves itself very nearly into a question of the structure of fish-tails . . . upon which so much stress has been laid by Prof. Agassiz.' Huxley's criticism concerns the structure and development of the tail in Recent teleosts; so far as it is not a play on words and their definition, I believe it is mistaken.

Darwin's caution about the three-fold parallelism was not matched by later evolutionists. The parallelism between ontogeny and palaeontology, which Darwin resisted using as evidence for his doctrine, was taken up with so much enthusiasm by Haeckel (1866) that the law now bears his name, rather than Agassiz' (cf. Hyatt 1894 : 390).

Huxley took up the three-fold parallelism in his two presidential addresses to the Geological Society (1862, 1870), on the theme of the fossil record and its bearing on theories of transformation. The first of these addresses was a pessimistic stock-taking, written in the terms of the three-fold parallelism; the second was a more optimistic progress report. In both, Huxley used the teleost *Beryx* as evidence for lack of change: 'In what respect is the *Beryx* of the Chalk more embryonic, or less differentiated, than *Beryx lineatus* of King George's Sound?' (1862 : li; 'embryonic' and 'differentiated' refer to the non-palaeontological terms of the three-fold parallelism); and 'off the coast of Portugal, there now lives a species of *Beryx*, which doubtless, leaves its bones and scales here and there in the Atlantic ooze, as its predecessor left its spoils in the mud of the sea of the Cretaceous epoch' (1870 : xlv). In drawing attention to 'persistent types' like *Beryx*, Huxley's intention was to support Darwinism, which allowed both persistence and change, against Agassizian creationism, which allowed change but not persistence. In the text accompanying the original of Fig. 1, Agassiz wrote 'having recognized that the species of each formation are always different from those of other epochs, I have drawn the lines separating the geological horizons across all the ascending lines of the families to show that the genealogical development of the species is repeatedly interrupted' (1844 : 170). In other words, 'species do not pass insensibly from one to another, but appear and disappear suddenly, without direct connection with their precursors . . . All these species have a fixed time of appearance and disappearance; their existence is likewise limited to a determined period' (1844 : 172).

Agassiz' theory is open to test here, for if it could be shown, for example, that a Recent species of teleost existed in the Cretaceous, Agassiz would be wrong, and Darwin, whose theory permitted such things, might be right. Hence Huxley's appeal to *Beryx*. Agassiz was prepared for such appeals, arguing that species which appeared to range through more than one period were due to inadequate systematics: 'The number of the species, still considered as identical in several successive periods, is growing smaller and smaller, in proportion as they are more closely compared' (Agassiz 1859 : 156). Huxley, in comparing Chalk and Recent *Beryx*, proposes that they are the same, whereas Agassiz believes that close comparison will show them to be different. At first, it seemed that Huxley was right, for following Woodward's (1902) account of the Chalk species *Hoplopteryx lewesiensis* (previously placed in *Beryx*), Regan (1911) transferred the Australian *Beryx lineatus* (one of the Recent species mentioned by Huxley) to the Cretaceous genus *Hoplopteryx*. But more detailed study of *Hoplopteryx* (Patterson 1964) showed that it differs from Recent Berycidae in many ways, and is better placed in the family Trachichthyidae. Subsequent work on Recent beryciform fishes (Rosen 1973, Zehren 1979) has shown that the relationship between Berycidae and Trachichthyidae is not particularly close, that the Trachichthyidae may not be a monophyletic group, and that the characters relating the Cretaceous *Hoplopteryx* to Recent trachichthyids are probably all primitive for the group Rosen (1973) called trachichthyoids. Thus here Huxley was wrong and Agassiz was right. Huxley's original question (1862) was 'in what respect is the *Beryx* of the Chalk more embryonic, or less differentiated, than *Beryx lineatus* . . . ?' One answer might be that in Recent berycids the caudal skeleton contains a compound element representing the fused first pre-ural and first and second ural centra, and the stegural; and the third and fourth hypurals are fused (Zehren 1979). In the Chalk *Hoplopteryx* the second ural centrum, the stegural and the third and fourth hypurals are all separate (Patterson 1968*b*). Since there is evidence that these parts of the caudal skeleton fuse during ontogeny in beryciforms, *Hoplopteryx* is 'more embryonic, or less differentiated' than Recent berycids.

Sauvage (1869), reviewing the fossil record of teleosts, wrote that 'Agassiz' first great law [that teleosts do not appear until the Cretaceous] seems to be true in general, and if Jurassic teleosts exist, they are relatively very rare. But the law of the successive development of organisms in accordance with embryonic types, a law laid down with assurance by Agassiz and by Vogt [Carl Vogt, Agassiz' assistant or student, 1839–44], is found wanting completely, so far as the leptolepids are concerned. These Jurassic teleosts are closer to the Halecoïdes than to any other group, and as Pictet & Humbert pointed out [(1866*a*)], in their monograph on the fishes of Lebanon, the herrings and salmons represent "in a way the archetype of the class, and possess its normal characters to the highest degree".' By his use of this quotation from Pictet & Humbert (the paper that Darwin read with such enthusiasm), Sauvage seems to imply that the leptolepids refute Agassiz' parallelism between ontogeny and palaeontology by conforming to his parallelism between systematics and palaeontology. Darwin and Huxley did not comment directly on this second aspect of the three-fold parallelism. This may have been due to the contrast between the Darwinian and Agassizian view of the ontological status of the natural system. To Agassiz, the elements of the natural system – species and higher taxa – were real: 'Species do not exist in nature in a different way from the higher groups' (Agassiz 1859 : 8); 'For many years past I have lost no opportunity of urging the idea that while species have no material existence, yet they exist as categories of thought, in the same way as genera, families, orders, classes and branches of the animal kingdom. Darwin's fundamental idea, on the contrary, is that species, genera, families, orders, classes and any other kind of more or less comprehensive divisions among animals do not exist at all, and are altogether artificial . . . If species do not exist at all, as the supporters of the transmutation theory maintain, how can they vary?' (Agassiz 1860*b* : 142–3). Darwin's answer to that last point was 'How absurd that logical quibble . . . As if anyone doubted their [i.e. species] temporary existence' (F. Darwin 1887, **2** : 333).

To Darwin, then, species were temporary, arbitrary segments of a continuum (Cracraft 1979). Darwin's view of higher taxa is more controversial; some believe that he regarded them as real, others that he thought higher taxa were also arbitrary chunks of a continuum (Ghiselin 1969, Hull 1973, Nelson 1974). By the 1860s, Huxley's view of species was presumably the same as Darwin's. On higher taxa, he wrote 'there may be as many classifications of any series of natural . . . bodies, as they have properties or relations to one another . . . so that . . . it might be more proper to speak of *a* classification than of *the* classification of the animal kingdom . . . Now, a morphological classification . . . answers the purpose of a *memoria technica* . . . But there is a second and even more important aspect . . . it expresses, firstly, a generalization . . . and, secondly, a belief . . . The generalization is that, in nature, the structures mentioned [in the definition of a group] are always found associated together: the belief is, that they always have been, and always will be, found so associated' (Huxley 1864 : 1–3, 1869 : 1–3). To Huxley, higher taxa are what Kitts (1977) called 'strictly universal hypotheses about character state association' – they seem to be as timeless and changeless as Agassiz' 'categories of thought' and far less real than Darwin's 'chunks of the genealogical nexus' (to use Ghiselin's 1969 phrase). Yet we should remember that the genealogical nexus has attributes of a category of thought, for it is not directly observable. Huxley's description of taxa does demand that they be definable, i.e. that they have characters.

Against this background, what of Sauvage's and Pictet & Humbert's appeal to leptolepids and Halecoïdes against the three-fold parallelism? The problem is that a group containing herring and salmon (Halecoïdes), and omitting, for example, esocids (cf. Fig. 1), is an ideal subject for talk of archetypes, since the group is uncharacterizable. It is an instance of what Eldredge & Cracraft (1980) call a 'not-A group', or what I prefer to call a non-group (Patterson 1980): one defined only by the absence of characters, and therefore lacking an empirical definition, or any existence in nature. The same seems to be true of leptolepids: they too are definable only by lack of the characters of Recent teleosts, with the added disadvantage that few are well enough known even to demonstrate these deficiencies. The conclusions drawn from comparison of two non-groups are unlikely to impinge on any general principle.

What, then, of Agassiz' three-fold parallelism? To him, at least, it was based on empirical observation, so perhaps he saw the fact of evolution without realising the implication. Jordan (1905, **1** : 381) quotes Agassiz in old age, referring to the time of his work on fossil fishes, saying 'At that time I was on the verge of anticipating the views of Darwin, but it seemed to me that the facts were contrary to the theories of evolution. We had the highest fishes first.' Here Agassiz seems to deny the three-fold parallelism, and in his posthumous criticism of Darwinism he wrote (1874 : 11; also Hull 1973 : 443) 'Let us look now at the earliest Vertebrates, as known and recorded in geological surveys. They should, of course, if there is any truth in the transmutation theory, correspond with the lowest in rank or standing. What then are the earliest known Vertebrates? They are Selachians (sharks and their allies) and Ganoids (garpikes and the like), the highest of all living fishes, structurally speaking.' In a footnote, Agassiz explains 'I use the terms low and high, throughout, in the zoölogical sense; with reference to specialization of structure, as comparative anatomists understand it'. In 1860 (1860*a* : 233) Agassiz said 'the earliest fishes are among the most perfect of their class, and have many reptilian characters'. Questioned about the apparent conflict between this statement and the parallel between embryology and palaeontology, and about the meaning of 'perfection', Agassiz replied that he took perfection 'to mean an embodiment of the highest combinations, the most complex representation of life. The embryo fish presents features of its type superior to those of the adult fish; the tendency to specialization increases with its growth, and the animal at last becomes only a fish, losing its embryonic type of the higher vertebrates. As a generalization or philosophic conception, the vertebrate egg is superior to man himself, inasmuch as it embodies all that may be produced from it.' If this is not mumbo-jumbo, it seems to be an attempt to reconcile von Baer's (1828) law, which Agassiz had previously rejected (Gould 1977 : 64), with a three-fold parallelism modified by equation of 'generalized' (in von Baer's sense) with 'high'. Darwin wrote 'Never use the words higher and lower' in the margin of his copy of *Vestiges of the Natural History of Creation* (Burrow 1968 : 33); and Gill (1872 : xxxvi) wrote 'Perhaps there are no words in science that have been productive of more mischief and more retarded the progress of biological taxonomy than those words, pregnant with confusion, HIGH and LOW, and it were to be wished that they might be erased from scientific terminology. They deceive the person to whom they are addressed; they insensibly mislead the one who uses them.'

To sum up Agassiz' achievement with respect to fossil teleosts, his production of Fig. 1, having initiated the investigation of fossil fishes virtually from scratch, is extraordinary. That he was mistaken in attempting to characterize Cycloidei and Ganoidei is a minor blemish, in part a consequence of the difficulty of characterizing groups with extinct members, and of assigning inadequately known fossils to groups, problems that are still with us. That Agassiz produced Fig. 1 without reference to, or belief in, theories of transformation is a salutary response to those who use such diagrams, with the addition of some dotted lines, as an expression or exposition of evolution. If Fig. 1 were redrawn using the current classification of teleosts, the pattern it reveals, of a sudden influx in the late Cretaceous and early Tertiary, would still exist. In a wider context, Agassiz first derived the three-fold parallelism from his work on fossil fishes. At first, he saw it as a powerful theory, offering a research programme uniting the whole of systematics and palaeontology with embryology. Later, like so many other theories, the three-fold parallelism seems to have degenerated as Agassiz added to it such things as 'prophetic types' and 'synthetic types' (1859), and as he maintained his opposition to any modification of the four Cuvierian basic plans in the animal kingdom. Through his adherence to such views, by the 1870s Agassiz had become what Hull (1973 : 449) called 'a living fossil'. Yet the three-fold parallelism had a glorious future, after it was taken up by Haeckel (Gould 1977), and its interest is not yet exhausted (Nelson 1978).

Darwin's (1859, 1872) comments on fossil teleosts, though more agreeable to modern sensibilities than Agassiz', show up the problems with his own theory as plainly as do Agassiz'. Whether teleosts appeared suddenly in the Cretaceous, as Agassiz supposed, or more gradually in the Jurassic or Triassic, as Heckel, Kner and Lütken supposed, are questions that can only be approached through systematics – characterization of groups – a field in which opinion and its substitute, authority, are still paramount. As Darwin's comments imply, no opinion or authority on such questions could run counter to his theory, for there is always the appeal to imperfection of the record, or to development within a 'perfectly enclosed basin, in which any great group of marine animals might be multiplied' (1859 : 306). Transformation offers an even more all-embracing research programme than the three-fold parallelism.

Huxley's comments on fossil teleosts were more factual than Darwin's. Where Huxley attempted direct criticism of Agassiz, as with the ontogeny of the teleost caudal skeleton and Cretaceous *Beryx*, Agassiz seems to have been right and Huxley wrong. Huxley's attempt to extend the fossil record of teleosts into the Palaeozoic, though now virtually forgotten, initiated what later became common practice in palaeontology – driving lineages back into the past without regard to adequate characterization of the group (lineage) by comparative analysis of its living members. Hence evolutionary palaeontologists' predilection for supposed demonstrations of polyphyly. The 'breakdown in logic' (Nelson 1969 : 528) behind such proposals has only recently been appreciated. Together with that appreciation, I see a revival of interest in Agassizian ideas like the three-fold parallelism (e.g. Nelson 1978) and the adequacy of the fossil record in demonstrating the sudden, rather than gradual, appearance of species and groups (e.g. Stanley 1979, Gould 1980).

The generalizations that Agassiz drew from fossil teleosts may seem to us mistaken, or tainted with outdated metaphysics. Yet they can only be favourably compared with the ideas of his British counterpart, Owen, whose general conclusion on fossil teleosts was 'that those species, such as the nutritious cod, the savoury herring, the rich-flavoured salmon, and the succulent turbot, have greatly predominated at the period immediately preceding and accompanying the advent of man, and that they have superseded species which, to judge by the bony Garpikes (*Lepidosteus*), were much less fitted to afford mankind a sapid and wholesome food' (Owen 1860 : 151). These seem to be the words of a pious victualler.

Agassiz and Darwin viewed the fossil teleosts in a context wider than the kitchen. To Darwin, they were one aspect of that 'mystery of mysteries', the origin of species, for which gradual transformation provided a material explanation. To Agassiz, the origin of species was no more mysterious than the observable transformations of ontogeny. He came to regard ontogeny as the overriding mystery (the only one worthy of the name evolution; 1874 : 92), and the only source of material explanations in systematics and palaeontology. That point of view still has advocates (Nelson 1978, Patterson in press).

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The Neanderthal problem and the prospects for direct dating of Neanderthal remains

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Synopsis

There is at present no satisfactory absolute chronological framework for the Upper Pleistocene interface between Neanderthal and anatomically modern hominids. Existing relative and radiocarbon dating methods provide only a secondary means of correlation, and many important fossil hominid specimens, for historical reasons, cannot even be assigned a satisfactory relative date. The development of a new method of radiocarbon dating by means of particle accelerators, which only requires small samples of organic material, offers the possibility of dating the fossil remains of Neanderthal man directly for the first time. This should allow the known fossil record, and also future discoveries, to be placed in a precise chronological and evolutionary framework.

Introduction

A remarkable fossil human cranium was discovered during work at the Forbes' Quarry, Gibraltar, in 1848 (Fig. 1; Oakley, Campbell & Molleson 1971). Its unusual appearance immediately attracted attention but it was not until 1865 that a scientific analysis of the specimen was published (Busk 1865). Thus by an accident of history the names 'Gibraltar man' and '*Homo calpicus*' (proposed by Falconer in a letter to Busk in 1864, after an ancient name for Gibraltar, Calpé) did not achieve scientific currency, for one year earlier the anatomist William King had designated a similar but more fragmentary fossil cranium from Germany as the type of the first recognizable archaic species of man, *Homo neanderthalensis* (King 1864, Oakley 1964, Oakley, Campbell & Molleson 1971). The specimen discussed by King had been discovered during quarrying operations which had penetrated a series of caves in the Neander Valley, near Düsseldorf, in 1856.

Much of the argument about these human fossils centred around their unusual cranial morphology, but although it was assumed by most workers that they represented ancient inhabitants of Europe, these historically important specimens could not be dated accurately since neither fossil was excavated systematically nor had associated faunal or archaeological remains. It was only after 1886, with the discovery at Spy, Belgium, of comparable remains unequivocally associated with a mammalian fauna which included the cold-adapted mammals *Coelodonta, Mammuthus* and *Rangifer,* that it could be inferred that the Forbes' Quarry and Neanderthal specimens probably dated from the same ancient glacial period. Even at the present time, no more accurate assessment of the relative or absolute age of these important fossils can be made than 'inferred Early Würm' (Oakley, Campbell & Molleson 1971).

A second and equally critical problem concerning the dating of Neanderthal hominids was their relationship to fossils of early anatomically modern (a.m.) *Homo sapiens* (used in the sense of Howells 1974). It had been realized for some time before 1886 that more modern-looking human fossils were also associated with faunas suggesting periglacial conditions, as

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Fig. 1 Right lateral view of the cranium discovered in Forbes' Quarry, Gibraltar, in 1848. BM(NH) reg. no. FC 278.7. × ½.

at French sites such as Cro-Magnon, Bruniquel and La Madeleine (Oakley, Campbell & Molleson 1971). Did, therefore, the populations of Neanderthal and modern man co-exist, or did one group antedate the other? The answer to this problem came through more careful excavation of a number of cave sites, and study of the stratigraphical relationships of archaeological remains. It was recognized that many of the fossil remains of a.m. *H. sapiens* found in French caves were associated with stone tool industries based on blades (long, narrow flakes of flint or other raw material, struck from prepared cores) and that much use was made of other raw materials such as bone, ivory and antler. Sometimes, stratified below these blade-tool industries, were industries of a different character without the predominance of blade-tools, and with little use of bone, ivory and antler. Such industries were found directly associated with Neanderthal skeletons at sites such as Spy, La Chapelle, La Quina, La Ferrassie and Le Moustier, and they were given the collective name Mousterian (also known as Middle Palaeolithic). This was to differentiate them from those of the succeeding Upper Palaeolithic industries, such as the Aurignacian, Perigordian, Solutrean and Magdalenian (Oakley 1964).

Thus by archaeological inference it was established that the Neanderthals probably antedated a.m. *H. sapiens* populations within what was eventually recognized as the last major glacial advance of the Pleistocene epoch. However, the extent of the time-gap between the two populations could only be guessed at before the advent of absolute dating methods, and the simple and abrupt archaeological division between the Mousterian and Upper Palaeolithic has become increasingly blurred following further research in Europe and south-west Asia (Bordes 1968, Lumley 1976).

The evolutionary significance of Neanderthal Man

Because of their use of caves as habitation sites and their introduction of burial practices, the Neanderthals are much better represented as fossils than any earlier Pleistocene hominids. The sample of Neanderthal fossils from Europe and Asia has grown markedly this century, and now represents several hundred individuals ranging in age from foetal to aged. While the majority of the specimens are fragmentary, several fairly complete skeletons have been excavated, and at some sites such as Krapina (Yugoslavia) and Shanidar (Iraq) many different individuals are represented (Smith 1976*b*, Trinkaus 1977, Wolpoff 1979). This has added to the importance of the Neanderthal sample since, in addition to detailed anatomical analysis, it is possible to attempt to study the actual biology of Neanderthal groups, investigating their health and population structure (e.g. level of sexual dimorphism, ages at death etc.) (Trinkaus & Howells 1979, Wolpoff 1979, 1980*a, b*, Trinkaus 1980, 1981, Smith 1980). But one of the difficulties with this kind of study, whether using material from one or from several sites, has been the problem of the time-span covered by the sample under investigation. Accurate dating of the Neanderthal specimens would allow much greater refinement in the study of their variability through time and space.

As already discussed, the stratigraphical position of Upper Palaeolithic industries, inferred to be the product of a.m. *H. sapiens,* above Mousterian industries, inferred to be the product of Neanderthal populations, demonstrated that Neanderthals existed in Europe at an earlier date than a.m. *H. sapiens.* From time to time the even earlier existence of a.m. *H. sapiens,* or a nearly-modern ancestral form, was claimed from sites such as Swanscombe (England) and Fontéchevade (France). If confirmed, this evidence would have relegated the Neanderthals to a side-branch of human evolution. However, the evidence for a modern morphology in these fossils is now regarded by most palaeoanthropologists as unconvincing (Stringer 1974, 1978, Wolpoff 1980*a, b*), so in looking for the ancestors of a.m. *H. sapiens* in Europe and south-west Asia, need we look any further than their immediate predecessors, the Neanderthals?

Two extremes of interpretation still dominate the arguments about the relationship between Neanderthal and a.m. *H. sapiens* populations, although there are also many intermediate viewpoints. One extreme view is that there must have been an evolving continuum in human populations of the Upper Pleistocene, with the Neanderthals gradually evolving into more modern-looking populations. Thus dating the Neanderthals accurately would be of critical importance since, in the simplest terms, the earliest Neanderthals would be less like modern humans, while the late Neanderthals would almost imperceptibly blend into the earliest a.m. *H. sapiens* populations (Brace 1964, Brose & Wolpoff 1971, Frayer 1978, Wolpoff 1981).

At the other extreme, the population-replacement model postulates that the Neanderthals were a specialized group of hominids with their own distinctive characteristics, and that they were replaced quite suddenly during the middle part of the last glaciation in Europe by more modern-looking populations. To test this view would also require accurate dating of the Neanderthal specimens, since they would be expected to show little evolutionary change in the direction of modern humans through time, and their replacement would have been abrupt, with a clear Neanderthal morphology existing right up to the sudden morphological discontinuity in the fossil record, represented by the appearance of completely distinct a.m. *H. sapiens* (Howells 1974, 1975, Stringer 1974, 1978). Furthermore, the sudden appearance of a.m. *H. sapiens* populations in western Europe would presuppose their existence at an earlier date in some other area; it would be expected that accurate dating would demonstrate the occurrence of early a.m. *H. sapiens* fossils in some areas contemporaneous with, or even earlier than, the Neanderthal fossils of western Europe (Stringer, Kruszynski & Jacobi 1981).

A less extreme view postulates a longer co-existence of the two forms of hominids in Eurasia, with some degree of gene flow and cultural diffusion between them, but in this case there must have been some adaptive or behavioural factors which maintained the discreteness of the two populations through time. Another model suggests that a.m. *H. sapiens* evolved out of some geographically restricted part of the Neanderthal range, perhaps in eastern Europe or south-west Asia, where it has been suggested that the Neanderthal populations of the Upper Pleistocene were less extreme in their characteristics (McCown & Keith 1939, Howell 1957). A comparable model is that of 'punctuated equilibria' (Gould & Eldredge 1977), whereby the change from a relatively stable Neanderthal morphology to a relatively stable a.m. *H. sapiens* morphology could have been achieved through a short burst of evolutionary change accomplished in a peripheral part of the Neanderthal population range. The evolutionary changes then spread rapidly from that area replacing the previous morphology. All of these models can only be tested adequately against the fossil and archaeological evidence if that evidence is well dated.

Archaeological evidence

The term 'Mousterian', as mentioned already, is the collective name first used in the last century for the stone tool industries which immediately preceded those of the Upper Palaeolithic in Europe, and which were attributed to Neanderthal populations. However, more recent excavations and study have shown that several well-defined and distinct assemblages can be recognized within the broad category of 'Mousterian'. This term in fact represents a stage of cultural evolution where flakes, made by the Levallois technique in some cases, were retouched to produce, in varying proportions, side-scrapers, notches and denticulates. Handaxes, Mousterian or Levallois points, and some 'Upper Palaeolithic' types of tools may also occur. The distinct variants of the Mousterian recognized in western Europe are the Mousterian of Acheulian Tradition, the Quina-Ferrassie, Denticulate and Typical Mousterian (Bordes 1968). Comparable kinds of industries have also been described elsewhere in Europe, in western and south-western Asia, and in north Africa (Bordes 1968). Although doubts have been raised about the significance of Mousterian assemblage variability (Binford 1973), it is possible that each of the Mousterian varieties had a long and predominantly independent evolution during the early part of the last glaciation and that they may have been the products of distinct co-existing ethnic groups. Relative chronologies have been proposed for some of the main archaeological sites and Mousterian varieties, and some of the most important Neanderthal fossils have been assigned a relative date by means of such correlations (Bordes 1973, Lumley 1976).

However, the simple equations 'Mousterian = Neanderthal' and 'Upper Palaeolithic = a.m. *H. sapiens*', which represent the underlying assumptions behind many evolutionary frameworks formulated in the absence of absolute dates, have given way in the last few years under the weight of new discoveries. Models closely linking technological change and human evolution, which also place much reliance on such a framework, must now be modified. Three sites have been critically important in emphasizing that the anatomy of the manufacturers of Mousterian or Upper Palaeolithic industries could *not* be assumed to be known in the absence of clear osteological evidence. Skhūl and Qafzeh, in Israel, are two sites where a Mousterian technology is clearly associated with fossil hominids representing a.m. *H. sapiens*, albeit an early and robust form (Howells 1970, Stringer 1974, 1978, Vandermeersch 1977). Excavations at the third site, Saint-Césaire, in France, have recently revealed an apparent Neanderthal burial in an early Upper Palaeolithic archaeological context – that of the Châtelperronian (Lévêque & Vandermeersch 1980). Interestingly, this last find has demonstrated for the first time that the continuity between the Mousterian of Acheulian Tradition and the Châtelperronian industries, which had been suggested by archaeologists, was apparently paralleled by a physical continuity in Neanderthal populations from Würm II–Würm III (French usage) (ApSimon 1980).

Thus it would appear that both Neanderthal and anatomically modern forms spanned the transition or gap between Mousterian and Upper Palaeolithic technologies, and this revelation will have tremendous repercussions on archaeological and anthropological thought. Certainly it appears an inescapable conclusion that in Eurasia a.m. *H. sapiens* evolved from an ancestor associated with the Mousterian level of culture. However, it is no longer safe to assume that therefore the antecedent was necessarily a Neanderthal *sensu stricto.* Moreover the likelihood that Neanderthal and a.m. *H. sapiens* populations co-existed in adjacent areas, if not the same areas, seems greatly increased by recent discoveries (Stringer *et al.* 1981). The Saint-Césaire evidence, if taken at face value, could also imply a survival of Neanderthal populations into Würm III (French usage), with the further implication that these populations could have contributed to the ancestry of a.m. *H. sapiens* populations of the late Pleistocene.

A further complication is the apparently sudden arrival in western Europe of the Upper Palaeolithic Aurignacian industry at about the same time as the Châtelperronian industry had completed its hypothesized evolution from the Mousterian of Acheulian Tradition. There are no convincing local archaeological antecedents for the Aurignacian in western Europe and it is tempting to correlate the spread of Aurignacian industries from eastern to western Europe with a movement of a.m. *H. sapiens* populations, or genes, in the same direction. But as many previous assumptions about the relationships of industries to hominids are demonstrably incorrect, such a model needs stronger corroborative evidence than is available at present. This is particularly so as there is no convincing ancestral industry for the Aurignacian anywhere else either, although it can possibly be traced back to eastern Europe more than 40,000 radiocarbon years before present (bp) (Kozłowski 1979). Accurate absolute dating would certainly clarify the relationships of European Upper Pleistocene hominids and industries.

South-west Asian evidence

For some time, south-west Asia has assumed particular significance in discussions about the origin of a.m. *H. sapiens.* It has been suggested as the source of Upper Palaeolithic industries (McBurney 1977) and of early European a.m. *H. sapiens* populations (Howell 1957, Stringer 1974, 1978, Vandermeersch 1977). The main fossil hominid finds from this area are associated with Levalloiso-Mousterian industries, with the exceptions of the Zuttiyeh specimen, which may be associated with the earlier Acheulian of Yabrudian facies (Gisis & Bar Yosef 1974, Schwarcz 1980), and a few Upper Palaeolithic specimens. The Zuttiyeh fossil may be a local equivalent of the 'early Neanderthals' of Europe, and may be metrically distinct from later Neanderthal fossils (Stringer 1978).

However, the main sample of Neanderthal finds from south-west Asia (those from Shanidar, Tabūn and Amud) shares a number of characters with its European counterpart. In some respects it is distinctive and more like a.m. *H. sapiens,* but in other characters it is as different from a.m. *H. sapiens* as the most extreme of the European Neanderthal specimens. The second relatively large sample of Pleistocene hominids from this area is also associated with Levalloiso-Mousterian industries, but has been recognized as representing a.m. *H. sapiens* (fossils from Skhūl, Qafzeh and perhaps Ksâr 'Akil) (Brothwell 1961, Howells 1970, 1974, 1975, Stringer 1974, 1978, Vandermeersch 1977, Trinkaus & Howells 1979, Stringer & Trinkaus 1981). The problem of relating these two hominid samples to each other taxonomically and chronologically has not been resolved, but the issues involved parallel those discussed for the European area. One difference from the European situation is that the samples from the sites of the Shanidar, Skhūl and Qafzeh are large and relatively well stratified. Furthermore the Neanderthal/a.m. *H. sapiens* interface appears to occur against a Mousterian technological background, and is likely to be earlier than the European interface which occurs against a terminal Mousterian/early Upper Palaeolithic background. The exact time relationships involved are uncertain, although it is at least possible that some of the early a.m. *H. sapiens* specimens are broadly contemporary with parts of the Neanderthal sample (Farrand 1979).

The implications of the south-west Asian evidence for the European Upper Pleistocene succession are important. Firstly, it would appear that a.m. *H. sapiens* in Eurasia evolved from a Mousterian technological background, although the evidence from Skhūl and Qafzeh implies that this is not at all the same thing as saying that this evolution was necessarily from a Neanderthal ancestor. Secondly, if dating evidence can confirm the apparent earlier appearance of a.m. *H. sapiens* in south-west Asia, this would provide a possible genetic source for the appearance of comparable populations in Europe, or evidence that an even older parent population for both groups existed somewhere. Finally, with more reliable dating evidence, the relatively large samples of stratified hominid material from sites such as Shanidar and Qafzeh may allow a more detailed examination of evolutionary trends in these samples than is at present possible in Europe. Moreover the evolutionary framework to be inferred may be applicable to the European fossil hominid samples. Thus the south-west Asian sample is a particularly significant one for any interpretation of the place of Neanderthal man in human evolution, and a reliable chronological framework for it is vital.

Dating

Relative dating

Chemical analysis (and more recently, activation analysis) of nitrogen, fluorine and phosphorus in fossil skeletal remains, and radiometric assay of uranium, are well established relative dating procedures. These methods have been intensively applied to the relative dating of fossil hominids over the last thirty years by K. P. Oakley and he has recently comprehensively reviewed the results obtained for Pleistocene and early post-Pleistocene hominid remains from Europe (Oakley 1980). Remains of Neanderthal and related hominids from sites in Europe, north Africa and south-west Asia are among those that have been analysed in this way and the results compared where possible with analyses of stratified faunal remains from the same sites (Oakley *et al.* 1971, 1975, 1977). It is of historical interest to note the early application of fluorine analysis to human bone from Krapina, Yugoslavia by the discoverer of the site, K. D. Gorjanović-Kramberger (1901). But while these methods of element analysis can often help to resolve the age relationships of a particular group of fossil skeletal remains from a given site, the results cannot provide an exact time scale or permit fossils from different localities to be placed in a temporal sequence, nor indeed have any such claims been made for these methods.

Before the advent of absolute methods of dating, the only other way of estimating the relative ages of fossil human remains was through correlation of the respective deposits in which they were found, on the basis of the available geological, faunal and associated archaeological evidence (A4 dating, Oakley *et al.* 1971). This was attempted by Zeuner (1940) for some of the principal Neanderthal remains known at the time. With the advances in detailed knowledge of the history of the last glaciation that have taken place since then (many of the foundations for which were laid by Zeuner), the environmental and archaeological background, though not able to provide an absolute time scale, assumes if anything even greater importance in the interpretative study of the fossil remains (Lumley 1976, Farrand 1979).

Absolute methods of dating

A number of methods of absolute dating appropriate to the expected time scale of the fossil hominids of the later Pleistocene may be mentioned. These include the thermoluminescence (Göksu *et al.* 1974, Wintle 1980), electron spin resonance (Ikeya 1978), uranium series (Schwarcz 1980), potassium-argon (Bishop & Miller 1972), amino-acid (Masters, in press) and radiocarbon methods. Some of these, for example thermoluminescence dating of burnt, humanly worked flint and electron spin resonance dating of bone, are not yet fully workable methods. A much more important consideration, however, is whether a method can be applied directly to the fossil remains in question (A1 dating in the terminology of Oakley

1964), rather than indirectly to some other, stratigraphically related, material. Only two of the methods mentioned above (amino-acid and radiocarbon dating) currently satisfy the former requirement and of these only the radiocarbon method has been at all well tested at present.

Approximately 70 radiocarbon dates have been published for sites in Europe (mainly France), north Africa and south-west Asia, that have yielded Mousterian (or Levalloiso-Mousterian) industries, some of which may be the handiwork of Neanderthal man (information based on a computer search of the contents of *Radiocarbon* volumes **1–16** (1959–74) stored on magnetic tape, and visual search of *Radiocarbon* **17–21** (1975–79)). This is a small number in comparison with the total of 50 000 or so radiocarbon dates now published (of which rather less than half are archaeological dates), but must reflect to some extent the paucity of associated organic material suitable for dating surviving on early sites and the relative rarity of the sites themselves. About half of these dates are based on bone (collagen or burnt bone) from the remains of hunted animals and half on charcoal; by far the greatest number has been contributed by the Groningen laboratory, mostly prior to 1970. About 45 of the dates are finite and lie in the range 30 000–55 000 bp, most lying towards the younger part of this age range (30 000–45 000 bp); the remainder are cited as 'greater than' 30 000 bp, four being > 45 000 bp. Probably even those published as finite dates with limits of error should be considered as minimum ages, because of the relatively greater effect that small amounts of younger contaminants, which it is very difficult to remove completely, can have on the apparent age of very old samples.

In all, 40 dates have been obtained, as summarized in Table 1, that relate to sites in Europe, north Africa, western and south-western Asia, at which the remains of Neanderthal and related fossil hominids have been found. Some of these dates merely provide a chronological basis for the stratigraphical sequence or a part of the sequence at a given site, not always that where the hominid remains were found. From these the dates of particular remains have been inferred, in some instances on very tenuous grounds, for example at Saccopastore, Italy. In other instances the primary objective has been to provide a date for the hominid remains and the association of the sample dated with the fossil remains is somewhat closer. Many of the remains that have been dated are, however, extremely sparse, some comprising only single teeth, and with certain exceptions (Shanidar, Iraq; Amud and Tabūn, Israel; Krapina, Yugoslavia; La Quina and Regourdou, France; Gibraltar) do not include some of the most complete fossils, nor those that are most significant from the evolutionary point of view. For many important fossils, for example the twenty or so individuals, some represented by fairly complete skeletons, from Qafzeh and Skhūl, Israel, absolute dates are lacking altogether and clearly many more dates are needed even for those remains for which some idea of the dating framework already exists. Minimum dates (that is, those given as greater than some lower limit of radiocarbon age, of which five are listed in Table 1) are inevitably of limited value. Clearly also, some of the dates listed in Table 1 (for example, the series for Amud and the date for the mandible from Bañolas, Spain) are too recent to be reconcilable with any credible model for the probable time scale of Neanderthal man's existence. Some others again, such as that for the temporal bone from Darra-I-Kur, Afghanistan, though perhaps falling closer to the age range that might reasonably be expected for the fossil remains, have been published with definite reservations as to their dependability (Krueger, in Dupree 1972). Most importantly of all, none of the dates at present available is an A1 date based directly on the fossil skeletal remains, that is on bone from an individual hominid, and it is in this important respect that there are now real prospects of a major advance.

Towards a direct and extended chronology

All the dates discussed above were obtained by the conventional gas-counting method for the measurement of low levels of radiocarbon, that is by detection of the radioactive beta-decay of atoms of ^{14}C. This is the basis also of the alternative conventional method of radiocarbon

Table 1 Neanderthal and related fossil hominid remains indirectly dated by radiocarbon. Sites have been arbitrarily listed by country from east to west and only finds from dated sites, or those for which correlations with other dated sites have been attempted, are included, together with the relevant radiocarbon dates. Following Oakley *et al.* (1971) the designations A2 and A3 in the date column denote the degree of association between the sample dated and the hominid remains. With the possible exceptions of dates obtained for remains from Bacho Kiro, Bulgaria (claimed early a.m. *H. sapiens* associated with an 'Aurignacoid' industry) and Vindija, Yugoslavia, for which full information was lacking, the list is believed to be complete. The information tabulated here was taken principally from *Radiocarbon*, New Haven, (*R*), vols **1–21** (1959–79) and from the (Oakley *et al.*) *Catalogue of Fossil Hominids* (*CFH*), parts **1–3** (1967–75; part **2** 2nd ed., 1977), as cited in the right-hand column of the table.

Site	Location	Date of discovery	Hominid remains	Radiocarbon date bp ($t_{\frac{1}{2}} = 5570$ yr)	Material dated and association	Lab. no.	Remarks	References
Darra-I-Kur, Afghanistan	36°44′N 69°59′E	1966	temporal bone	$30\,300^{+1900}_{-1200}$ (A2)	charcoal and soil organic matter	Gx–1122	sample associated with Middle Palaeolithic flakes and cores Mousterain	Dupree (1972): 3–84 (not published in *Radiocarbon*)
Shanidar, Iraq	36°50′N 44°13′E	1953, 1957–60	remains of at least 9 individuals represented by partial skeletons (Layer D; Shanidar 1–9)	50 600 ± 3000 46 900 ± 1500 (A2/3)	charcoal from hearth in top of Layer D	GrN–1495 GrN–2527	dates Shanidar 1 and by inference from stratigraphy, Shanidar 3 and 5; date of *c.* 60 000 bp inferred on this basis for Shanidar 2, 4, 6, 8 and 9; Shanidar 7 (infant) is stratigraphically older Mousterian	*R* **5** (1963): 173 *CHF* **3** (1975): 122 Trinkaus (1977): 9–33
Ksâr 'Akil, Lebanon	33°55′N 35°37′E	1947	fragmentary maxilla (Complex 3; Ksâr 'Akil 2)	43 750 ± 1500 (A3)	charred bone from layer 1 m below maxilla	GrN–2579	Mousterian/Upper Palaeolithic	*R* **5** (1963): 174 *CFH* **3** (1975): 164
Ras el-Kelb, Lebanon	33°56′N 35°36′E	1959	adult premolar (Ras el-Kelb 1)	> 52 000 (A2/3)	charred bone	GrN–2556	date for sample from correlated layer Levalloiso-Mousterian	*R* **6** (1964): 349 *CFH* **3** (1975): 165
Amud, Israel	32°52′N 35°30′E	1961, 1964	remains of 5 individuals, including cranium, mandible and most of skeleton (Amud 1) (Layer B;	10 600 ± 400 10 500 ± 140 9010 ± 160 11 500 ± 250 7340 ± 150 14 700 ± 310 15 700 ± 370 18 300 ± 400 11 700 ± 200	collagen and carbonate fractions of animal bone from Layer B1–B4	TK–12 TK–33a N–763 N–764 N–765 N–766 N–767 N–768 N–785	contamination suspected; fission track dating of bone from Layer B1–4: 28 000 ± 35% BP "Transitional" or mixed Levalloiso-Mousterian/Upper Palaeolithic	*R* **11** (1969): 511 *R* **11** (1969): 512 *R* **19** (1977): 81–83 *CFH* **3** (1975): 126

			Amud 1–5)	10 700 ± 190 13 100 ± 230 14 400 ± 350 (A2)		N–786 N–852 N–854		
Mugharet et-Tabūn, Israel	32°40′N 35°05′E	1929–34	fragmentary remains, mainly teeth, of 6 individuals (Layer B; Tabūn B1–BC6);	39 700 ± 800 (A2)	charcoal from Layer B	GrN–2534	Levalloiso-Mousterian	*R* **5** (1963) : 172 *CFH* **3** (1975) : 144, 146 Farrand (1979) : 376–377
			fragmentary cranium, mandible and partial skeleton of adult female, remains from	40 900 ± 1000 (A2)	charcoal from Layer C	GrN–2729		
			at least 4 other individuals (Layer C; Tabūn C1–C7)	$51\,000^{+4800}_{-3000}$ (A2)	Layer C	GrN–7409		
Geulah (Cave A), Mt Carmel, Israel	32°40′N 35°05′E	1962	fragmentary ulna and 2 fragmentary tibiae (Layer B2; Geulah 1)	42 000 ± 1700 (A2)	bone ash from Layer B2	GrN–4121	Levalloisian	*R* **9** (1967) : 119 *CFH* **3** (1975) : 134
Mugharet el-Kebarah, Israel	32°33′N 34°57′E	1964, 1965	fragmentary remains of 2 infants	> 30 000 (A3)	charcoal from upper Levalloiso-Mousterian level	L–336d	dated samples not directly associated with hominid remains Mousterian	*Science, N.Y.* **126** (1957) : 1324 *R* **5** (1963) : 174 *CFH* **3** (1975) : 137, 140
				35 300 ± 500 41 000 ± 1000 (A3)	charcoal from underlying Layer F	GrN–2551 GrN–2561		
Haua Fteah, Libya	32°50′N 22°10′E	1952, 1955	2 fragmentary mandibles (Layer 33; Haua Fteah 1 and 2)	$47\,000^{+3200}_{-2300}$ (A2)	charred bone from Layer 33	GrN–2023	Levalloiso-Mousterian	*R* **5** (1963) : 171 *CFH* **1** (1977, 2nd ed.) : 68
Velika Pećina, Yugoslavia	46°17′N 16°02′E	1961	frontal bone (Layer j; Velika Pećina 1)	33 850 ± 520 (A3)	charcoal from top of Layer i	GrN–4979	not Neanderthal proto-Aurignacian	*R* **14** (1972) : 60 *CFH* **2** (1971) : 342
Veternica, Yugoslavia	45°51′N 15°53′E	1955	calotte (Veternica 1)	> 43 200 (A2/3)	charcoal from immediately underlying layer	GrN–4984	not Neanderthal– intrusive to Mousterian?	*R* **14** (1972) : 61 *CFH* **2** (1971) : 342

Table 1—*cont.*

Site	Location	Date of discovery	Hominid remains	Radiocarbon date bp ($t_{\frac{1}{2}} = 5570$ yr)	Material dated and association	Lab no.	Remarks	References
Krapina, Yugoslavia	46°10′N 15°52′E	1899	fragmentary remains of perhaps more than 70 individuals, the majority immature	30 700 ± 750 (A2 ?)	charred bone from unrecorded level	GrN–4299	dated sample not necessarily associated with hominid remains Mousterian	*R* **14** (1972) : 59 *CFH* **2** (1971) : 338–340 Smith (1976*b*) Wolpoff (1979) : 67–114
Sacco-pastore, Italy	41°57′N 12°32′E	1929	2 adult crania, one fragmentary (Levels 5 and 7; Saccopastore 1 and 2)	58 000 ± 500 (A3)	wood	GrN–2572	date (obtained after isotopic enrichment) for sample from remote correlated deposit; date of *c.* 60 000 bp inferred for hominid remains Mousterian	*R* **9** (1967) : 103 *CFH* **2** (1971) : 254
Saint-Brais, Berne, Switzerland	47°19′N 7°09′E	1955	adult incisor (depth 2·9 m; Saint-Brais 1)	33 400 ± 1700 (A3)	bone of *Ursus* from 2·4 m depth	B–838	date of *c.* 40 000 bp inferred for Saint-Brais 1 presumed final Mousterian	*CFH* **2** (1971) : 306 (not publ. in *Radiocarbon*)
Arcy-sur-Cure (Grotte du Renne), Yonne, France	47°36′N 3°46′E	1950–58	teeth (Bed 8; Arcy 14–22)	33 860 ± 250 (A2)	charred bone	GrN–1742	Châtelperronian with Mousterian element	*R* **5** (1963) : 166 *CFH* **2** (1971) : 77
Combe-Grenal, Dordogne, France	44°48′N 1°12′E	1953	juvenile mandible, fragmentary adult cranium and mandible, teeth, fragmentary skeleton (Bed 25; Combe-Grenal 1 and 2)	39 000 ± 1500 (A2)	charred bone and ash from Layer E2	GrN–4304	Mousterian of La Quina type	*R* **9** (1967) : 112 *CFH* **2** (1971) : 102

Regourdou, Dordogne, France	45°03′N 1°11′E	1957	adult mandible and partial skeleton (Bed 4; Regourdou 1)	45 500 ± 1800 (A2)	wood from Bed 4	GrN–4308	Mousterian	*R* **9** (1967) : 112 *CFH* **2** (1971) : 164
La Quina, Charente, France	45°30′N 0°19′E	1908–15, 1920, 1965	fragmentary remains of at least 20 individuals (Bed 1–4; Quina H1–H27)	35 250 ± 530 (A3)	charred bone from Bed 1	GrN–2526	dates latest Mousterian occupation level	*R* **5** (1963) : 165 *CFH* **2** (1971) : 162
Bañolas, Spain	42°07′N 2°45′E	1887	adult mandible (Bañolas 1)	17 600 ± 1000 (A2)	travertine matrix	UCLA–93	date is very late for Neanderthal remains, but the accuracy of a radio-carbon age based on travertine is uncertain as there is the possibility of subsequent exchange with more recent carbon; no archaeological associations.	*R* **8** (1966) : 480 *CFH* **2** (1971) : 288
La Cotte de St Brelade, Jersey, C. I.	49°12′N 2°12′W	1910–11	adult teeth (St Brelade 1)	47 000 ± 1500 (A3)	charcoal (black ashes)	GrN–2649	Mousterian	*R* **5** (1963) : 1965 *CFH* **2** (1971) : 37
Forbes' Quarry & Devil's Tower Gibraltar	36°08′N 5°18′W	1848, 1926	adult cranium (Gibraltar 1); fragmentary cranium and mandible of child (Gibraltar 2)	47 700 ± 1500 49 200 ± 3200 >47 000 (A3)	charcoal from Layer G (uppermost Mousterian layer) in Gorham's Cave, Gibraltar	GrN–1473 GrN–1556 GrN–1678	dating based on correlation with Gorham's Cave Mousterian (Gibraltar 2)	*R* **6** (1964) : 350 *CFH* **2** (1971) : 218, 219
Jebel Irhoud, Morocco	31°56′N 8°52′W	1961	adult cranium and calvaria, mandible of child (Irhoud 1, 2, and 3)	>32 000 (A2)	animal bone from same layer	Ny–73	Levalloiso-Mousterian	*R* **10** (1968) : 123 *CFH* **1** (1977, 2nd ed.) : 81

age measurement, liquid scintillation counting. In practice, the far limit of methods of dating based on measurement of radioactive decay is normally some ten half-lives, when only about one-thousandth of the initial activity is left. The half-life of ^{14}C is 5730 ± 40 years (although the original, 3% lower, Libby value of 5570 ± 30 years is used for calculating conventional radiocarbon ages; Godwin 1962), and the specific activity of ^{14}C in nature is about 14 disintegrations per minute per gram of carbon so that the initial level is low. The practical limit of radiocarbon age measurement by conventional counting methods is about 50 000 years although by isotopic enrichment the range can be extended by a further 20 000 years (Erlenkeuser 1979, Grootes 1977, Grootes & Stuiver 1979, Grootes *et al.* 1980, Haring *et al.* 1958). In addition, natural variations in the concentration of ^{14}C over past millennia have resulted in discrepancies between the radiocarbon time scale and solar years and no very exact allowance can yet be made for this beyond the far limit of the bristlecone pine calibration at about 8000 calendar years before present (BP) (Olsson 1970).

Measurement of the amount of ^{14}C in any given sample by detecting the relatively infrequent decay of ^{14}C atoms is an inefficient procedure in comparison with the theoretical ideal of determining the total number of ^{14}C atoms present by direct measurement of some physical constant such as their mass (Stuiver 1978*a*). It is essentially by this means, using a mass spectrometer to detect specific ions, that the concentration of stable (that is, non-radioactive) ^{13}C in ^{12}C, the common stable isotope of carbon, is measured. The natural abundance of ^{13}C is, however, about 1·1%, whereas that of ^{14}C in ^{12}C in modern living material is about 1 part in 10^{12}, some ten orders of magnitude less than the relative abundance of ^{13}C. Hitherto, no mass spectrometric methods were available with the sensitivity necessary to allow the direct detection of such small amounts of any element, still less the residual amounts of ^{14}C in ancient organic material in which appreciable radioactive decay has occurred (for example 1 part in 10^{13}, 1 in 10^{14} and 1 in 10^{15} of ^{14}C in ^{12}C in 20 000, 40 000 and 60 000 year-old material, respectively). Now the long-sought ideal of direct measurement of ^{14}C, previously regarded as unattainable, is near to realization.

In recent years there has been increasing interest among nuclear physicists in the development of methods for the detection of long-lived radioisotopes having a very low natural abundance, and half-lives of the order of several hundred-thousand to several million years (Allen 1980). Some of these nuclides (for example the cosmogenic radionuclides ^{10}Be, ^{26}Al and ^{36}Cl) may eventually become the basis of geological dating methods if their geochemistry proves favourable, while others (for example ^{129}I) have a particular bearing on such questions as the age of the solar system and the ages of meteorites. The search for these rare or very rare elements as well as other, more fundamental, research in nuclear physics, has provided much of the impetus for the design of particle accelerators and cyclotrons for use as high energy mass spectrometers. A logical development from this is the application of the same methods to the detection and measurement of the relatively much shorter lived and much more abundant cosmogenic radionuclide ^{14}C (Bennett *et al.* 1977, 1978, Gove 1978, Muller 1977, 1979, Muller *et al.* 1978, Nelson *et al.* 1977, Stephenson *et al.* 1979). The methodology of high energy mass spectrometry is well described in the references cited here and at the end of the next paragraph. Here it is sufficient to note the higher energy (some 10^3 times that typical for conventional mass spectrometers) needed to obtain good resolution of the closely similar masses of the three isotopes of carbon, ^{12}C, ^{13}C and ^{14}C, and the need (much more difficult to satisfy) for virtually 100% discrimination against unwanted ions of the same mass (for example, ^{14}N).

Accelerators or cyclotrons built primarily for nuclear physics research are not necessarily either ideal or routinely available for radiocarbon dating, so that 'dedicated' machines are needed for the purpose. Of the possible alternatives, accelerators based on the tandem Van de Graaff principle have been preferred for the high energy mass spectrometers now under construction for radiocarbon dating, for example the dedicated machine being built at Oxford with the support of the Science Research Council (Doucas *et al.* 1978, Hall 1980, Hedges 1981).

The high capital cost of accelerator-based laboratories probably implies that relatively few will ever be built even on a world-wide basis and that they will not supersede conventional radiocarbon dating laboratories for most purposes, but for some applications high energy mass spectrometric methods will have unassailable advantages over existing methods of radiocarbon dating and these can be summarized very quickly. Firstly, the efficiency of detection of ^{14}C by accelerator methods is several orders of magnitude higher than that of methods based on radioactive counting. Thus samples of only a few milligrams or less of carbon will be needed, compared with the amounts of several grams needed for most conventional radiocarbon age measurements. Secondly, the increased sensitivity of accelerator methods will allow age measurements to be made to within the same statistical accuracy as that attainable by conventional methods, but in a much shorter time (minutes or hours rather than days). Thirdly, the age range will be greater than that of conventional methods and may ultimately be extended to 100 000 years bp with the aid of laser enrichment (Hedges & Moore 1978). Small gas counters of a few millilitres in volume, with very low background counting rates and excellent long-term stability, have recently been successfully developed (from solar neutrino research) for the measurement of samples of a few milligrams of carbon (Harbottle *et al.* 1979), but long counting times are needed (typically 70 days) and the far limit of age attainable without enrichment is likely to be about 20 000 years for 10 mg samples. Although for some applications the role of small counters will be complementary to that of accelerators, their performance will not rival that of accelerators for very old samples.

Contamination, particularly by younger organic substances, is a limiting factor in the accuracy of radiocarbon dating and becomes increasingly important as the true age of samples increases. This applies equally to all radiocarbon age measurements whether made conventionally or by high energy mass spectrometry. Time-consuming chemical pretreatment is necessary to remove potential contaminants from almost all of the organic materials commonly used as samples for radiocarbon dating. This preliminary chemistry requires roughly the same expenditure of time and effort whatever final method of measurement is used. On the other hand, the very small amounts of sample required for radiocarbon age measurement by high energy mass spectrometry will allow refined chemistry and chemical methods to be used for the separation of ultra-pure specific substances (for example, hydroxyproline, the amino-acid exclusive to bone collagen; Hedges 1981) for reduction to elemental carbon (graphite) for introduction to the ion source of the accelerator. Less than 1 g (possibly as little as 0·2 g) of compact bone, or about one five-hundredth of the amount normally required for dating, will probably be needed to provide an adequate sample of hydroxyproline.

The implications of all this for the more exact dating of the fossil remains of Neanderthal man are clear, although it may be some time before the full potential of the accelerator method can be realized and the desired accuracy of measurement of better than ±0·5% attained in practice for samples 50 000–75 000 radiocarbon years old. Some of the most important remains of Neanderthal man from the evolutionary point of view are from historic excavations of sites that were dug under what would be regarded today as non-ideal conditions with inadequate stratigraphical and other controls. Direct sampling of these remains should enable these important fossils to be accurately dated and placed in their correct chronological sequence, allowing present doubts and arguments about stratigraphical correlations to be finally resolved. For more recently excavated remains where the stratigraphy is not in doubt and for further discoveries that may be made in the future, the value of direct dating of skeletal remains, without the need to sacrifice appreciable quantities of palaeontologically important material, will be very great.

The survival of sufficient collagen for dating (and by inference, of hydroxyproline) in very ancient bone has yet to be demonstrated, but it is likely that it will be possible to date human bone directly by this means at least within the normal range of the conventional methods of radiocarbon age measurement. Production of ^{14}C *in situ* through capture by ^{14}N of thermal neutrons arising from cosmic radiation does not ordinarily have a significant effect on radiocarbon samples at or near sea level (Harkness & Burleigh 1974), but might have to be taken

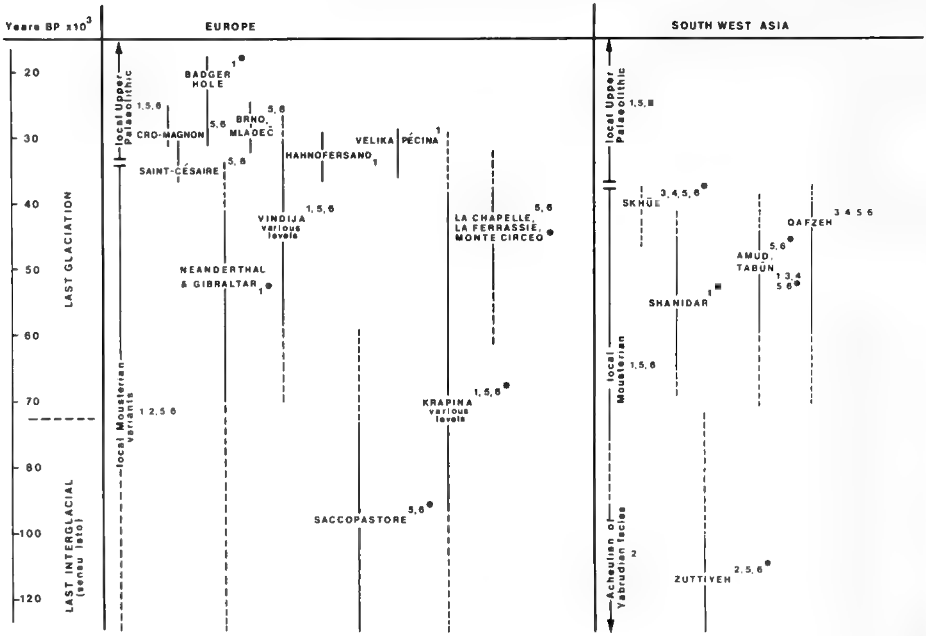

Fig. 2 Ranges of uncertainty in dating Neanderthal and other fossil hominid material of the Upper Pleistocene. The vertical arrangement of sites has no evolutionary significance. 1 = indirect ^{14}C date; 2 = uranium series date; 3 = direct amino-acid racemization date; 4 = amino-acid racemization date (faunal); 5 = sedimentological or stratigraphic correlation; 6 = faunal correlation. References used in the compilation of this table and not quoted elsewhere are Bräuer (1980), A. J. Jelinek (in press), J. Jelínek (1976), Smith (1976*a*).

into account in nitrogenous material (such as collagen) more than 50 000 years old. Another possible uncertainty relates to the occurrence of natural ^{14}C variations in the remote past for which only indirect evidence, suggesting that these were not inordinately large, is available at present (Barbetti 1980, Stuiver 1978*b*). In the longer term, measurement by the accelerator method of ^{14}C in carbon dioxide occluded within the annual layers of polar ice cores, or in carbonates (foraminifera) from ocean sediments correlated by magnetostratigraphy, together with conventional $^{13}C/^{12}C$ (and $^{16}O/^{18}O$) measurements, may allow the extent of natural ^{14}C variations during the upper Pleistocene to be more fully determined.

Concluding remarks

The above review of our present state of knowledge concerning the dating of Neanderthal and related hominids has shown the severe limitations of present methods of relative and absolute dating in resolving the crucial evolutionary problems of this period of the Upper Pleistocene. The present powers of resolution of the various methods available, and the associated chronological ranges of uncertainty for specific hominid sites are summarized in Fig. 2. It is evident that the application of radiocarbon dating using particle accelerators has the potential to resolve many of the areas of uncertainty embodied in Fig. 2 and much of the fossil material listed is already available for measurement, as indicated by an asterisk. The direct dating of such hominid finds from the Upper Pleistocene should be a primary task of this new method as soon as it comes into operation. This will be of inestimable value to our understanding of the more recent stages of human evolution.

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Hippoporidra edax (Busk 1859) and a revision of some fossil and living *Hippoporidra* (Bryozoa)

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Synopsis

Hippoporidra edax, the type species of *Hippoporidra* Canu & Bassler 1927, has been revised following a study of type and other specimens from the Pliocene Coralline Crag of Suffolk. Recent British bryozoans previously referred to *H. edax* are considered to be a distinct species, *H. lusitania* sp. nov. This and four established species of *Hippoporidra* are distinguished by a key which uses the form of the interzooidal avicularium and the shape of the autozooidal orifice. Miocene and Pliocene fossil populations of *H. edax* from Europe compare closely with some living populations from the western Atlantic but differ from the four recognizable living species of *Hippoporidra* from the eastern Atlantic.

Introduction

The first major publication on British fossil bryozoans was George Busk's monograph of bryozoans from the Pliocene and Pleistocene Crags of East Anglia, published in 1859. Busk's type material is now in the palaeontological collections of the British Museum (Natural History). This includes specimens of a particularly interesting cheilostome, *Cellepora edax* Busk 1859, which was subsequently designated as the type species of *Hippoporidra* by Canu & Bassler (1927). Several Recent and fossil species have been referred to *Hippoporidra*, including supposed living examples of *H. edax*. The major objective of this paper is to present a systematic revision of *H. edax*, based on a study of type and additional specimens from the Pliocene Coralline Crag, and to explore its implications for fossil and Recent species of *Hippoporidra*.

All described material is housed in either the palaeontological or zoological collections of the British Museum (Natural History).

Historical review

Early interest in *H. edax* focussed on the relationship between the bryozoan and the host substrate, always a gastropod shell. Busk (1859) believed *H. edax* to be a parasite of the gastropod because, although the shape of the bryozoan colonies he studied (Fig. 1) attested to their origin as gastropod associates, he could rarely find any trace of the original gastropod shell. This, he thought, was because the bryozoan was a shell-dissolving parasite of the gastropod. Hincks (1862), working on Recent *Hippoporidra*, agreed with Busk that the bryozoan had the ability to dissolve its shell substrate, later adding (Hincks 1880 : 313) that the bryozoan zoarium 'supplies a good and solid substitute for the house which it has supplanted'. Although Wood (1872 : 55) also suspected *H. edax* to be a parasite of

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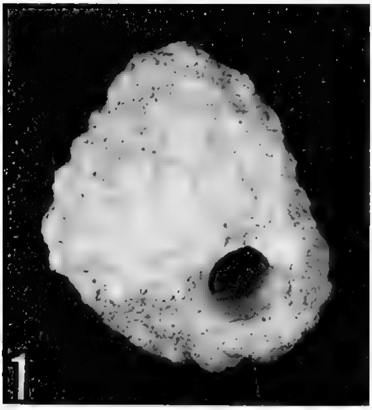

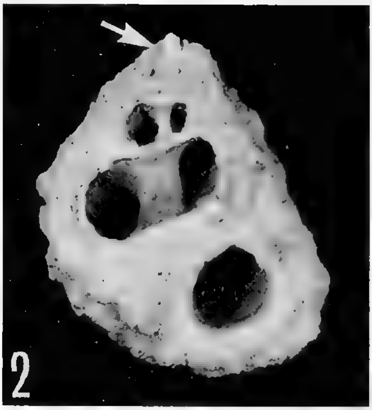

Figs 1, 2 *Hippoporidra edax* (Busk). Coralline Crag, Suffolk. Fig. 1, lectotype B1620, showing typical thick encrustation developed on a gastropod shell; ×2·5. Fig. 2, 23459a, fractured specimen showing helicospiral chamber constructed by bryozoan colony growth and the tiny gastropod shell substrate (arrowed); ×2·5.

gastropods, he thought that the gastropod destroyed its own shell, 'in order to lighten its heavy and inconvenient incumbrance'.

It is now known that most colonies of *Hippoporidra* are associates not of living gastropods but of hermit crabs which occupy empty gastropod shells (e.g. Cook 1964, 1968). Bryozoan growth during pagurid tenancy mimics gastropod shell growth by forming a helicospiral coil originating at the aperture of the gastropod shell. Helicospiral bryozoan growth is presumably a direct result of the presence of a pagurid whose curved body, adapted to fit a helicospiral gastropod shell, acts as a template around which the bryozoan grows. The original gastropod shell substrate may be left deeply embedded within the apex of the bryozoan colony (Fig. 2). This explains why Busk was rarely able to locate the original gastropod shell and why he was misled into believing that *H. edax* was a shell-dissolving parasite. It should, however, be noted that some bryozoans have the capacity to etch calcareous substrates (Pinter Morris 1975) or to bore into them (Pohowsky 1978).

Busk (1859) further commented on the likeness between the 'basal lamina' of *H. edax* (i.e. the wall lining the helicospiral pagurid living chamber) and the undersurface of *Lunulites* colonies. The basal wall in the free-living bryozoan *Lunulites* is now known to be an interior wall (*sensu* Boardman & Cheetham 1973) consisting of a calcified layer which accreted beneath a cover of hypostegal coelom (Håkansson 1973). The presence of a chamber-lining interior wall (Fig. 6b, p. 249) has been recently established in *Hippoporidra* and its formation and role in the development of *Hippoporidra* colonies will be discussed elsewhere (Cook & Taylor, in preparation).

Systematic descriptions

Order **CHEILOSTOMATA**

Suborder **ASCOPHORA**

Family **CLEIDOCHASMATIDAE** Cheetham & Sandberg, 1964

Genus ***HIPPOPORIDRA*** Canu & Bassler, 1927

[*Hippoporidra* Canu & Bassler, 1927 : 8; Canu & Bassler 1929 : 418; Osburn 1940 : 454; Osburn 1952 : 354; Lagaaij 1952 : 147; Buge 1957 : 320; Cook 1964 : 22; Cook 1968 : 196; Pouyet 1973 : 54 (*partim*); Hayward & Ryland 1979 : 214; Cook in press].

Description. Colony generally encrusting pagurid-tenanted gastropod shells, multilamellar,

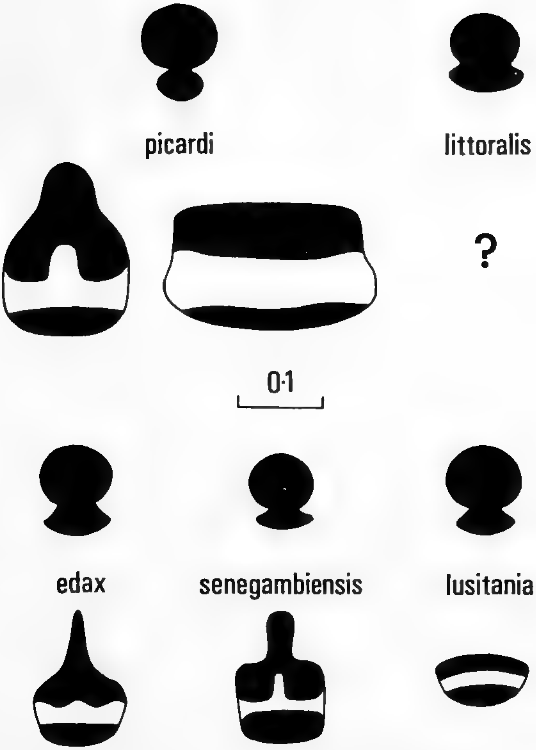

Fig. 3 Shape of the autozooidal orifice and rostrum of the interzooidal avicularium in five species of *Hippoporidra*. Interzooidal avicularia were not located in studied specimens of *H. littoralis*. Scale bar is 0·1 mm.

monticulate and occasionally branched. Autozooids with marginal pores and scattered or absent frontal pores. Calcified frontal shields cryptocystidean, with overlying hypostegal coelom. Orifice cleithridiate with strong lateral condyles; oral spines absent. Most autozooids are frontally-budded between monticules and are irregularly shaped. Cortical zooids, situated on monticules, are larger than autozooids but have a smaller orifice. Ovicells are hyperstomial, imperforate, with an uncalcified frontal area, and are not closed by the operculum. Avicularia are small and adventitious or large and interzooidal.

Type species. *Cellepora edax* Busk 1859, by original designation; Pliocene, Suffolk.

Remarks. Using established correlates of character states of orifice shape and avicularian skeletal morphology (cf. Hayward 1978), five species of *Hippoporidra* may be recognized (see key below and Fig. 3) : *H. edax* (Busk), *H. lusitania* sp. nov., *H. littoralis* Cook, *H. picardi* Gautier and *H. senegambiensis* (Carter). The only species known as a fossil is *H. edax* and this is present in deposits of the early Miocene onwards. Living North American species of *Hippoporidra* are inadequately known and, in addition to probable *H. edax*, include some undescribed species.

Lepralia edax forma *janthina* Smitt 1873 was formerly regarded as *Hippoporidra janthina* (Smitt) but has since been shown to be a species of *Hippotrema* (Cook in press).

Key to species of *Hippoporidra* (see Fig. 3).

1. Narrow rounded poster; interzooidal avicularia with either broad (simple pivotal bar) or pear-shaped (ligulate pivotal bar) rostra . . . . ***H. picardi***

– Broad poster, wider than anter; interzooidal avicularia absent or rare . . . . ***H. littoralis***
– Broad poster, the same width as or slightly narrower than anter 2

2\. Interzooidal avicularium with pointed rostrum and doubly constricted pivotal bar . . . . ***H. edax***
– Interzooidal avicularium with spatulate rostrum and ligulate pivotal bar . . ***H. senegambiensis***
– Interzooidal avicularium with transversely elliptical rostrum and simple pivotal bar ***H. lusitania***

Hippoporidra edax (Busk, 1859)

? 1847 *Cellepora parasitica* Michelin : 326; pl. 78, fig. 3.
1859 *Cellepora edax* Busk : 59; pl. 9, fig. 6; pl. 22, fig. 3.
non 1859 *Cellepora parasitica* Michelin; Busk : 61; pl. 9, figs 11, 13 [= *Osthimosia parasitica*].
1872 *Cellepora edax* Busk; Wood : 54; pl. 5, fig. 25.
1873 *Lepralia edax* forma *calcarea* Smitt : 63; pl. 11, figs 220–223.
non 1873 *Lepralia edax* forma *janthina* Smitt : 63; pl. 11, figs 224–225 [= *Hippotrema janthina*].
? 1904 *Lepralia maculata* Ulrich & Bassler : 423; pl. 115, figs 8, 9; pl. 118, fig. 7.
1912 *Cellepora edax* Busk; Leriche : 805, text-figs 41, 41a, 42, 42a.
1923 *Cellepora minuta* Canu & Bassler : 182; pl. 25, figs 10–13.
? 1923 *Cellepora maculata* (Ulrich & Bassler) Canu & Bassler : 182; pl. 25, figs 14–20.
1924 *Cellepora edax* Busk; Duvergier : 186; pl. 6, figs 5–10.
1928 *Hippoporidra edax* (Busk); Canu & Bassler : 139; pl. 22, figs 1–4.
1928 *Hippoporidra calcarea* (Smitt); Canu & Bassler : 140; pl. 22, figs 5, 6; text-fig. 30.
1929 *Hippoporidra calcarea* (Smitt); Canu & Bassler : fig. 163 C–H.
? 1948 *Cellepora parasitica* Michelin; Roger & Buge : 461; pl. 17, figs 1, 4–7, 10–13.
? 1948 *Hippoporidra edax* (Busk); Roger & Buge : 465; pl. 17, figs 8, 9.
1949 *Hippoporidra edax* (Busk); Vigneaux : 81, fig. 32.
1952 *Hippoporidra edax* (Busk); Lagaaij : 147; pl. 15, fig. 13; pl. 16, fig. 6.
1957 *Hippoporidra edax* (Busk); Buge : 320; pl. 12, figs 3–6 only [pl. 11, fig. 2 = *H. senegambiensis*].
? 1962 *Cellepora parasitica* Michelin; Buge & Lecointre : pl. 18, figs 1, 5 only [pl. 18, fig. 2 = *H. senegambiensis*].
1964 *Hippoporidra edax* (Busk); Cook : 26 (*partim*); pl. 3, fig. 7 only.
1973 *Hippoporidra edax* (Busk); Pouyet : 120; pl. 2, figs 4–6; pl. 13, fig. 1; pl. 16, fig. 2.

Revised diagnosis. Autozooid orifice with poster slightly narrower than anter; interzooidal avicularium with an acute rostrum and doubly constricted pivotal bar.

Lectotype (designated by Lagaaij 1952). BM(NH) Palaeontology Dept. no. B1620; Coralline Crag, Sudbourne, Suffolk (Busk 1859 : pl. 9, fig. 6a–c).

Material. All Coralline Crag of Suffolk: 23459a–d, Sudbourne, Daniels Coll.; 60338a–b, Sutton, Bell Coll.; 60463a–b, Butley River Marshes; 60475a–c, 60477, Boyton, Charlesworth Coll.; B1012a–b, Gedgrave, Tennant Coll.; D6699, D6700–2, D6704–6, D6755, D6756 (? Busk 1859 : pl. 22, fig. 3c), D6757, D6758a–b, D6759 (? Busk 1859 : pl. 22, fig. 3b), D6761 (? Busk 1859 : pl. 22, fig. 3a), D6767, Wood Coll.; D52744, near Orford Castle; G3967 (Wood 1872 : pl. 5, fig. 25a), near Orford, Wood Coll.

Recorded occurrence. Miocene of France (Loire, Aquitaine) and the eastern U.S.A.; Pliocene of England (Suffolk), France, Italy (Valle Botto), Belgium, Holland and the eastern U.S.A.; Recent of the east coast of the U.S.A. and the Gulf of Mexico.

Description. Colonies monticulate (Fig. 1), multilamellar, exclusively encrusting gastropod shells. Autozooids (Figs 4B, 5a) with marginal pores, some frontal pores, suboral area imperforate and sometimes developed as an umbo. Orifice with strong lateral condyles dividing a poster from a slightly broader, rounded anter. Cortical zooids (Figs 4A, 5c) umbonate, larger than autozooids with a slightly smaller orifice. Adventitious avicularia (Fig. 4B) acute, small. Interzooidal avicularia rostra (Fig. 5b) broad proximally with a doubly constricted pivotal bar, narrow terminally and acute. Ovicells (Fig. 5d) rounded with a frontal area.

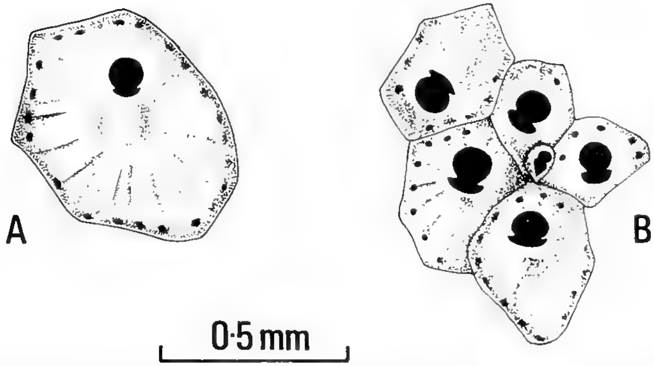

Fig. 4 *Hippoporidra edax* (Busk). Coralline Crag, Suffolk. A, cortical zooid drawn from the lectotype B1620; B, irregularly-shaped, frontally-budded autozooids and an adventitious avicularium drawn from specimen 23459b.

DIMENSIONS. Autozooid orifice length 0·10–0·11 mm, width 0·07–0·08 mm; cortical zooid orifice length 0·09–0·10 mm, width 0·07 mm; interzooidal avicularium rostrum length 0·15–0·17 mm, width 0·13–0·14 mm.

REMARKS. Michelin's (1847) type specimens of *Cellepora parasitica* are apparently lost (Roger & Buge 1948) and neither his figure nor his description are sufficient to permit positive identification of the species. The *Cellepora parasitica* Michelin of Busk (1859) may not be the same species as that described by Michelin. It has been redescribed by Lagaaij (1952) under the name *Osthimosia parasitica* (Busk, ? *non* Michelin).

Specimens of the N. American species *Cellepora minuta* Canu & Bassler (1923) in the collections of the BM(NH) confirm its synonymy with *H. edax*. The closely similar *Lepralia maculata* Ulrich & Bassler (1904) may be also a junior synonym.

Lepralia edax forma *calcarea* Smitt 1873, described from the Recent of Florida, has interzooidal avicularia identical with those of Coralline Crag *H. edax*, suggesting its synonymy.

Hippoporidra lusitania sp. nov.

1861 *Cellepora edax* Busk; Busk : 154, figs 3, 3a.
1862 *Cellepora edax* Busk; Hincks : 304.
1880 *Lepralia edax* (Busk) Hincks : 311 (*partim*); pl. 24, figs 7, 8 only [fig. 7a = *H. edax*].
1929 *Hippoporidra edax* (Busk); Canu & Bassler : fig. 163A, B.
1937 *Lepralia edax* (Busk); Moore : 202.
1964 *Hippoporidra edax* (Busk); Cook : 26 (*partim*); pl. 3, figs 5, 6 only.
1979 *Hippoporidra edax* (Busk); Hayward & Ryland : 214, fig. 91A–E.

DIAGNOSIS. Autozooid orifice with poster slightly narrower than anter; interzooidal avicularium with a transversely elliptical rostrum and a simple pivotal bar.

HOLOTYPE. BM(NH) Zoology Dept. no., 1911.10.1.1143a; Guernsey, Norman Coll.

PARATYPES. 1899.5.1.1517a–b, Plymouth, Hincks Coll.; 1899.7.1.1410, Coast of Devon, Busk Coll. (? Busk 1861 : figs 3, 3a); 1899.7.1.1410A, Guernsey ?, Busk Coll.; 1911.10.1.1143 b–i, Guernsey, Norman Coll.; 1963.3.30.273, Scilly Isles (35 fathoms), Buskill Coll.; 1963.4.16.1, ? Guernsey, Busk Coll. All BM(NH) Zoology Dept. numbers.

DISTRIBUTION. Recent of British coastal waters. Hayward & Ryland (1979) record the species from the Isle of Man, the western English Channel, the Scilly Isles, the north and south coasts of Devon and Cornwall, and also the Gulf of St Malo.

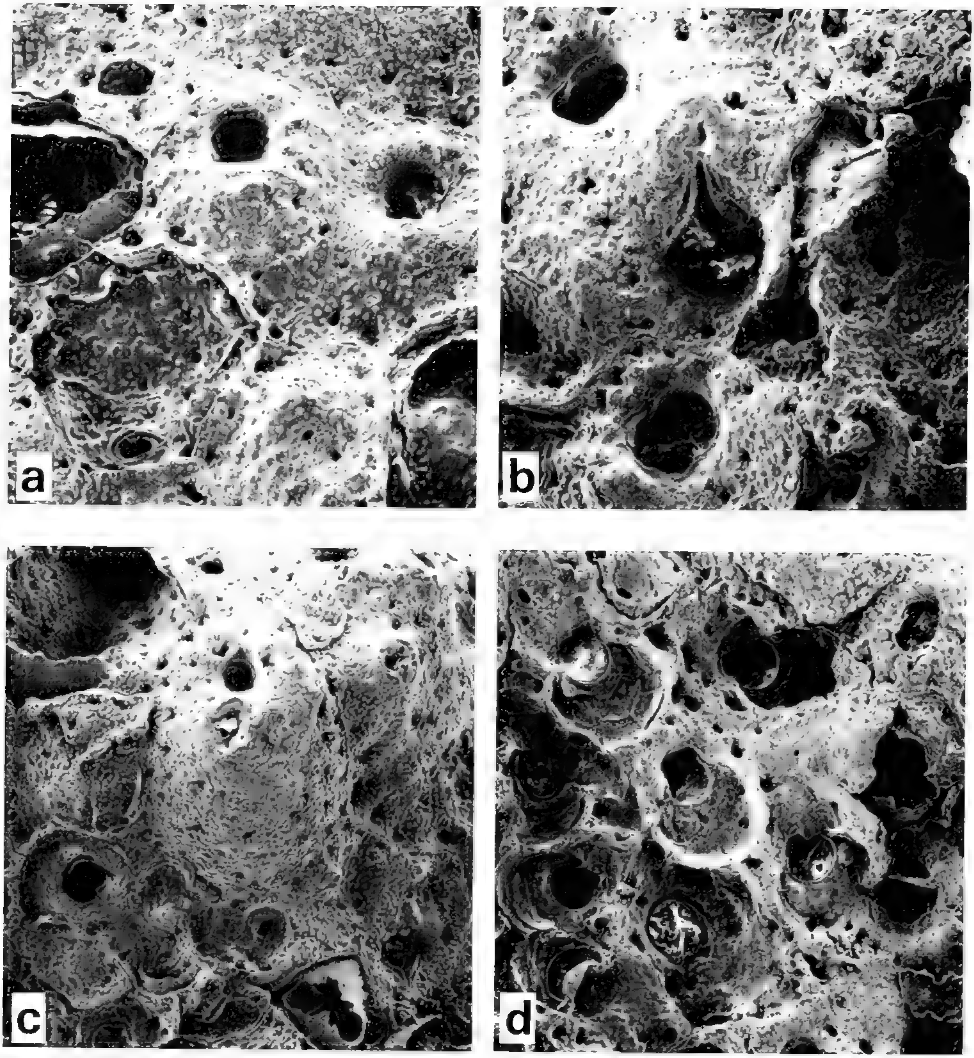

Fig. 5 *Hippoporidra edax* (Busk). Coralline Crag, Suffolk. Scanning electron micrographs of specimen 23459c. a, autozooids and a frontal bud (bottom left), ×90. b, interzooidal avicularium, ×110. c, cortical zooid with broken umbo, ×60. d, ovicelled zooids with frontal part of ovicell wall missing and basal wall penetrated by septulae, ×80.

DESCRIPTION. Colonies monticulate, multilamellar, exclusively encrusting gastropod shells inhabited by pagurids. Autozooids (Fig. 6c) with marginal and some frontal pores; suboral area imperforate, variably umbonate. Cortical zooids (Fig. 6a) large but with orifice distinctly smaller than that of autozooids. Adventitious avicularia (Fig. 6d) ovate, small. Interzooidal avicularia (Fig. 3) with a transversely elliptical rostrum and a simple, curved pivotal bar. Ovicells (Fig. 6d) rounded to semi-ovoid with a distally-placed frontal area.

DIMENSIONS. Autozooid orifice length 0·09–0·10 mm, width 0·07–0·08 mm; cortical

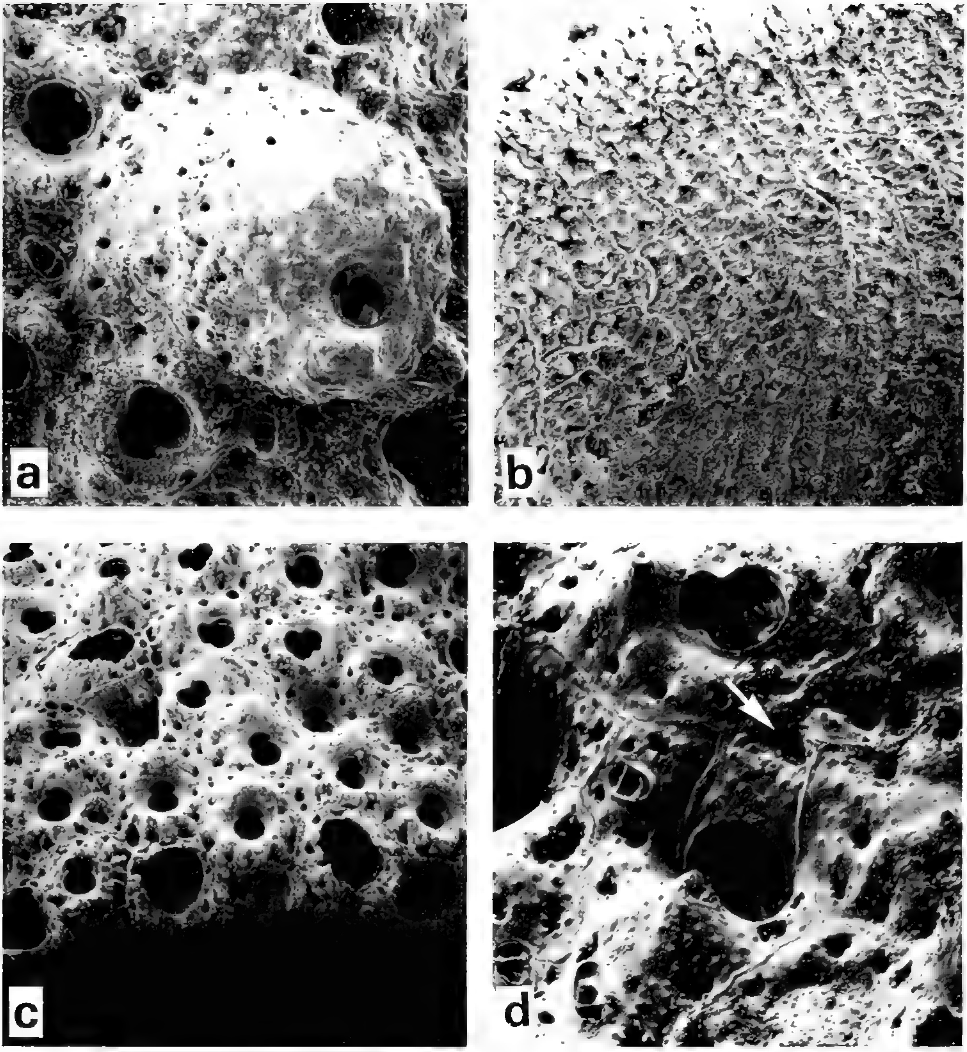

Fig. 6 *Hippoporidra lusitania* sp. nov. Recent, Guernsey. Scanning electron micrographs of **holotype,** 1911.10.1.1143a. a, cortical zooid, autozooids and small adventitious avicularia, × 100. b, bryozoan interior wall lining pagurid living chamber and showing septulae and cuticular traces, × 50. c, frontally-budded autozooids at the free edge of the pagurid aperture, x 50. d, ovicelled zooid (uncalcified frontal area arrowed) and small adventitious avicularia, × 180.

zooid orifice length 0·07–0·09 mm, width 0·05–0·06 mm; interzooidal avicularium rostrum length 0·04–0·05 mm, width 0·07 mm.

REMARKS. This new species has been created to accommodate some Recent *Hippoporidra* previously referred to *H. edax* but differing from that species principally in the structure of the interzooidal avicularium. In *H. edax* this has an acuminate rostrum and a doubly constricted pivotal bar, whereas in *H. lusitania* it has an oval-shaped rostrum, with a transverse long axis, and a simple curved pivotal bar. The adventitious avicularia are generally more rounded in *H. lusitania,* while the ovicells are often less rounded and appear to have a more distally restricted frontal area. *H. lusitania* also has cortical zooids with smaller orifices than those of *H. edax,* so that there is a greater contrast in orifice size between autozooids and cortical zooids within a colony.

Discussion

This brief survey of fossil and living *Hippoporidra* and revision of the type species *H. edax* has some interesting biogeographical implications.

The only species of *Hippoporidra* with a well-documented fossil history is *H. edax,* which had a pan-Atlantic distribution during Miocene and Pliocene times. *H. edax* seems to be restricted to the western side of the Atlantic at the present day. Supposed *H. edax* now living off the western and south-western coasts of the British Isles and the Channel Islands has been shown to be a different species, *H. lusitania* sp. nov. This living population was previously suspected (Hayward & Ryland 1979) to represent the relic of a declining population of *H. edax,* abundant in Europe during the Neogene. Known distributions of *Hippoporidra* in time and space lead to the tentative suggestion that the living eastern Atlantic species of *Hippoporidra, H. lusitania, H. picardi, H. littoralis* and *H. senegambiensis,* arose through allopatric speciation which followed fragmentation of the initially widespread *H. edax* populations.

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The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria

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Contents

Synopsis

English Upper Jurassic marine reptiles of the superfamily Plesiosauroidea are reviewed in depth. Four genera and six species are recognized and described from previously known material, these being *Cryptoclidus eurymerus* (Phillips), *C. richardsoni* (Lydekker), *Muraenosaurus leedsii* Seeley, *M.*

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beloclis Seeley, *Tricleidus seeleyi* Andrews and *Colymbosaurus trochanterius* (Owen). In addition a skull from the Kimmeridge Clay of Dorset is described as *Kimmerosaurus langhami* gen. et sp. nov. The genus *Cryptoclidus* is described first and is taken subsequently as a model for comparison with other genera. A restoration of the skeleton of *C. eurymerus* is offered, and the skulls of *Cryptoclidus*, *Tricleidus* and *Kimmerosaurus* are reconstructed for the first time. A further three generic and twenty-five specific names are listed, discussed and rejected: some are junior synonyms but most are *nomina dubia.*

Published work on the phylogeny and classification of the order Plesiosauria is reviewed critically. Differing family-level classifications have been produced through the arbitrary weighting of differing characters of the postcranial skeleton. Thirty-eight plesiosaur characters used by taxonomists are discussed in the light of the present work, and of these fifteen (seven being skull characters) are of importance in distinguishing phyletic lineages.

The evolution and phylogeny of the Plesiosauria is discussed, three main lineages are identified, and a new classification is proposed. The order is divided into two superfamilies and four families. The Pliosauroidea represent one line of evolution and contain the single family Pliosauridae. The Plesiosauroidea contain an ancestral family (Plesiosauridae) and two descendant families (Cryptoclididae and Elasmosauridae). Diagnoses of these groups are given and referred genera listed. The Cryptoclididae comprise the genera *Cryptoclidus* and *Kimmerosaurus* together with the South American Upper Cretaceous genus *Aristonectes* Cabrera, hitherto considered an aberrant pliosaur. The genera *Muraenosaurus*, *Tricleidus* and *Colymbosaurus* are primitive elasmosaurs, as also is the English Lower Jurassic genus *Microcleidus* Watson.

Introduction

The order Plesiosauria is a group of the reptilian subclass Sauropterygia, and comprises reptiles which dominated the seas throughout the Jurassic and Cretaceous periods. On the basis of features which include the form of the skull and the comparative length of the neck they are divided into two superfamilies, the Plesiosauroidea and the Pliosauroidea. The vernacular names 'plesiosaur', 'plesiosauroid' and 'pliosauroid' (also 'pliosaur') refer to members of the order and the two superfamilies respectively.

Plesiosaur material is plentiful from most stages of the Jurassic System in Europe, and in particular from England. European specimens become scarce in the Cretaceous, and the principal remains are then to be found in North America. By the Upper Cretaceous the group had achieved a world-wide distribution, but in common with most groups of large reptiles it became extinct by the close of the Mesozoic era.

Most plesiosaur material was found and described in the nineteenth century. Early collectors depleted the coastal exposures, and by about 1910 most quarries became mechanized, this severely limiting the collection of fossil material before it was destroyed. After this date finds of new material were few, and although taxonomists continued to adjust the classification, very little redescription was attempted. Excellent as was much of the original description for its time, it proved to be an inadequate basis for subsequent work, and the need arose for a complete review. In more recent years Welles (1943, 1952, 1962; Welles & Gregg 1971) has reviewed the Cretaceous plesiosaurs, and Tarlo (1960) has reviewed the Upper Jurassic pliosaurs.

Most material of Upper Jurassic plesiosauroids has been recovered from English deposits, and especially from the two great clay formations, the Oxford Clay (mainly Callovian Stage) and the Kimmeridge Clay (Kimmeridgian Stage). The nomenclature of all genera is based on English type specimens in the collections of the British Museum (Natural History) (specimens with numbers prefixed by R or without prefix); the Sedgwick Museum, Cambridge (S.M.C.; numbers prefixed by J); the University Museum, Oxford (U.M.O.; numbers prefixed by J) and the Hunterian Museum, University of Glasgow (H.M.G.; numbers prefixed by V). Additional useful material is preserved in the National Museum of Wales, Cardiff (N.M.W.), the Castle Museum, Norwich (C.M.N.) and the Manchester Museum, University of Manchester (M.M.). During the course of the present study all these museums were visited and their collections examined. Further material in the Museum of the Royal College of Surgeons of England, London (R.C.S.), which was catalogued by Owen in 1854, was destroyed in 1941 by a fire caused by enemy action.

Almost all the plesiosauroid material from the Oxford Clay was collected in the late nineteenth century by one man, Alfred N. Leeds. His collection was made from brick-pits near and to the south of Peterborough; a map indicating the geography of these pits was published in a biographical work by the collector's son (Leeds 1956). Mechanization now prevents the collection of almost all specimens from these sites, but a few good finds, including an almost entire skeleton of *Cryptoclidus eurymerus* (see Charig & Horrell 1971), have been recovered in recent years through the cooperation and good will of the London Brick Company.

The bulk of the Leeds Collection, including most of the best specimens, was sold to the British Museum (Natural History) where it was catalogued and described by Andrews (1910, 1913). His description is full and largely accurate, and now requires only to be emended and supplemented. Plesiosauroids from the Kimmeridge Clay and higher deposits, on the other hand, are known only from isolated finds which are separately described and located. The present work is the first general review of these forms.

Examples are known of plesiosauroid individuals ranging from half-grown to full-grown. Differences of osteological structure of specimens of a single species, attributable entirely to ontogeny, have in the past been misinterpreted and used to produce taxonomic divisions. This, together with misinterpretation of other characters used in taxonomy, has led to the publication of a hyperabundance of generic and specific names, and a proliferation of schemes of classification based upon these. In order to facilitate description and the study of ontogeny, specimens are here allocated to one of three categories which represent growth stages, as follows:

(i) 'Juveniles', in which the neural arches of the vertebrae are not fused to the centra;

(ii) 'Adults', in which fusion of neural arches and centra has taken place, and

(iii) 'Old adults', in which the neural arches and centra are fused, and in addition further characters of advanced ossification are found.

Throughout the present work, the use of inverted commas indicates these special meanings of the words 'juvenile', 'adult' and 'old adult'.

Systematic descriptions

In the descriptive sections which follow, English Upper Jurassic plesiosauroid genera and species are described and discussed objectively, without reference to higher classification. There then follows a discussion of the phylogeny and classification of plesiosaurs; a new classification of the Plesiosauria is subjectively proposed and the genera of plesiosaurs are assigned to family-group taxa.

Genus ***CRYPTOCLIDUS*** Seeley, 1892

1892 *Cryptoclidus* Seeley: 145 (as a subgenus).
1895*a* *Cryptoclidus* Seeley; Andrews: 333 (as a genus).
1909 *Cryptocleidus* Andrews: 418 (incorrect subsequent spelling).
1915 *Apractocleidus* Smellie: 341 (subjective-objective synonym *sensu* Blackwelder 1967).

TYPE SPECIES. *Plesiosaurus eurymerus* Phillips, 1871.

ADDITIONAL ENGLISH SPECIES. *Cryptoclidus richardsoni* (Lydekker, 1889).

DIAGNOSIS. Plesiosauroids in which tooth ornament is reduced; the dentary bears 24 to 26 teeth on each ramus; the premaxillae bear 6 teeth each, of which the first (most anterior) is small and the second to sixth are large; the parietals form a sagittal crest; the paroccipital process of the exoccipital-opisthotic is of moderate length; the occipital condyle is not ringed by a groove, and extends onto the pedicles of the exoccipitals; there are about 55 presacral vertebrae, of which usually 32 are cervical; the cervical vertebrae have relatively amphicoelous centra, the length of which very rarely exceeds the height; the clavicles are triangular and well developed, lie visceral to the ventral rami of the scapulae, and meet in the midline; the interclavicle is absent or rudimentary; the coracoids meet the scapulae in the ventral midline in 'adults'; the width across the posterior cornua of the coracoids exceeds the interglenoid width in 'adults' by up to 40%; the elements of the pectoral girdle tend to fuse in old individuals; there are normally only two epipodials in the manus; a foramen only appears between the epipodials in specimens showing advanced ossification. (Diagnostic characters of the skull are taken only from the type species.)

Cryptoclidus eurymerus (Phillips, 1871)

(Figs 1–18, 43a, 44a)

1869 *Plesiosaurus oxfordiensis* Seeley. Published as *P. oxfordiensis* Phillips, MS (*nomen nudum*).
1871 *Plesiosaurus oxoniensis* Phillips: 307, figs 113–117 (*nomen dubium*).
1871 *Plesiosaurus eurymerus* Phillips: 315, fig. 120.
1874*b* *Muraenosaurus oxoniensis* (Phillips) Seeley: 448.
1888 *Plesiosaurus oxoniensis* Phillips; Lydekker: 352.
1888 *Plesiosaurus eurymerus* Phillips; Lydekker: 352.
1889 *Cimoliosaurus eurymerus* (Phillips) Lydekker: 205, figs 66–68 (mis-spelling of *Cimoliasaurus* Leidy, 1852).
1889 *Cimoliosaurus oxoniensis* (Phillips) Lydekker: 209.
1892 *Cimoliosaurus eumerus* ('Phillips'); Seeley: 145 (*lapsus*).
1892 *Plesiosaurus durobrivensis* (Lydekker) Seeley: fig. 5.
1892 *Muraenosaurus (Cryptoclidus) platymerus* Seeley: 145, figs 13–15.
1895*a* *Cryptoclidus oxoniensis* (Phillips) Andrews: 333, figs 1–4.
1895*a* *Cryptoclidus platymerus* (Seeley) Andrews: 335.
1895*b* *Cryptoclidus oxoniensis* (Phillips); Andrews: 241, fig. 1, pl. 9.
1896 *Cryptoclidus oxoniensis* (Phillips); Andrews: 145, fig. 1.
1909 *Cryptoclidus oxoniensis* (Phillips); Bogolubov: 44.
1909 *Cryptoclidus eurymerus* (Phillips) Bogolubov: 48.
1909 *Cryptoclidus platymerus* (Seeley); Bogolubov: 50.
1909 *Cryptocleidus oxoniensis* (Phillips); Andrews: 418.
1910 *Cryptocleidus oxoniensis* (Phillips); Andrews: 164, text-figs 78–94, frontispiece, pls 9, 10.
1915 *Apractocleidus teretipes* Smellie: 341, fig. 1.
1916 *Apractocleidus teretipes* Smellie; Smellie: 609, text-figs 1–9, pl. 1.
1959 *Cryptocleidus eurymerus* (Phillips); Delair: 66.
1959 *Cryptocleidus oxoniensis* (Phillips); Delair: 67.
1962 *Cryptoclidus oxoniensis* (Phillips); Welles: 8.
1962 *Cryptocleidus oxoniensis* (Phillips); Welles: tables 1, 4.
1963 *Cryptocleidus oxoniensis* (Phillips); Persson: 24.
1963 *Cryptocleidus eurymerus* (Phillips); Persson: 24.
1964 *Cryptocleidus oxoniensis* (Phillips); Novozhilov: figs 303, 304.
1964 *Apractocleidus teretipes* Smellie; Novozhilov: 320, fig. 304.
1964 *Cryptocleidus eurymerus* (Phillips); Novozhilov: 320.

LOST HOLOTYPE. A forelimb formerly in the Woodwardian (= Sedgwick) Museum, Cambridge. The specimen was described and figured by Phillips (1871) from a plaster cast then in the University Museum, Oxford. It was originally misidentified as a hindlimb, and was named *Plesiosaurus eurymerus.* Andrews (1910) states that vertebrae similar to those of *P. oxoniensis* Phillips, 1871, were associated with the limb.

The lost holotype was from Bedford, England, taken from Oxford Clay, and therefore of Callovian or, improbably, Lower Oxfordian age. (No English plesiosauroid material of certain Oxfordian age is known.)

The holotype was realized to be missing in 1958, since when repeated searches of the Sedgwick Museum have been fruitless. Furthermore, there is no documentary record relating to its existence in that museum (personal communication, Dr C. L. Forbes). The plaster cast in Oxford University Museum is also missing (personal communication, Mr H. P. Powell). I am therefore obliged to propose a neotype.

NEOTYPE. Specimen R.2860, a Leeds Collection specimen in the BM(NH). This is one of the most complete 'adult' plesiosaur skeletons known, and was described, figured extensively and reconstructed by Andrews (1910 : 164; frontispiece; text-figs 78c, 78d, 91a, 91b, 94; pl. 9 figs 1, 1a, 2, 3). The forelimbs show the same distinctive characters as Phillips' figure of the lost holotype (1871 : fig. 120); these are included in the diagnosis below.

The neotype is from an unspecified brick-pit near Peterborough, England. Its horizon is Upper Jurassic, Callovian Stage, from the lowest deposits of the Oxford Clay, which includes the zones of *Kosmoceras jason, Erymnoceras coronatum* and *Peltoceras athleta* (see Andrews 1910 : vii).

DIAGNOSIS. Members of the genus *Cryptoclidus* in which the teeth have a characteristic ornament of longitudinal ridges: two opposing axial ridges (mesial and distal) rise from the base of the crown and almost meet over the tip, and between these rise from 4 to 7 lingual ridges which extend from the base to approximately one-third of the height of the crown; there are usually no buccal ridges. The humerus is greatly expanded distally by an anterior expansion of the portion bearing the radial facet. The radius is enlarged by anterior expansion of the portion bearing the humeral facet, which may be up to twice as long as the facet for the radiale, so causing the anterior margin to describe a sigmoid curve. The ulna is much wider than long.

DISTRIBUTION AND RANGE. Diagnostic material is known only from the Peterborough and Bedford districts. Upper Jurassic; Callovian Stage only.

REFERRED SPECIMENS. Since remains of this species are comparatively abundant, only those specimens mentioned in the text are listed below; a fuller list is given elsewhere (Brown 1975). All specimens are from the Oxford Clay in the Peterborough area.

R.2412. Incomplete 'adult' postcranial skeleton partly figured by Seeley (1892 : figs 13–15) as the holotype of *Muraenosaurus (Cryptoclidus) platymerus*, and by Andrews (1910 : text-figs 79, 80, 83, 84, 90c) as *C. oxoniensis.*

R.2416. Incomplete 'juvenile' postcranial skeleton partly figured by Andrews (1895*a* : fig. 3b; 1910 : text-figs 89a, 90b) as *C. oxoniensis.*

R.2417. 'Juvenile' skeleton (mounted) figured by Andrews (1895*b* : pl. 9; 1910 : text-figs 78a, 78b, 90a, 92, pl. 9 figs 4, 4a, 5, 6) as *C. oxoniensis.*

R.2616. Incomplete 'adult' postcranial skeleton partly figured by Andrews (1895*a* : figs 1, 2; 1896 : fig. 1; 1910 : text-fig. 87, pl. 10) as *C. oxoniensis.*

R.2862. Postcranial skeleton of an 'old adult'. Gastralia figured by Andrews (1910 : text-fig. 86) as *C. oxoniensis.*

R.3538. Pectoral girdle of an 'adult'. Figured by Andrews (1910 : text-fig. 88) as *C. oxoniensis.*

R.3703. Incomplete 'adult' postcranial skeleton. Hindlimb figured by Andrews (1910 : text-fig. 93) as *C. oxoniensis.*

R.3730 (Figs 6, 7). Incomplete 'adult' skeleton. Jaws figured by Andrews (1910 : pl. 9 fig. 7) as *C. oxoniensis.*

R.8621 (Figs 3–5). Lower jaw, two teeth and postcranial skeleton of an 'adult'. Figured *in situ* by Charig & Horrell (1971).

H.M.G. V.1091. Postcranial skeleton of an 'old adult', lacking a tail (mounted with the tail of V.1104). Figured by Smellie (1915 : fig. 1; 1916 : figs 1–9, pl. 1) as the holotype of *Apractocleidus teretipes.*

H.M.G. V.1104 (Figs 8–9, 11–12, 14–18). Postcranial skeleton of an 'adult'.

H.M.G. V.1807. Coracoids, scapulae and humeri of an 'old adult'.

H.M.G. V.1809. Right forelimb of an 'old adult'.

H.M.G. V.1835. Right humerus of an 'old adult'.

Discussion of synonymy

Phillips (1871 : 307–312) described as *Plesiosaurus oxoniensis* various dissociated plesiosaur remains from the Oxford Clay of Long Marston, Oxfordshire. This included several vertebrae, a hindlimb and a pectoral girdle (figured upside down and described by Phillips as a pelvis). Subsequent opinions regarding the affinities of the limb and girdle differed (Seeley 1874*b*; Lydekker 1888; Andrews 1895*a*, 1910); they are in fact plesiosauroid, but generically non-diagnostic. Andrews (1910) concluded that the only parts of Phillips' material to which the name *P. oxoniensis* could be applied were the vertebrae. In the same work of 1871, Phillips (: 315–316) described and figured a forelimb from the Oxford Clay of Bedford as *Plesiosaurus eurymerus*, misidentifying it as a hindlimb.

After visiting the private collections of A. N. Leeds at Eyebury, near Peterborough, and studying several almost complete skeletons, Lydekker (1888) identified the holotype of *P. eurymerus* as a forelimb and recognized its association with vertebrae similar to those of *P. oxoniensis.* Believing Leeds' specimens to be of significantly larger size, he retained both names, *P. eurymerus* being used to refer to the larger species. In 1889 he referred both species to the genus *Cimoliasaurus* Leidy, and figured as *C. eurymerus* a cervical vertebra and associated forelimb of a partial skeleton (R.2412) acquired by the BM(NH) from Mr Leeds.

In 1892, Seeley made R.2412 the holotype of *Muraenosaurus (Cryptoclidus) platymerus,* new subgenus and species. His subgeneric distinction was based on the form of the clavicles which he described for the first time; but he did not distinguish between the forelimb and that of the holotype of *P. eurymerus*, and so his introduction of a new specific name was not justified.

During the succeeding two decades the BM(NH) received numerous specimens from the Leeds Collection which were then described and catalogued by Andrews. He believed (1895*a*, 1910) that *P. oxoniensis* and *P. eurymerus* were sexual dimorphs, differing only in size, of a single species for which he used the name *Cryptoclidus oxoniensis.*

Subsequent to Andrews' work, a second species of the genus *Cryptoclidus* (*C. richardsoni*) has been recognized. The two species differ in the structure of the forelimb but their vertebrae together with those of *Tricleidus seeleyi* are mutually indistinguishable. The type vertebrae of *P. oxoniensis* are therefore non-diagnostic, and this name is a *nomen dubium.* The valid name for the present species is *Cryptoclidus eurymerus* (Phillips, 1871).

In 1915, Smellie described a Leeds Collection plesiosauroid in the Hunterian Museum, University of Glasgow, as *Apractocleidus teretipes.* It is argued below that the holotype (V.1091) is an 'old adult' individual of *C. eurymerus.*

Description of material

The skull. Andrews (1910) described the skull of *C. eurymerus* only by comparative reference to that of *Muraenosaurus.* It is known from several rather fragmentary specimens, the most complete of which is that of R.2860 (the neotype), and it differs in several important respects from those of its contemporaries. The reconstruction which is now presented (Figs 1, 2) is based largely upon R.2860, together with details of the dentition taken from R.3730. These skulls are now described, together with additional skull material.

SKULL OF R.2860 (NEOTYPE). This skull is preserved as 12 separate fragments: (A) most of the right premaxilla, the left premaxilla and the anterior part of the left maxilla; (B) a small part of the right premaxilla and the anterior part of the right maxilla; (C) the posterior part of the right maxilla; (D) the posterior part of the left maxilla, both frontals, both parietals, the supraoccipital and a small part of the left squamosal; (E) both the fused exoccipital-opisthotic elements, the basioccipital and the basisphenoid; (F) most of the left squamosal; (G) the right squamosal and right quadrate; (H) the vomers, upon which are compressed fragments probably of the premaxillae and frontals; (I) the left ramus of the dentary and the anterior portion of the right; (J) the posterior portion of the right ramus of the dentary; (K) the left angular, surangular and articular; and (L) the right angular, surangular and articular.

The dorsal surface of the premaxillae (fragments A, B) is much roughened by an irregular ornament of pits and ridges. The right element is better preserved than the left, and includes a complete toothrow containing the sockets for six teeth. With the exception of the small first

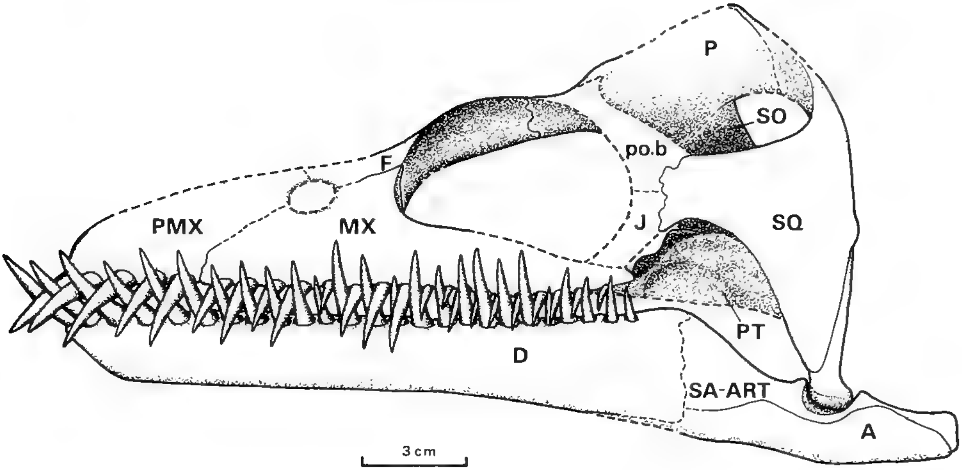


Fig. 1 *Cryptoclidus eurymerus* (Phillips). Composite reconstruction of skull in lateral view. A, angular; D, dentary; F, frontal; J, jugal; MX, maxilla; P, parietal; PMX, premaxilla; po.b, postorbital bar; PT, pterygoid; Q, quadrate; SA–ART, fused surangular-articular; SO, supraoccipital; SQ, squamosal.

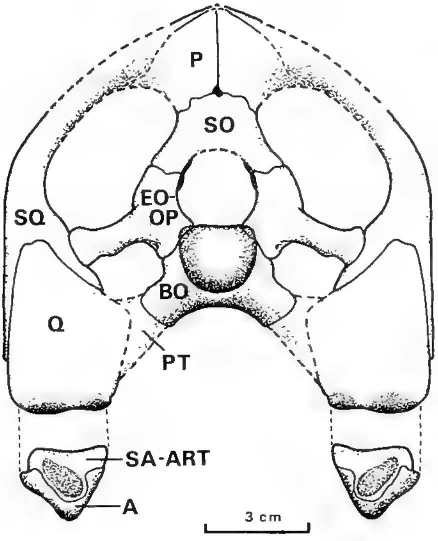


Fig. 2 *Cryptoclidus eurymerus* (Phillips). Composite reconstruction of skull in occipital view. A, angular; BO, basioccipital; EO–OP, fused exoccipital-opisthotic; P, parietal; PT, pterygoid; Q, quadrate; SO, supraoccipital; SQ, squamosal.

socket these are all of relatively large size. The third to sixth sockets remain on the left side, the fifth containing the only tooth preserved with the present specimen. The tip of this tooth is broken off; but the remaining part is ornamented with only 5 or 6 ridges which are widely spaced and confined to the lingual side. It is thus of the same characteristic type as the teeth of R.2417, R.3730 and R.8621 (see below). Both premaxillae are broken and eroded dorsally, and there is no evidence for their suture with the frontals or for the margin of the external nares. Posteriorly the sutures with the maxillae remain intact.

The maxillae (fragments A, B, C, D) have been somewhat eroded dorsally, but the alveolar regions are better preserved, and the left toothrow is complete. This contains sockets for 21 teeth, the posterior sockets appearing as grooves due to the loss of their lingual halves. The teeth evidently formed a graded series, showing a gradual reduction in diameter posteriorly.

The antorbital process of each maxilla extends dorsally to an extensively overlapping suture with the frontal, without any evidence for the existence of a discrete prefrontal or lacrimal element. From this suture the orbital margin is preserved downwards and backwards in an arc for about 3 cm on either side, but posterior to this point the edge of the bone is continuously broken back to the posterior end of the toothrow. The anterior margin of the antorbital process is also missing. There is therefore no evidence for the position of the external naris or of posterior sutures of the maxilla with other elements.

The frontals (fragment D) are relatively narrow posteriorly, where they meet the parietals and separate the dorsal margins of the orbits by only 3 cm; but more anteriorly they expand to carry the orbital margins outwards and upwards in an arc which reaches 1 cm above the median suture before continuing in descent to the sutures with the maxillae. The anterior expanded part of each frontal is thin, but ventrally it is strengthened by two thicker bony bars set at an angle of about 40°. One bar follows the median suture anteriorly towards the premaxillae; the other forms the orbital margin.

The parietals (fragment D) are fused, there being no trace of their suture on the skull table. Anteriorly they meet the frontals in a complex interlaminating suture which is split in the midline by the pineal foramen; this foramen is contained largely within the parietals, but on the dorsal aspect the frontals form a small part of its anterior margin.

Posterolateral to the pineal foramen the parietals are expanded to form the bases of the postorbital bars. These are not preserved; but the position of the squamous suture of at least the postfrontal element is indicated by ridges on the parietals and posterolateral margins of the frontals. This evidence suggests that the postorbital bar was thin, and that its plane was tilted downwards and backwards at an angle of about 30° to the plane of the skull table.

Behind the postorbital bars the parietals form a high and narrow sagittal crest, which is flanked by deep excavations for the temporal musculature. Behind these excavations each parietal is produced into a process which unites with the squamosal to form the post-temporal bar. On the left side a portion of this bar remains with the dorsal margin preserved to within 3 mm of the midline. At this point the bar is formed largely from the parietal; but above this is sutured the squamosal, which here has the form of a thin strand of bone tapering towards the midline, where it probably just met its opposite at the skull vertex.

The parietals form the uppermost 2·5 cm of the occipital surface of the skull, and in this part the median suture is still visible. Ventrally they unite with the supraoccipital.

The supraoccipital (fragment D) forms an arch over the dorsal half of the foramen magnum. In the midpoint of the suture with the parietals is a small foramen (observed in all plesiosauroid skulls studied) which may have housed the origin of a nuchal ligament. Ventrally the facets for the prootics and exoccipitals are of approximately equal size, the anterior prootic facets being grooved for the dorsal part of the posterior vertical semicircular canals.

The fused exoccipital-opisthotic elements together with the basioccipital and the basisphenoid (fragment E) were described and figured by Andrews (1910 : 166; pl. 9, figs 1, 1a, 2) in union with the supraoccipital and the posterior part of the parietals. The fusion of the exoccipital and opisthotic appears to be usual in all plesiosaurs. The opisthotic part contains half the utriculus (identified as the ampulla of the posterior vertical semicircular

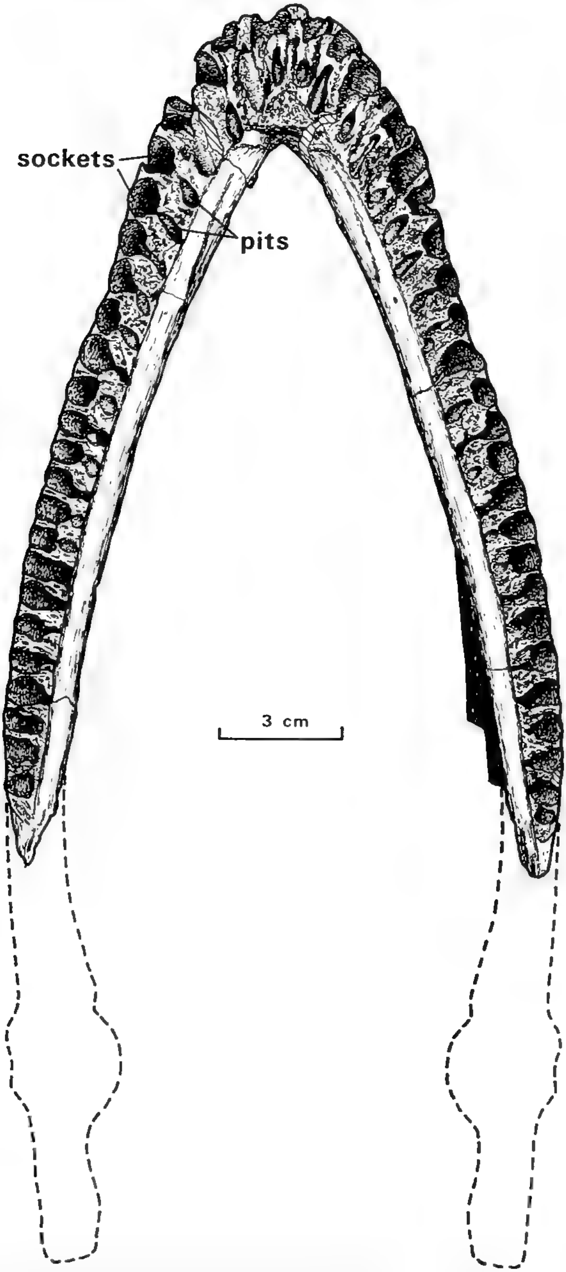


Fig. 3 *Cryptoclidus eurymerus* (Phillips), R.8621. Dentary in dorsal view. Outline of posterior elements of jaw (Fig. 4b) in dashed lines.

canal by Andrews, 1910) and parts of the posterior vertical and horizontal semicircular canals. The paroccipital process is relatively shorter than in *Muraenosaurus* and *Tricleidus*, yet longer than in *Kimmerosaurus*.

The occipital condyle of *Cryptoclidus eurymerus* differs markedly from all contemporary species. It is formed largely from the basioccipital, but includes a small part of the pedicles of the exoccipitals, whereas in the genera *Muraenosaurus* and *Tricleidus* (see below) the condyle is formed entirely from the basioccipital, and is separated from the exoccipitals by a groove.

The squamosals (fragments F, G) are triradiate in structure: the dorsal ramus forms the major part of the post-temporal bar and curves dorsomedially to meet its opposite above the parietals (these rami have been eroded heavily and cannot now be fitted to the parietals); the anterior ramus forms the zygoma and probably met the postorbital bar; the ventral ramus is a vertically-orientated plate of bone extending downwards almost to the jaw articulation and largely obscuring the quadrate in lateral view.

On the inner surface of the squamosal just beneath the base of the dorsal ramus is a flange which, together with the ventral ramus, forms a ventrally-orientated socket housing the primary head of the quadrate (Fig. 2). On the medial surface of this flange there is a large oval facet which matches in size and shape the head of the paroccipital process. It is therefore evident that the opisthotic articulated with the squamosal, and not with the quadrate as has been suggested by Andrews (1910) and Welles (1952).

The right quadrate (fragment G) is a strongly-built element and is preserved *in situ* with the right squamosal. At its ventral end it bears two ovoid condyles for articulation with the lower jaw. These are positioned at right angles to the skull axis, with the lateral condyle slightly larger than the medial. The process for suture of the quadrate with the pterygoid is broken away close to the medial condyle, and their precise arrangement cannot be determined. The combined quadrate and squamosal elements have been flattened a little in preservation, and the natural angle between them widened; this has been taken into account in the reconstruction (Figs 1, 2).

The only parts of the palate which have been preserved are the fused vomers (fragment H). Onto these have been compressed small parts of the premaxillae and frontals, and the whole fragment has been eroded heavily. The vomers were probably similar in form to those of *Muraenosaurus* and *Tricleidus*; a part of the margin of the right internal naris can be identified in the same relative position.

Small discontinuities of the toothrow are present on both rami of the dentary (fragments I, J), but the number of sockets per ramus may be estimated, 26 being the most probable figure. This compares with 24 sockets per ramus in R.8621, 24 or 25 in R.2417 and 25 in R.3730, these being the only specimens in which the dentary is preserved.

The posterior elements of the lower jaw (fragments K, L) do not differ significantly from those of R.8621 (described below).

The skull reconstructions (Figs 1, 2) were based as far as possible on the present specimen. It was necessary to restore the general outlines of the postorbital bar and jugal element from a consideration of plesiosauroid skull reconstructions by Andrews (1910) and Welles (1943, 1952, 1962). The dentition was restored by reference to specimens R.3730 and R.8621.

SKULL OF R.8621. With the exception of a small unidentifiable fragment, only the lower jaw and two isolated teeth remain of this skull. These are very well preserved, and have been prepared fully in the British Museum (Natural History).

The toothrow of the dentary (Fig. 3) has been preserved intact and without any post-mortem distortion, but all mature teeth have been lost. Each ramus bears sockets for 24 teeth, the largest (implying that these held the largest mature teeth) being the 4th, 5th and 6th. The anterior sockets are only slightly smaller than these; posteriorly they decrease regularly in size from the 6th to 22nd, then reduce abruptly to the small 24th.

The sockets are inclined outwards at a considerable angle from the vertical. This angle increases from 40° posteriorly up to 60° or more in anterior sockets. They are also inclined forwards, again this inclination increasing from behind forwards.

The present specimen exhibits the characteristic structure of the sauropterygian toothrow in which large tooth sockets, which held the functional teeth, are paired on the lingual side with small pits in which the replacement teeth developed. The pits take the form of small depressions or sometimes elevations, the surfaces of which are evenly textured, resembling the appearance of fine sandpaper. This surfacing contrasts with the surrounding bone, which is smooth and shows grain. Each pit is connected to the socket by a fine line or groove. The crowns of developing replacement teeth appear to pass from the pit outwards along this line until they occupy the socket; stages of this process are to be found in relation to the left 2nd, 4th and 7th, and the right 1st, 2nd, 4th, 9th and 14th sockets.

The pits appear on the surface of the bone lingual and posterior to their associated sockets, but owing to the inclination of the sockets, they are actually sited immediately above the socket bases. It is evident that the developing teeth move downwards into the socket; the apparent lateral movement of the crowns as seen on the surface of the bone is caused by increase in the length of the outwardly-inclined tooth crown coupled with a downward movement of the whole tooth.

The specimen shows the characteristic plesiosauroid 'short symphysis', which represents a simple unexpanded union of the left and right rami between the first alveoli. The dorsal

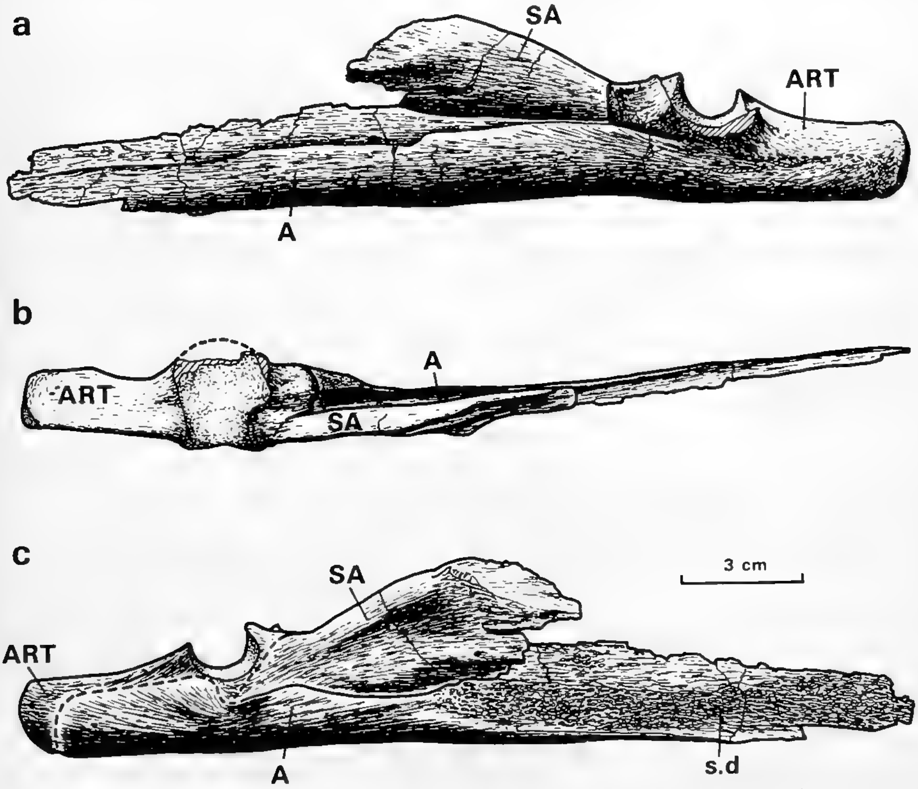


Fig. 4 *Cryptoclidus eurymerus* (Phillips), R.8621. Posterior elements of right lower jaw ramus: a, medial; b, dorsal; c, lateral aspect. A, angular; ART, articular; SA, surangular; s.d, surface for union with dentary. Sites of fusion between the articular, angular and surangular (indicated by

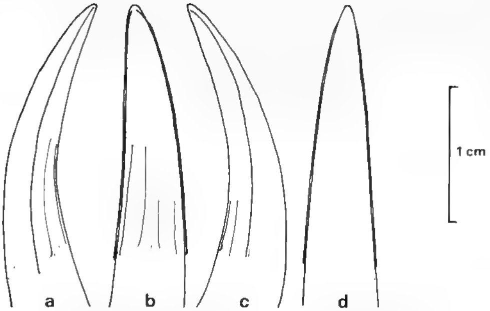


Fig. 5 *Cryptoclidus eurymerus* (Phillips), R.8621. Tooth showing ornamental ridges: a and c, axial; b, lingual; d, buccal aspect.

length of the symphysis is 3·2 cm and the length of the left ramus is 22·4 cm; the symphysis is therefore comparatively much shorter than in pliosaurs (cf. measurements given by Andrews, 1913).

The internal surface of the dentary is grooved deeply for the reception of the surangular and possibly a splenial. Thin broken fragments perhaps of this latter element remain in place anteriorly on both rami.

The posterior elements of the right lower jaw ramus are preserved united in a second piece (Fig. 4), and consist of the fused articular-surangular together with the angular. There is no separate coronoid element in this species.

Fusion of the articular and surangular appears to occur in all plesiosaurs. The combined elements form the glenoid for articulation with the skull. This is laterally expanded, and has two concavities to fit the double condyles of the quadrate.

In the present specimen the articular-surangular is in the process of fusing with the angular. Anteriorly the suture is clearly visible, but fusion has been completed posteriorly, the line of fusion being still traceable from the growth-pattern of the elements. Posteriorly the angular is a thin lamina in plesiosaurs, which is wrapped round the sides and ventral surface of the massive and cylindrical articular. Anteriorly it takes the form of a thin vertical lamina which unites externally with the inner surface of the dentary. Its medial surface is folded to produce a dorsally orientated meckelian groove for the insertion of jaw

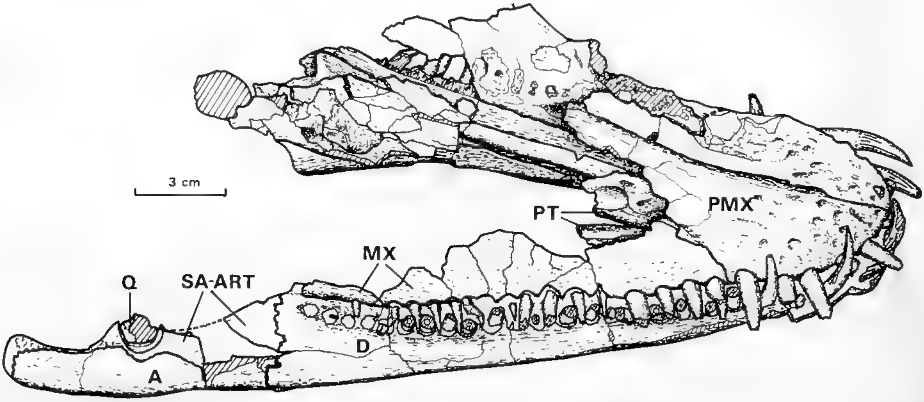


Fig. 6 *Cryptoclidus eurymerus* (Phillips), R.3730. Skull in right dorsolateral view. Broken bone hatched, clay matrix stippled. Abbreviations as in Fig. 1, p. 259.

musculature. A fragment consisting of part of the left angular and surangular is also preserved.

Two isolated teeth were found near the jaw. The smaller tooth is well preserved (Fig. 5) and shows clearly the characteristic ornament found in this species (see description in diagnosis).

SKULL OF R.3730. The preserved parts of this skull are the upper and lower jaws together with the frontals, parietals and supraoccipital. These latter elements (which comprise a separate fragment) resemble closely those of R.2860, and add nothing to the description. Despite much post-mortem flattening, however, the jaws (Figs 6, 7) retain almost the full set of teeth, and have been compressed together in such a way as to preserve their interlocking arrangement. This arrangement has been incorporated into the skull reconstruction (Fig. 1).

There are 25 teeth in each ramus of the lower jaw (cf. 26 sockets in R.2860), the largest being the anterior six. In conformity with the sockets of R.8621 they show a gradual decrease in size posteriorly, but only the most posterior tooth could be described as small. In this respect the lower and upper teeth differ. The most anterior tooth in the premaxilla is very small, and the left and right teeth are very close together. The remaining five premaxillary teeth are large, being as large as the dentary teeth with which they interlock. Each maxilla bears 18 teeth (cf. 21 sockets in R.2860) of which the anterior eight (the 7th to 14th upper teeth) are approximately equal in size to the 7th to 14th lower teeth. Posterior to these the upper teeth diminish considerably, becoming much smaller than their adjacent teeth in the dentary.

On the right side of the jaw (Fig. 6) the detailed interlock of the teeth has been very well preserved. The most anterior teeth in the combined jaws are the first upper teeth, which bite together in advance of the first lower teeth. Thereafter, upper and lower teeth interlock in a one-to-one fashion anteriorly, with the upper teeth biting in advance of the lower. Behind the 10th teeth the interlock becomes disrupted occasionally, with two upper or lower teeth biting together between their opposites. At such places invariably one or more mature teeth have been lost and their places only partly occupied by smaller developing replacement teeth. The fully detailed interlock on the left side (Fig. 7) could not be determined, but it was apparent that the sites of confused interlock did not coincide with those of the right side. All teeth show the characteristic ornamentation.

The tooth crowns curve towards the vertical (i.e. the lingual side is shorter), this curvature amounting to 40° posteriorly but reducing to about 20° in the most anterior teeth. From a consideration of the orientation of empty sockets in R.8621 it is evident that in posterior teeth the curvature fully counteracts the outward inclination of the socket such that the tooth

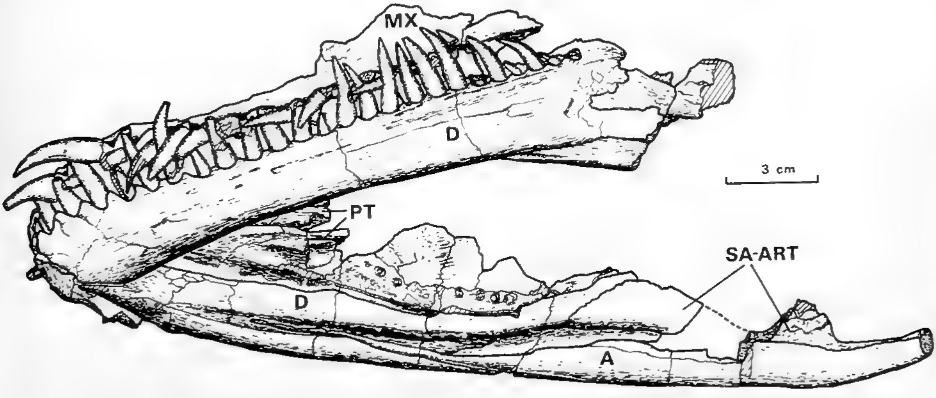


Fig. 7 *Cryptoclidus eurymerus* (Phillips), R.3730. Skull in left ventrolateral view. Abbreviations as in Fig. 1, p. 259.

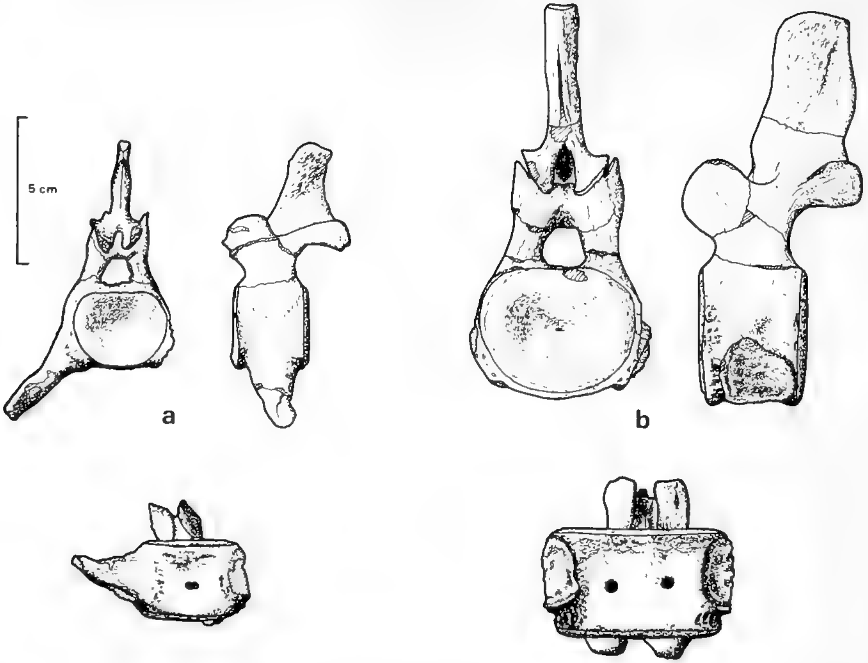


Fig. 8 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. a, fifth and b, twenty-fifth cervical vertebrae: posterior, left lateral and ventral views.

tip was vertical; in the most anterior teeth the tip may have had a natural orientation of as much as 40° from the perpendicular.

A scale lateral reconstruction of the appearance of the closed jaws was produced by reference to the right jaws of R.3730 and the toothless jaw of R.8621, as above. This was then reversed (so as to appear to face to the left) and reduced slightly until it fitted the toothless restoration of R.2860. In this way the composite lateral reconstruction (Fig. 1) was derived.

SKULL OF R.2417. The skull of this 'juvenile' individual is very fragmentary, and has been mounted on thin steel bars to which the fragments have been glued. It is less complete than that of R.2860, and adds little to the description.

Three teeth, preserved *in situ* on the premaxillae, show the diagnostic ornamentation. Fragments of the frontals and parietals are preserved, and the supraoccipital, exoccipital-opisthotics, basioccipital and basisphenoid were figured by Andrews (1910 : pl. 9, figs 4, 4a, 5; the 'median foramen' in the basisphenoid, figured and labelled *for.*, is actually a hole that has been drilled to facilitate mounting on a steel peg). The form of the occipital condyle, in which the exoccipitals are involved, is exactly as in R.2860. Parts of the right squamosal and both quadrates are also preserved.

The right ramus of the lower jaw (Andrews 1910 : pl. 9 fig. 6) contains 24 tooth sockets with posteriorly a small depression suggestive of a 25th socket developing. The left ramus is heavily eroded. In this 'juvenile' specimen the angular extends slightly posterior to the ossified part of the articular, which was completed posteriorly in cartilage.

The postcranial skeleton. The detailed description of the postcranial skeleton of this species which was given by Andrews (1910 : 168–202, text-figs 78–94, frontispiece, pl. 10) is largely accurate, and a complete redescription is unnecessary. In the following account several details are added concerning ageing and osteological development; some misconceptions regarding characters of taxonomic importance are clarified and Andrews' reconstruction (1910 : text-fig. 94) is modified (Fig. 10).

VERTEBRAE. Five types of vertebrae are distinguished in describing the vertebral column of plesiosaurs, these being cervical, pectoral, dorsal, sacral and caudal. Pectoral vertebrae (defined by Seeley, 1874*a*) are transitional between cervicals and dorsals; in these the rib articulates with both the centrum (as in cervicals) and the neural arch (as in dorsals). In sacral vertebrae the centrum and neural arch together form a large facet for the modified sacral rib, and in the caudals the rib articulates only with the centrum, this usually possessing additional ventral facets for the chevrons.

Pectoral vertebrae (Fig. 9) can be identified and counted easily in 'juveniles' since the neural arches and centra are free, but in 'adults' these elements fuse and the line of fusion cannot be traced. It is therefore necessary to estimate the numbers of cervical, pectoral and dorsal vertebrae in 'adults' by comparison with the appearance of these vertebrae in 'juvenile' specimens. The boundary between dorsal and sacral regions is always obvious, and in entire specimens the number of presacral vertebrae may be counted reliably.

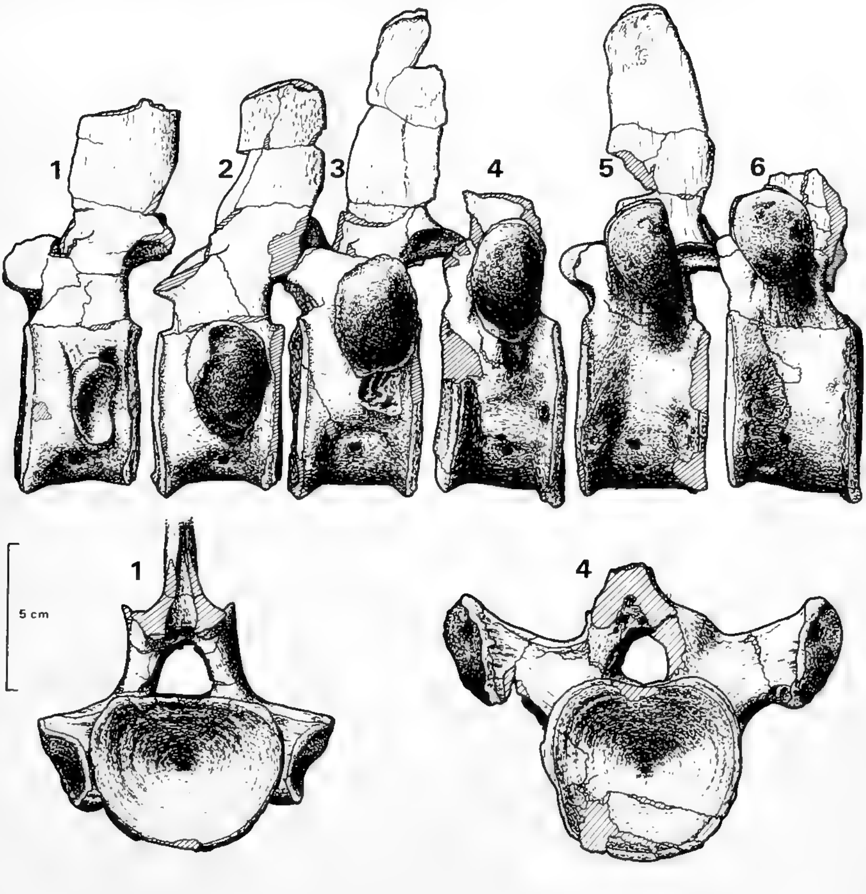


Fig. 9 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. 1–3, pectoral vertebrae; 4–6 anterior dorsal vertebrae (first, second and third dorsals). Left lateral view, with posterior views of two vertebrae.

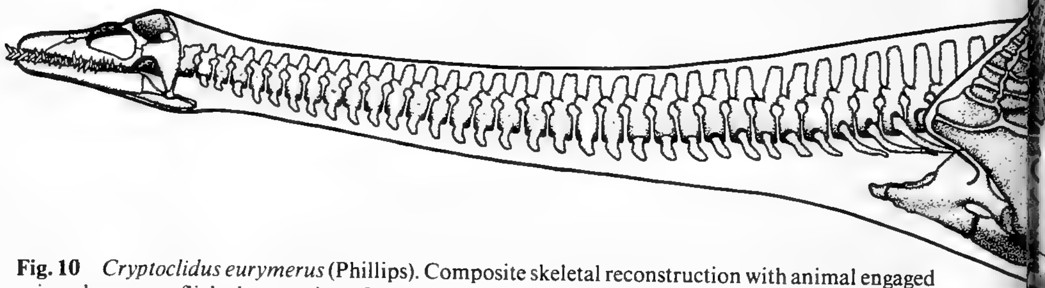


Fig. 10 *Cryptoclidus eurymerus* (Phillips). Composite skeletal reconstruction with animal engaged in subaqueous flight locomotion. Overall length of adult about four metres. See 'Note on the reconstruction', p. 280.

There are three specimens of *C. eurymerus* in which 55 presacral vertebrae are preserved. In R.2417, which is a 'juvenile', there are 32 cervicals, 3 pectorals and 20 dorsals, and this is also the estimated distribution of vertebral types in the 'adult' specimen R.2860. In the 'old adult' V.1091 the estimate of 29 cervicals, 3 pectorals and 23 dorsals suggests that the position of the transition from cervicals to dorsals is subject to variation. If a constant number of presacral vertebrae in this species is assumed from the evidence of 3 specimens with the maximum recorded number, then it must also be assumed that specimens with rather less than 55 presacrals (such as R.2862 with 53, R.2416 with 48) have been incompletely collected. Since the bones are disarticulated and entirely clear of the matrix, this cannot be checked but seems probable.

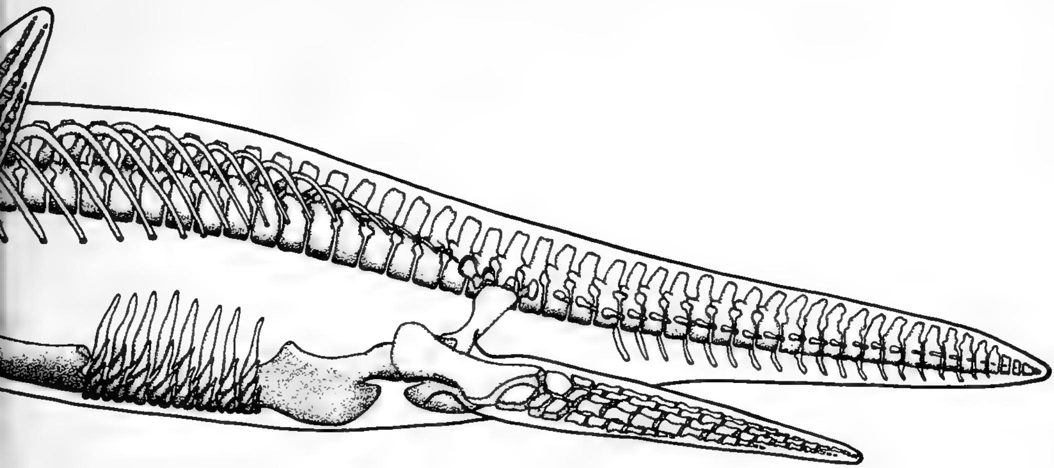
The vertebral column of plesiosaurs shows several features which do not vary significantly throughout the suborder but have sometimes been used erroneously for taxonomic purposes. These include relative size of vertebral types; proportional length of neural spines; relative diameter of the neural canal; relative development of zygapophyses and presence of nutritive foramina. In these features the present species is typical of all forms.

In any individual the largest vertebrae are the mid-dorsals, and these have proportionally (as well as actually) the longest neural spines. The diameter of the neural canal is maximal in the posterior dorsal vertebrae, and reduces both posteriorly and anteriorly.

The zygapophyses of dorsal and caudal vertebrae are small and weak, whereas those of cervical vertebrae are large and well developed. Williston (1914) thought that this indicated a relative lack of flexibility of the neck, but the reverse is more likely, since the spaces for cervical intervertebral discs are large, and the zygapophyses are constructed so as to limit only rotational movements.

Nutritive foramina are present in all vertebral centra. In the most anterior cervicals the paired foramina are very close together and are separated by a mid-ventral ridge; they may occasionally coalesce into a single median foramen as in Fig. 8a. They become progressively further apart in posterior cervicals and are laterally placed in pectorals, dorsals and sacrals. In caudals the nutritive foramina again become ventral, and tend to become subdivided.

Proportions of vertebral centra in plesiosaurs vary from species to species, and hence are of genuine taxonomic importance; however, taxonomists have frequently found difficulty in delimiting and defining taxonomic characters involving central proportions, and so their usefulness has been restricted. For example, Welles (1952, 1962) devised a 'vertebral index' system involving comparison of all three dimensions of centra (length, width and height) together with absolute measurements, but found this system to be too complicated to be of use other than for distinguishing plesiosauroid and pliosauroid material.



All plesiosauroid specimens here studied show the same pattern of variation in shape of the posterior articular facet. Maximum width always exceeds minimum central height, and their average ('average centrum diameter') is maximal in mid-dorsal vertebrae. Cervical, sacral and anterior caudal centra have oval articular facets, whereas these become rounded in dorsals and posterior caudals. If significant interspecific variation of this pattern were to occur, it would affect to only a small extent the strength and possibly the mobility of the column.

In contrast, interspecific variation of relative centrum length occurs and is of taxonomic importance since, being cumulative, it may affect considerably the overall proportions of the animal. However, proportional length of the centrum also increases with ontogeny, and shows individual variation, different regions of the column having differently proportioned centra; this must be understood before interspecific variation may be distinguished and employed as a taxonomic character. If the midventral centrum length is calculated as a percentage of the posterior average centrum diameter, the resulting index ('vertebral length index') may be plotted against vertebral number and used to analyse and distinguish these different variants.

When the graph of vertebral length index against vertebral number is plotted for one individual, this illustrates the pattern of intraindividual variation. If the graphs of conspecific individuals of different ages are plotted together (as in Fig. 13), this tests the relationship of the pattern of intraindividual variation to ontogeny and at the same time permits an analysis of the ontogenetic increase in central proportional length for each region of the vertebral column.

In *C. eurymerus* (Fig. 13) the anterior cervicals are proportionally the longest vertebrae; yet centrum length never exceeds average centrum diameter, and they cannot be described as elongated. The centra become proportionally shorter towards the pectorals; then posterior to these they increase in proportional length and reach a peak at or just before the anterior sacrals. The index then falls abruptly, the posterior sacral and anterior caudals being proportionally the shortest vertebrae. The proportional length of the centrum again increases towards the tip of the tail. This pattern of intraindividual variation is exhibited by individuals of all growth categories. In Fig. 13 the centra of the 'juvenile' individual (R.2417) have proportional lengths approximately 20% (20 index points) less than the corresponding centra of the 'old adult' specimen (V.1091). The graph also illustrates the fact that the anterior cervicals of 'juvenile' individuals may have the same central proportions as posterior cervicals of 'old adults'.

In the present species the centra are always amphicoelous, and there is sometimes a small notochordal pit. The vertebrae of 'juveniles' are smoother and neater in general appearance than those of older individuals, which generally have a rough and more wrinkled surface.

RIBS. These have been described by Andrews (1910) and Smellie (1915). All ribs are single-headed. Cervical and caudal ribs become fused to the centra in 'adults', but pectoral, dorsal and sacral ribs always remain free.

The anterior cervical ribs develop an anterior flange halfway along their length, giving

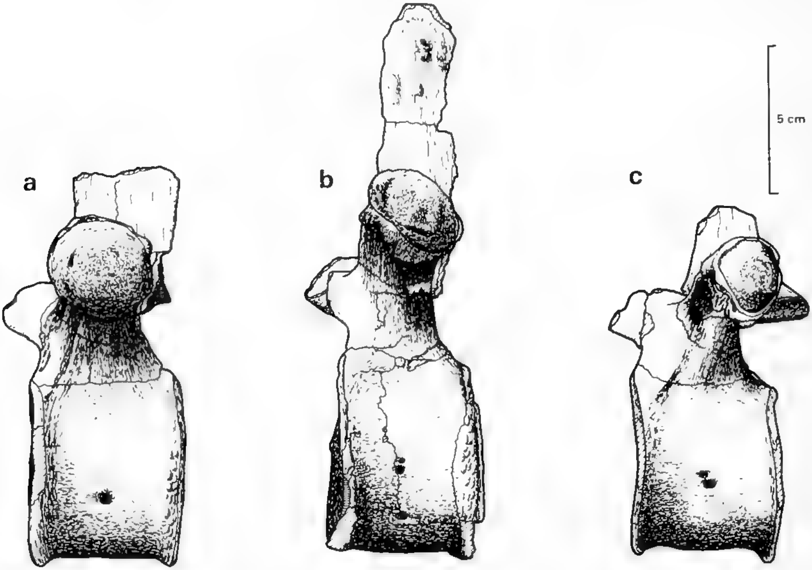


Fig. 11 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. a, eighth; b, fifteenth and c, twentieth dorsal vertebrae. Left lateral view.

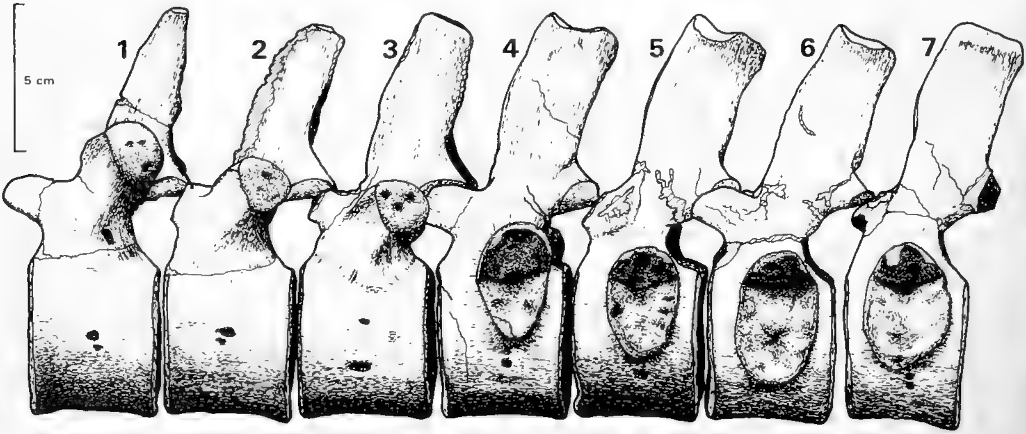


Fig. 12 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. 1–3, posterior dorsal vertebrae; 4–7, sacral vertebrae. Left lateral view.

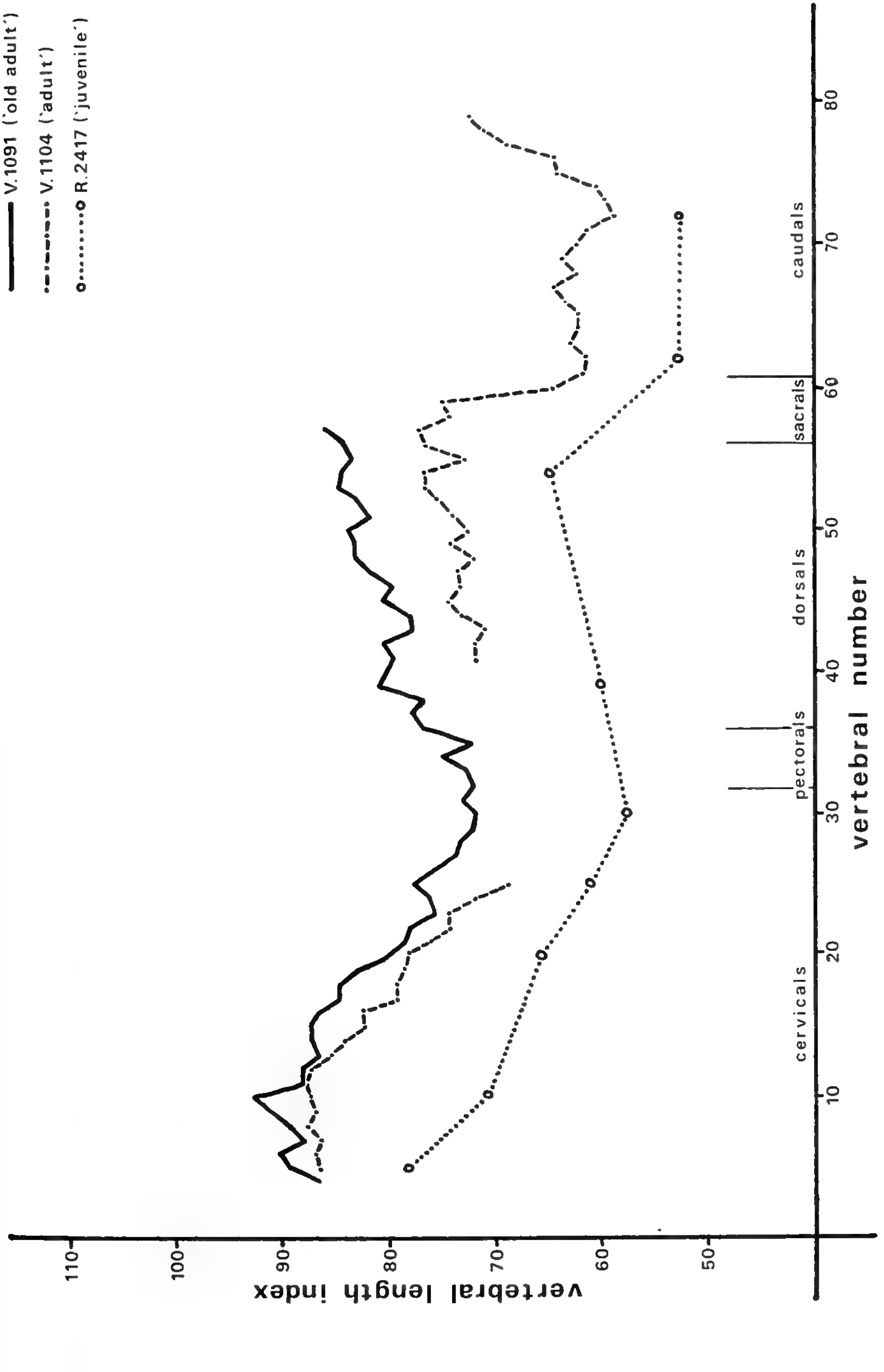


Fig. 13 *Cryptoclidus eurymerus* (Phillips). Graph of vertebral length index against vertebral number for three specimens of differing age, showing relationship of vertebral length index to topography and ontogeny. Measurements of R.2417 from Andrews (1910).

them an appearance which Andrews described as 'hatchet-shaped'. This flange is most prominent in 'old adults', but its development is irregular and may differ markedly in adjacent ribs.

Pectoral ribs are more elongated and curved than cervicals. Facets on the curved distal portions were observed in several specimens, and indicate that they overlapped one another to form a strengthened area for the attachment of the scapulae.

The anterodorsal and mid-dorsal ribs are long and curved, but posteriorly they become much shorter and straighter. The shape of the articulation with the transverse process changes with position on the column (see Fig. 11) and this enables ribs to be positioned with reasonable accuracy. When held in articulation with the respective transverse processes they can be spatially orientated; observations made using this approach have been taken into account in the drawing of the reconstructed skeleton (Fig. 10).

The sacral ribs are short and massive. On the anterior and posterior aspects of their dorsal ends they bear facets or depressions where they contacted and moved against adjacent sacral ribs. The 1st and 4th ribs are longer than the 2nd and 3rd, and they are orientated by their respective vertebrae so as to converge distally (Fig. 14). The shape of the dorsal end of the ilium matches the distal outline of the proximated sacral ribs, and it seems probable that the resulting joint was relatively mobile with respect to the vertebrae.

The caudal ribs are straight, dorsoventrally flattened, and orientated in a horizontal plane. They decrease in size posteriorly, and are absent from the terminal segments of the tail.

CHEVRONS. These paired bones are shorter than the corresponding caudal ribs, are slightly curved, and are orientated almost in a vertical plane. They are proportionally shorter in 'juveniles' and may fuse to the caudal centrum in 'old adults'. Chevrons are present from the 3rd caudal vertebra to within about four segments from the tip of the tail. Anterior to the 8th caudal vertebra their single heads articulate only with the facets on the posterior edge of the ventral aspect of the centrum; but posteriorly they articulate between vertebrae, and the 8th or 9th and subsequent caudal centra also bear anterior chevron facets.

PECTORAL GIRDLE. This has been described and figured by Andrews (1895*a*; 1910 : text-figs 87–89) and by Smellie (1915), and consists of the clavicles, scapulae and coracoids. An interclavicle is known only in specimen R.3538, in which it is a rudimentary splint of bone (Andrews 1910 : text-fig. 88).

The clavicles are comparatively large in 'juveniles', but grow at a much slower rate than the ventral rami of the scapulae, which come to meet superficial to them in 'adults' (Andrews 1895*a*). Their simplest shape is that of a right-angled triangle, with the right angle at the posteromedial corner, as in R.2616; more frequently the posterior border is concave, with the posterolateral corner drawn out into a short process as in R.2860, R.3538, R.3730 and V.1091. The two elements meet in the midline.

The 'adult' scapula is not distinctive, and has the usual triradiate structure. It consists of a strong vertically-orientated dorsal ramus, a short posterior ramus which forms the anterior half of the glenoid, and an expanded plate-like ventral ramus which meets its opposite superficial to the clavicles in the ventral midline and is prolonged posteriorly to meet the coracoids, thus forming a median keel-like scapulocoracoid bar. A rough prominence on the lateral border of the ventral ramus and prominent rugosities along the posterior margin of the dorsal ramus indicate the origin of powerful muscles at these sites.

The 'adult' coracoids are large plates which are thin in section except for the lateral margins and the anterior region between the glenoids. In the interglenoid region a horizontal bar is formed to resist the inward forces produced by the paddles in locomotion (Watson 1924, Robinson 1975). The lateral margins are thickened to form bars which curve posterolaterally and terminate as the posterior cornua. When developed fully in 'adults' and 'old adults' the distance between the tips of the two cornua is up to 40% wider than the distance across the posterior margins of the glenoids, a character which distinguishes the genus *Cryptoclidus* from its contemporaries. In 'juveniles' the coracoids cannot be distinguished since the cornua are incompletely formed.

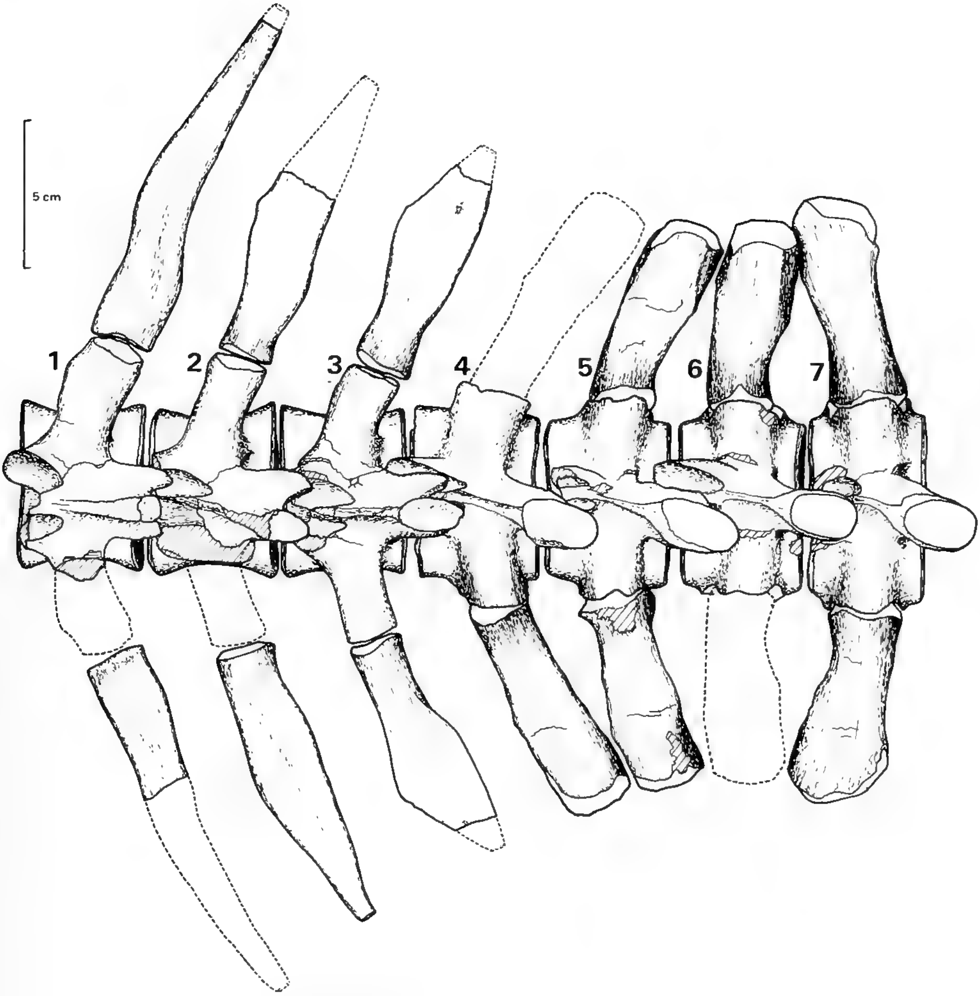


Fig. 14 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. 1–3, posterior dorsal vertebrae and ribs; 4–7, sacral vertebrae and ribs. Dorsal view.

The posterior margin of the coracoids does not ossify fully until the 'old adult' stage. The thin median part of the coracoids then extends backwards well behind the cornua, and on either side of this extension rounded notches are developed. The extension is best shown by specimen V.1807, but is beginning to develop in V.1091 (Smellie 1915 : text-fig. 7a) in which the position of the notches is apparent. It seems probable that the median posterior growth was visceral to the most anterior gastralia, which then curved upwards and inwards through the notches. In this way a fairly firm union between the pectoral girdle and the gastralia would be formed.

The glenoid is a large oval facet which is elongated anteroposteriorly and is only shallowly cupped. It is formed equally by the scapulae and coracoids. On the surrounding dorsal and ventral surfaces of these elements are numerous small foramina, the apertures of which face towards the glenoid. These are also found in abundance around the head of the humerus, and were associated with capsular ligaments. Comparison of the relatively small humeral head with the large glenoid indicates that the capsule was large, and the joint must have been very flexible. Elevation and depression of the humerus in the glenoid, as would occur with the sub-aqueous flight locomotion postulated by Robinson (1975), is osteologically unrestricted; whereas full rotation of the humerus to produce a rowing stroke as suggested by Watson (1924) is not possible, since the humeral tuberosity and anterior margin of the coracoid would coincide spatially.

In 'juvenile' individuals the clavicles appear relatively large and the ventral rami of the scapulae do not meet in the midline. In the 'adult' stage the ventral rami in the midline meet anterior processes of the coracoids to form the scapulocoracoid bar, but the six elements still remain separate. In 'old adults' progressive fusion of the pectoral girdle takes place, as is shown by specimens V.1091, V.1807 and R.2862. In all these specimens the coracoids are fused, and the scapulae are fused. In V.1091 the sutures between scapulae and coracoids in the scapulocoracoid bar are fusing, but those behind the glenoids remain open, and the single clavicle preserved with this specimen is quite free. In V.1807 all sutures between the scapulae and coracoids are fully fused; unfortunately the clavicles are not preserved, but their absence demonstrates that they were still free from the scapulae. Finally in R.2862 the clavicles are fused to each other and are also fused posteriorly onto the visceral surface of the ventral rami of the scapulae. Thus in this specimen the pectoral girdle is a single composite structure.

PELVIC GIRDLE. This has been described and figured adequately by Andrews (1896, 1910 : text-fig. 92), and is indistinguishable from the pelvic girdles of contemporary plesiosauroids. The pubes and ischia form expanded ventral plates which meet their opposites in the midline, and they were probably connected by a median cartilaginous bar which divided the obturator foramen; this bar is sometimes ossified in Cretaceous elasmosaurs (Welles 1962). The ischium is proportionally shorter than this element in pliosaurs. The ilium contacts the ischium only, and is reduced to a bar which ascends posteromedially from the acetabulum to the sacrum. The acetabulum has an elongated oval shape, and differs from the pectoral glenoid by facing posterolaterally rather than laterally.

GASTRALIA. In plesiosaurs the gastralia form a well-developed basket which functioned as a ventral carapace. In the present species this comprises eight complete rows of elongated cylindrical elements, each row consisting of a median element and three pairs of lateral elements (1st, 2nd and 3rd laterals). Posterior to these are a further two rows which lack the median element.

Median elements show bilateral symmetry and are the most massive. In dorsal view the left and right rami meet at an angle of about 165°, with the apex directed anteriorly. Laterally the anterior surface of each ramus forms a large concave facet into which fits the medial end of the 1st lateral element. In anterior or posterior view the median element is very slightly curved, giving the ventral surface of the animal a very gentle convex shape.

The 1st and 2nd lateral elements are closely similar. In dorsal view they appear twisted into a gentle S-shape as a result of excavations for the articulation of adjacent elements. The

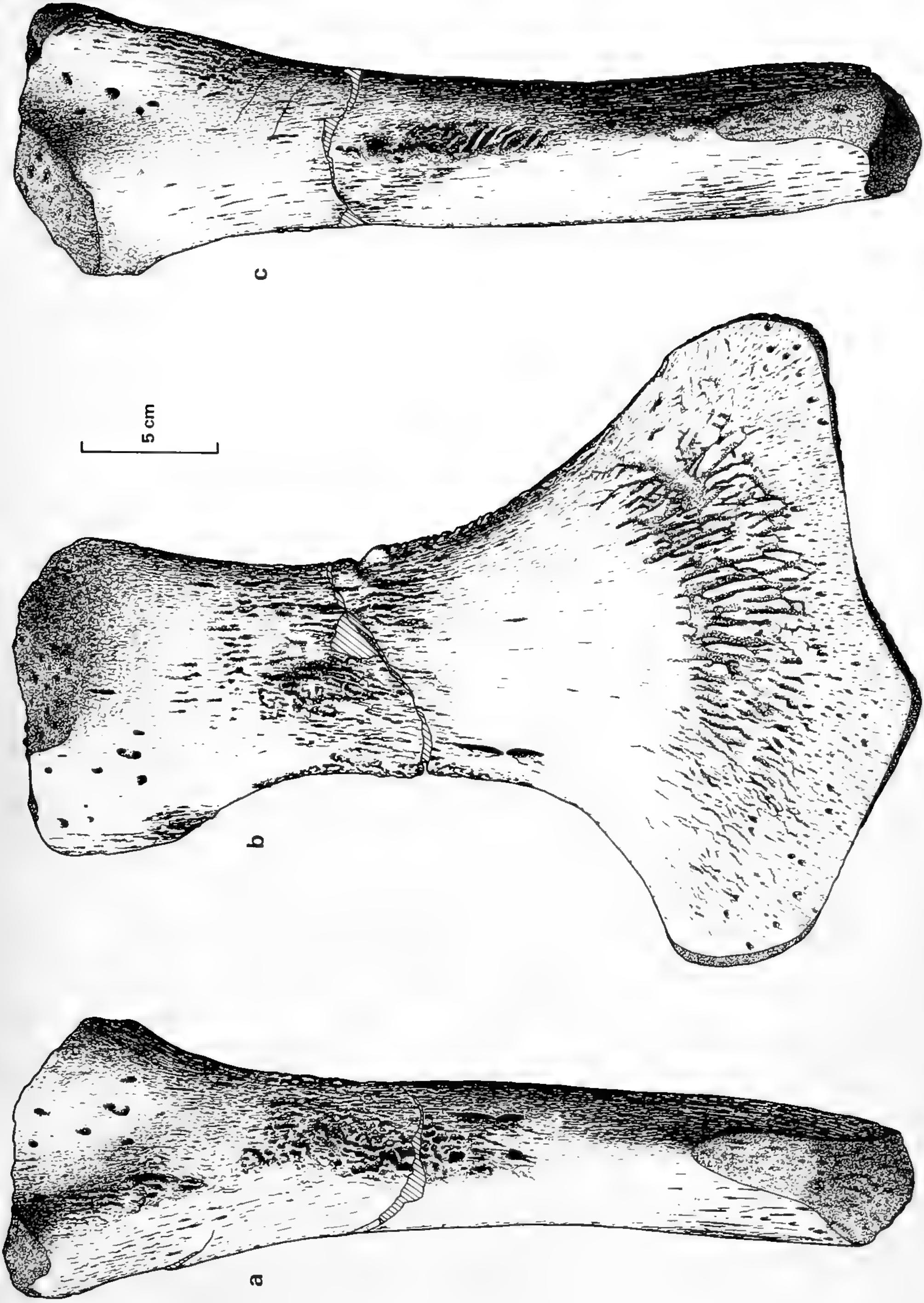


Fig. 15 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. Left humerus: a, posterior; b, ventral; c, anterior aspect.

1st lateral has a long posterior facet on the medial end for articulation with the median element, and the lateral end is hollowed on its anterior aspect for the reception of the 2nd lateral. Similarly, the 2nd lateral articulates posteromedially with the 1st lateral and anterolaterally with the 3rd lateral element. 1st and 2nd laterals may be orientated spatially by the form of their ends: the medial end is the most gently tapering and pointed, and the lateral end shows more curvature in the vertical plane. When 1st and 2nd laterals are compared, the 2nd laterals show more vertical curvature and their lateral ends are more tapered.

Third lateral elements show more vertical curvature than other elements, and are easily distinguished as there is only one posteromedial facet for articulation with the 2nd lateral. The outer end is somewhat flattened and bluntly terminated.

In specimen R.2862 the plastron has been preserved *in situ* because of an unusual concretion of the surrounding clay matrix (Andrews 1910 : text-fig. 86). The elements of each row are closely associated, and in addition the plastron is strengthened by the interlocking of the tips of gastralia of adjacent rows. Lying superficial to the anterior margins of the pubes are the incomplete 9th and 10th rows, the 9th lacking the median element and the 10th consisting only of a forked piece of bone representing the medial end of a lateral element. In V.1104 this forked gastralium is almost entire and was probably the only element in the row. It has a small anterior facet towards the lateral end, where it probably contacted the posterior surface of the 9th row laterals.

FORELIMB. This has been described and figured by Andrews (1910 : text-figs 90, 91A) and by Smellie (1915). In the 'adult' the humerus, radius and ulna are diagnostic of the species, whereas the distal parts of the paddle are indistinguishable from those of contemporary species. The length of the entire limb may exceed 1 m, and the overall span of the outstretched paddles may be 3 m in a specimen of overall length 4 m.

The 'adult' humerus (Figs 15, 16a, 17a, 17b) is characterized by a disproportionate enlargement of the anterodistal part which forms the radial facet. In 'juveniles' this character is insufficiently developed to be diagnostic.

Rugosities on the surface of the bone indicate the positions of muscle insertions. Prominent rugosities are present running axially down both the anterior and posterior borders of the humeral shaft (Figs 15a, 15c), and between these on the ventral surface is a prominent band of rugosities which is most developed midway anteroposteriorly and at about one third of the humeral length from the proximal end (Fig. 15b). The dorsal surface of the shaft (Fig. 16a) is smooth and without evidence of muscle attachments. It is not possible from a study of rugosities to distinguish and outline all the numerous muscle insertions shown in the reconstructed figures of the humerus of *Cryptoclidus* given by Robinson (1975) or of *Muraenosaurus* given by Watson (1924).

Rugosities are present on the prominent tuberosity of the humerus, being most evident on the anterior and posterior edges and the proximal part of the dorsal surface (Figs 15a, 15c and 16a). These probably mark the insertions of the rotator cuff musculature. In the 'old adult' the tuberosity may become separated from the head by the development of a strip of finished periosteal bone surface which divides the usually single proximal cartilaginous area (Fig. 17a) into two, as in V.1835.

On the dorsal and ventral surfaces of the distal end of the humerus there are extensive areas of shallow grooves and ridges, which become more prominent distally. In addition this area, together with the surfaces of all the epipodials and mesopodials, is marked by numerous small foramina, the apertures of which face peripherally. The distal paddle bones have roughened surfaces. All these various markings indicate the presence of a tough yet thin covering of ligaments and small muscles whose function was to strengthen and slightly stiffen the paddle, making it streamlined and only slightly flexible.

Even in small 'juveniles' the radius of this species has a characteristic shape, being greatly expanded proximally and anteriorly to match the expansion of the humerus. The bone thus has a sigmoid anterior outline which is convex proximally and concave distally, and by this

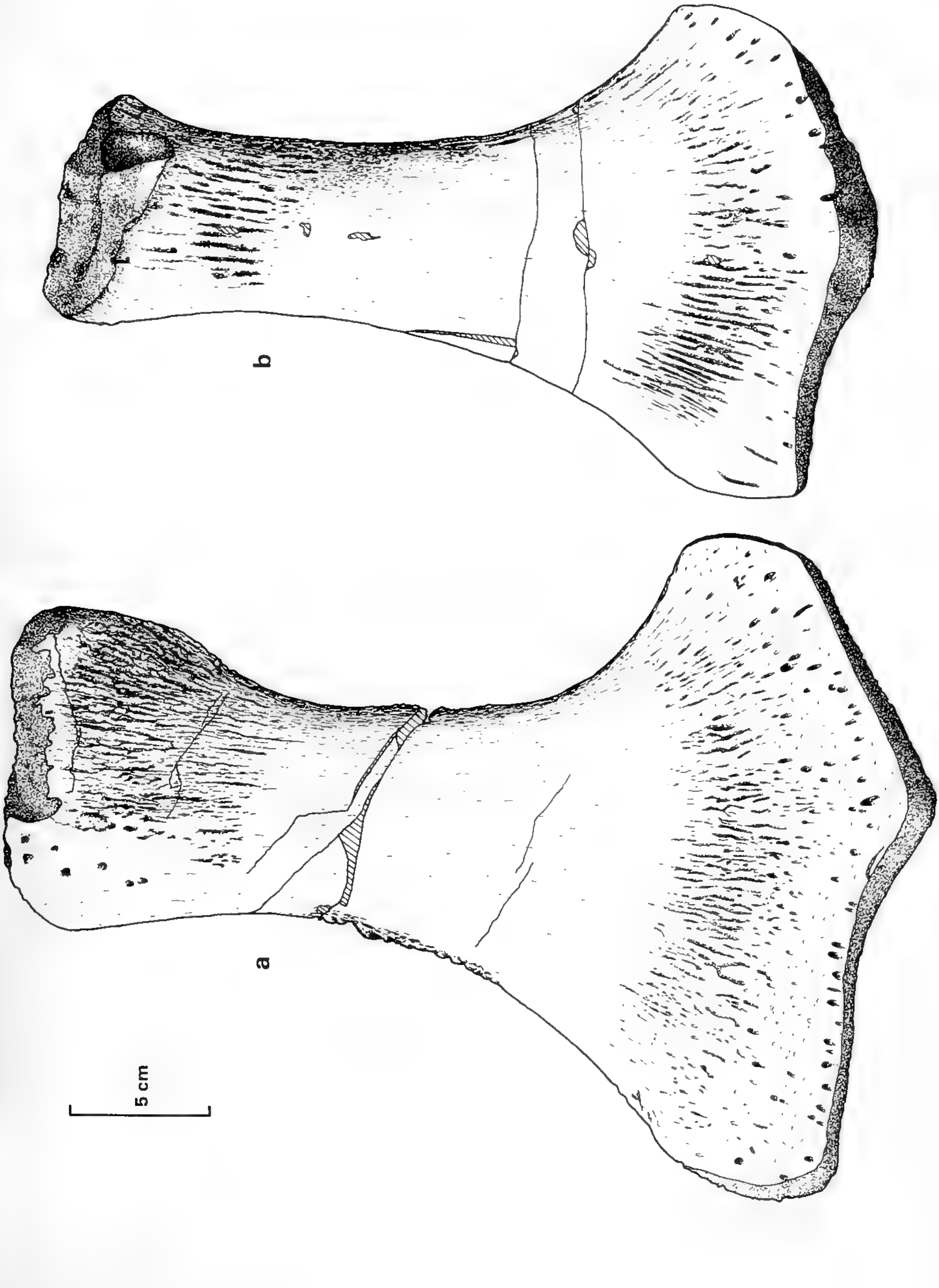


Fig. 16 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104: a, left humerus; b, left femur: dorsal aspects.

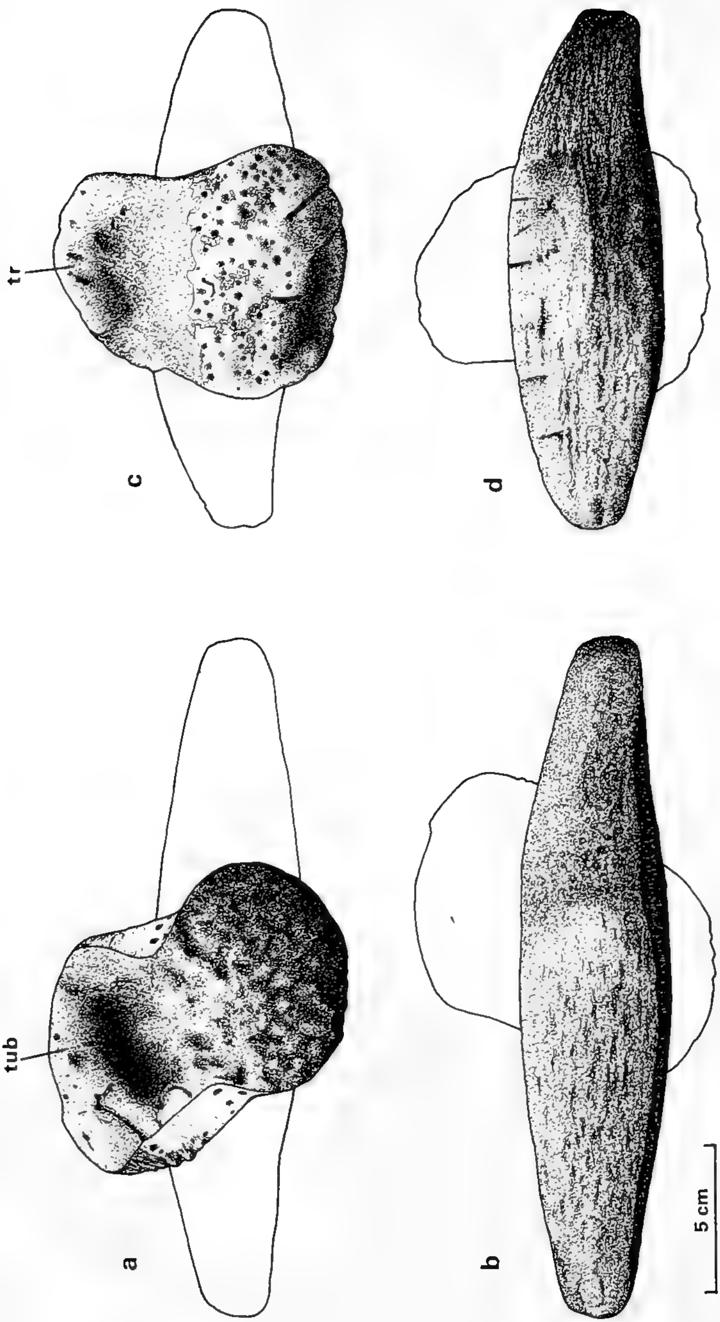


Fig. 17 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. Left humerus: a, proximal; b, distal aspect. Left femur: c, proximal; d, distal aspect. tub, tuberosity of humerus; tr, trochanter of femur.

character it may be distinguished from the radius of all contemporary species in which the anterior margin is concave throughout.

The ulna is generally very short and wide, its anteroposterior width being approximately twice its length. Occasionally, as in V.1091, there is evidence that it may ossify from two distinct centres.

The combined shape of the radius, ulna and distal end of the humerus results in the distal part of the paddle being orientated backwards at an angle of about 25° to the axis of the humeral shaft, with the characteristic expansions of the humerus and radius forming a prominent elbow in this species.

In all plesiosaurs the radius and ulna are separated by a gap or foramen, presumably for the passage of interosseous nerves and blood vessels. This foramen is usually evident at all stages of growth, but in the present species it is visible only when the advanced ossification of the 'old adult' stage is reached, as in V.1091, V.1809 and R.2862.

There are essentially six carpals (mesopodials), arranged in two rows of three, the proximal row consisting of the radiale, intermedium and ulnare. There is a considerable tendency to develop additional elements (accessory ossicles) which may be preaxial or postaxial, or both, and which may remain free or fuse to an adjacent epipodial or carpal. They usually result in asymmetry between left and right paddles of an individual, and are of no taxonomic significance.

The first (most anterior) metacarpal is flattened and resembles a carpal, whereas the second to fifth are cylindrical and phalangiform. The fifth metacarpal, characteristically for plesiosaurs later than the Lower Jurassic, is displaced proximally into the distal metacarpal row and articulates with the ulnare.

The exact number of phalanges in each digit cannot be stated since the paddles have usually suffered from post-mortem disturbance and in the past were generally collected without due attention being paid to their position. The longest digits (3rd and 4th) probably consist of about 15 phalanges, with the 2nd, 5th and 1st containing decreasingly fewer.

HINDLIMB. This has been described and figured by Andrews (1910). It is slightly shorter and a little more slender than the forelimb, and is very similar to the hindlimbs of contemporary species. The femur and tibia differ from the humerus and radius, but the fibula, tarsals, metatarsals and phalanges are indistinguishable from the corresponding elements of the forelimb.

In 'juveniles' the femur (Figs 16b, 17c, 17d, 18) may be closely similar to the humerus, but these elements are distinguished readily in the 'adult'. The distal anterior portion of the femur is not so expanded; the trochanter is not so well developed as the tuberosity of the humerus and does not form so prominent an angle at its posterodorsal margin; and the proximal portion of the femoral shaft is circular in section, whereas that of the humerus is oval, with definite anterior and posterior margins.

The rugosities marking muscle insertions on the proximal portion of the femur have the same general appearance as in the humerus, but differ in two details. The anterior marginal area of rugosities is less prominent than in the humerus, and is surrounded by an area of smooth bone (cf. Figs 18c and 15c); the rugosities on the ventral surface of the femoral shaft tend to be aggregated around two centres, one on either side of the ventral midline of the shaft, rather than around one as in the humerus (cf. Figs 18b and 15b). It is not possible from these rugosities to delimit the insertions of a large number of individual muscle blocks in the way suggested by Robinson (1975).

Surface evidence for the presence of capsular ligaments, rotator cuff musculature and the ligaments and small muscles of the paddle are exactly as in the pectoral girdle and limb. Several deep posterior foramina at the base of the distal expansion probably held the origins of large postaxial collateral ligaments. As in the humerus, the trochanter of 'old adults' may become separated from the head by the development of a strip of finished periosteal bone surface which divides the usually single cartilaginous area into two; this is seen in specimen V.1810.

The tibia is a rectangular, almost square bone, differing from the radius in that it lacks the proximal anterior expansion. A foramen between the tibia and fibula is evident only when the 'old adult' stage is reached, as in R.2616.

The left hindlimb of R.3703 (Andrews 1910 : text-fig. 93) is believed to be complete, and has a phalangeal formula of 3 : 9 : 13 : 13 : 12.

Note on the reconstruction

Fig. 10, pp. 268–9, represents a reconstructed lateral view of a swimming 'adult' individual of *Cryptoclidus eurymerus*, and was based so far as possible on the neotype specimen R.2860. The skull is a proportional reduction of Fig. 1. The outlines of the vertebrae were drawn from the frontispiece in Andrews (1910) (a photograph of the mounted skeleton) but with spacing to allow for intervertebral discs. The ribs (which were incorrectly 'hung' in order to fit the specimen into the narrow showcase) have been reorientated after study of specimens R.2860, V.1104 and V.1091 (the latter specimen has been mounted correctly in this respect). The girdles were drawn from R.2616 in which they are mounted accurately, and the gastralia were reconstructed from R.2860, R.2862 and V.1104.

The limbs were drawn largely from R.2860, with the full complement of phalanges of the forelimb taken from R.2864 (a specimen of *Muraenosaurus leedsii*). The orientation of the active paddles conforms with the theory of subaqueous flight locomotion of plesiosaurs discussed by Robinson (1975, 1977).

The body shape of this animal is flatter and wider than in the reconstruction of Andrews, and the neck is proportionally longer. There is little if any support for the argument presented by Robinson (1977 : fig. 12) and followed by Taylor (1981) that the vertebral column and the ventral skeletal elements (girdles and gastralia) were analogous in shape to an archer's bow and taut bow-string respectively; they are of almost equal length. However, the arrangement of the pectoral ribs, the close association of the gastralia with the girdles, and the structural arrangement of the sacrum and ilia strongly support her contention that these functioned as tensional force-transmitting elements. In the present reconstruction the hydrostatic pressure of the viscera assists in tensioning the ventral skeletal elements in a gently curving configuration, and the flattened body shape provides additional dorsoventral stabilization during subaqueous flight locomotion as in marine turtles.

Cryptoclidus richardsoni (Lydekker, 1889)

(Fig. 44b)

1889 *Cimoliosaurus richardsoni* Lydekker: 240, figs 73, 74 (mis-spelling of *Cimoliasaurus* Leidy, 1852).
1889 *Cimoliosaurus richardsoni* Lydekker; Mansel-Pleydell: 171, fig. 1; pl. 1.
1909 *Cryptoclidus richardsoni* (Lydekker) Bogolubov: 48.
1959 *Crytpocleidus richardsoni* (Lydekker); Delair: 66 (lapsus).
1959 *Cryptocleidus richardsoni* (Lydekker); Delair: 67.
1963 *Cryptocleidus richardsoni* (Lydekker); Persson: 24.

HOLOTYPE. Specimen R.6696, an almost complete postcranial skeleton which was discovered and collected by Nelson M. Richardson of Dorset and identified initially as *Plesiosaurus plicatus* Phillips (a *nomen dubium*) by Mansel-Pleydell (1888). The pectoral girdle was figured by Lydekker (1889) and the whole (then mounted) skeleton was described and figured by Mansel-Pleydell (1889). No other specimen is known.

TYPE LOCALITY AND HORIZON. A label with the holotype states that it was found 'in a brick-field between Montevideo House [near Weymouth] and Chickerell, at a depth of 30 feet'. Upper Jurassic, Callovian or Oxfordian Stage. From the Oxford Clay, which includes (Arkell 1933) the six ammonite zones from the zone of *Kosmoceras jason* to the zone of *Cardioceras cordatum*.

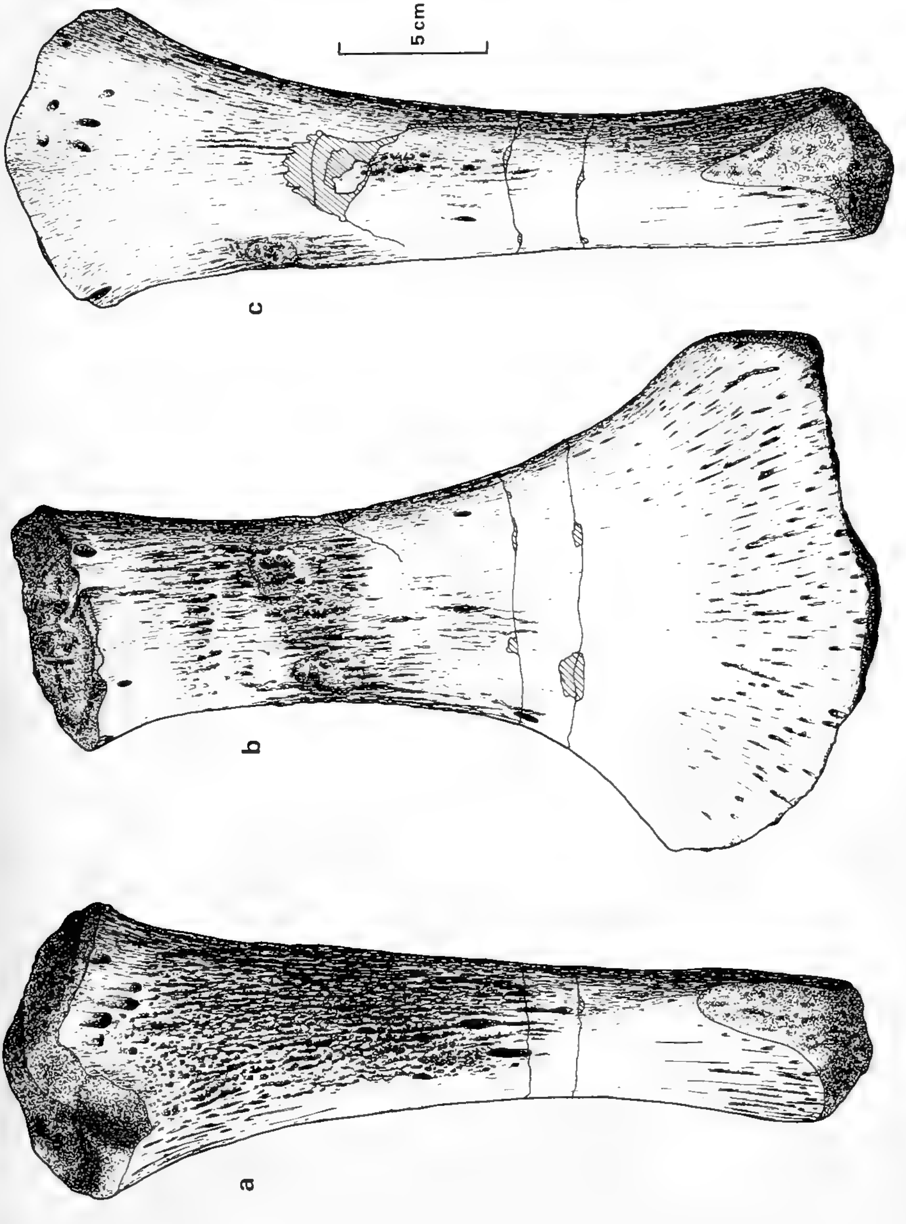


Fig. 18 *Cryptoclidus eurymerus* (Phillips), H.M.G. V.1104. Left femur: a, posterior; b, ventral; c, anterior aspect.

Diagnosis. Member of the genus *Cryptoclidus* in which the distal anterior portion of the humerus is not greatly expanded; the radius has a concave anterior border, and the humeral facet is only slightly longer than the facet for the radiale; the ulna is approximately square.

Description of material. Specimen R.6696 is an 'old adult', and resembles closely 'old adult' specimens of *C. eurymerus* in size, proportions, structure and degree of ossification. The skull and the right hindlimb are missing.

The vertebrae have been crushed, distorted and broken so that not all can be orientated or identified positively. They bear numbers in white paint in two series, but this is neither original nor reliable. Parts of 73 vertebrae are preserved and are here tentatively identified as 32 cervicals, 3 pectorals, 17 dorsals, 2 sacrals and 19 caudals. Three or four caudal centra are required to complete the tip of the tail. It is quite possible that 2 dorsals, 2 sacrals and a few caudals are missing; these would bring the vertebral count up to that of *C. eurymerus*. The neural arches and the cervical and caudal ribs are fused to the centra throughout, and an 'old adult' feature is the fusion of the chevrons to the caudal centra; all these are now largely broken away and missing.

The scapulocoracoid bar and the thin areas of the coracoids have been eroded away. The remaining parts of the pectoral girdle have been broken into several pieces which can be fitted together. Anteriorly the specimen has suffered from postmortem decay of the spongy bone such that the outer lamellar parts are separated. A piece of bone (numbered '7' in white paint) which has suffered in this way appears to be part of the right clavicle, and shows that it was large and triangular in outline as in *C. eurymerus*.

The scapulae and coracoids agree in structure with those of *C. eurymerus*, and are fused together (an 'old adult' feature). The posterior cornua of the coracoids are not quite complete to their tips, but on the right side are preserved parts of the lateral and posterior margins of this element. Extrapolation of these margins indicates that the cornua were developed to the same extent as in *C. eurymerus*.

The pubis and ischium do not differ from the corresponding elements in *C. eurymerus*, but the dorsal head of the ilium is smaller and more rounded.

The humerus lacks the anterodistal expansion characteristic of *C. eurymerus*. The distal expansion is produced very largely by posterior growth of the posterodistal part, and thus resembles closely that of *Muraenosaurus leedsii* (see Fig. 44). The radial facet is larger than that for the ulna. Both humeri have been slightly squashed so that the shaft appears a little too wide in dorsal aspect.

The femur is not quite so expanded distally as in *C. eurymerus*, and this expansion is greater posterior to the axis of the shaft.

The epipodials of both limbs resemble those of *Muraenosaurus leedsii*. A foramen is formed between each pair as in 'old adult' specimens of *C. eurymerus*. Numerous phalanges and fragments of ribs and gastralia are also preserved, and show no distinctive characters.

Genus ***MURAENOSAURUS*** Seeley, 1874

1874*a* *Muraenosaurus* Seeley: 197.
1909 *Picrocleidus* Andrews: 421 (subjective synonym).
1940 *Tremamesacleis* White: 463 (subjective-objective synonym).

Type species. *Muraenosaurus leedsii* Seeley, 1874.

Additional English species. *Muraenosaurus beloclis* Seeley, 1892.

Diagnosis. Plesiosauroids in which the teeth are ornamented by many longitudinal ridges; the dentary bears 19 to 22 teeth on each ramus; the premaxillae bear 5 teeth each, of which the 1st and 5th are small and the 2nd to 4th are large; the most anterior maxillary tooth (6th upper tooth) is small and the 8th and 9th upper teeth are large; the parietals form a sagittal crest; the quadrate overlaps the quadrate ramus of the pterygoid posteromedially; the paroccipital process of the exoccipital-opisthotic is relatively long and slender; the occipital condyle is ringed by a groove, and is formed from the basioccipital only; there are about 66 presacral vertebrae, of which usually 44 are cervical; the cervical vertebrae have relatively platycoelous centra, the length of which exceeds the height in anterior vertebrae, and exceeds or is approximately equal to the height in posterior vertebrae; the clavicles are reduced or absent; the interclavicle is developed and may be plate-like or reduced and lanceolate; the coracoids meet the scapulae in the midline in 'adults'; the width across the posterior cornua of the coracoids is about equal to or only just in excess of the interglenoid width in 'adults'; the elements of the pectoral girdle tend to fuse in old individuals; there are normally only two epipodials in the manus; a foramen is present between the epipodials even in 'juveniles'.

Muraenosaurus leedsii Seeley, 1874
(Figs 19–21, 43b, 44c)

1871 *Plesiosaurus plicatus* Phillips: 313, figs 118, 119 (*nomen dubium*).
1874*a* *Muraenosaurus leedsii* Seeley: 197; pl. 21.
1881 *Plesiosaurus leedsii* (Seeley) Whidborne: facing p. 480.
1888 *Plesiosaurus plicatus* Phillips; Lydekker: 351.
1888 *Muraenosaurus leedsi* 'Seeley'; Lydekker: 351 (incorrect subsequent spelling).
1889 *Cimoliosaurus durobrivensis* Lydekker: vii (mis-spelling of *Cimoliasaurus* Leidy, 1852).
1889 *Cimoliosaurus plicatus* (Phillips) Lydekker: 234.
1892 *Muraenosaurus platyclis* Seeley: 139, figs 6, 7.
1895*c* *Muraenosaurus plicatus* (Phillips) Andrews: 429, figs 1–3.
1909 *Muraenosaurus leedsi* 'Seeley'; Andrews: 418.
1909 *Muraenosaurus platyclis* Seeley; Andrews: 418.
1909 *Muraenosaurus durobrivensis* (Lydekker) Andrews: 418.
1910 *Muraenosaurus leedsi* 'Seeley'; Andrews: 120, text-figs 44, 59, 62, 63; pls 3, 4, 6 fig. 6.
1910 *Muraenosaurus durobrivensis* (Lydekker); Andrews: 127, text-figs 43, 45, 49–57, 60, 65, 67; pl. 5.
1910 *Muraenosaurus platyclis* Seeley; Andrews: 134, text-figs 48, 58, 68, 69; pl. 6 figs 1–5.
1940 *Muraenosaurus leedsi* 'Seeley'; White: 463.
1940 *Tremamesacleis platycleis* ('Seeley') White: 463, fig. 9d (mis-spelling).
1940 *Tremamesacleis durobrivensis* (Lydekker) White: 463.
1959 *Muraenosaurus leedsi* 'Seeley'; Delair: 60.
1959 *Muraenosaurus plicatus* (Phillips); Delair: 60.
1962 *Muraenosaurus leedsii* Seeley; Welles: 7; table 4.
1962 *Muraenosaurus leedsi* 'Seeley'; Welles: table 1.
1962 *Muraenosaurus durobrivensis* (Lydekker); Welles: tables 1, 4, 5.
1962 *Muraenosaurus platyclis* Seeley; Welles: 9; table 1.
1963 *Muraenosaurus leedsi* 'Seeley'; Persson: 24.
1963 *Muraenosaurus plicatus* (Phillips); Persson: 24.
1963 *Tremamesacleis platyclis* (Seeley); Persson: 24.
1963 *Tremamesacleis durobrivensis* (Lydekker); Persson: 24.
1964 *Muraenosaurus leedsi* 'Seeley'; Novozhilov: 321, figs 305–307.
1964 *Tremamesacleis platycleis* ('Seeley'); Novozhilov: fig. 308.

Holotype. The Leeds Collection specimen R.2421, an almost complete 'adult' postcranial skeleton. It was described initially by Seeley (1874*a*), and was described and figured extensively by Andrews (1910 : pl. 3 figs 1, 1a, 2, 2a, 3, 3a, 6; pl. 4 figs 1–10). Note that the teeth figured by Andrews (1910 : pl. 3 figs 4, 4a and 5), stated to belong with this specimen, are crocodilian and probably referable to the genus *Metriorhynchus.*

Type locality and horizon. An unspecified brick-pit near Peterborough, England; Upper Jurassic, Callovian Stage. From the lowest deposits of the Oxford Clay, which includes the zones of *Kosmoceras jason, Erymnoceras coronatum* and *Peltoceras athleta* (see Andrews 1910 : vii).

Diagnosis. Members of the genus *Muraenosaurus* in which the cervical ribs rarely develop a prominent anterior flange; the interclavicle is plate-like with a median anterior notch and a median posterior projection; in the manus the intermedium has a very small contact with the radius and a large articulation with the ulna; the overall length of the 'adult' is 4·5 to 5·2 metres.

Distribution and range. Diagnostic material is known only from the Peterborough area. Upper Jurassic, Callovian Stage only.

Referred specimens. Since remains of this species are comparatively abundant, only those specimens mentioned in the text are listed below; a fuller list is given elsewhere (Brown 1975). All specimens are from Oxford Clay in the Peterborough area.

R.2422 (Fig. 20). Incomplete 'old adult' skeleton. Neurocranium figured by Andrews (1910 : text-fig. 44).

R.2424. Incomplete 'juvenile' postcranial skeleton. Clavicle figured by Seeley (1892 : fig. 8).

R.2426. Incomplete 'old adult' postcranial skeleton. Interclavicle figured by Seeley (1892 : fig. 9).

R.2628 (Fig. 21d). Incomplete 'juvenile' postcranial skeleton partly figured by Andrews (1895*c* : figs 1–3; 1910 : text-figs 65, 67; pl. 5 figs 1–9, 11, 12). Holotype of *M. durobrivensis.*

R.2678 (Fig. 21a). Incomplete 'adult' skeleton partly figured by Seeley (1892 : fig. 7) and by Andrews (1910 : text-figs 48, 68, 69; pl. 6 figs 1–5) as the holotype of *M. platyclis.*

R.2861. Incomplete 'adult' skeleton partly figured by Andrews (1910 : text-figs 43, 45) as *M. durobrivensis.*

R.2863. Incomplete 'juvenile' skeleton.

R.2864. 'Adult' skeleton. Limbs figured by Andrews (1910 : text-figs 59, 63).

R.3704 (Fig. 21b). Pectoral girdle of an 'old adult'. Figured by Andrews (1910 : text-fig. 62; pl. 6 figs 6, 6a).

Discussion of synonymy

In 1871, Phillips described thirteen vertebrae from the Oxford Clay of St Clements, near Oxford, under the new name *Plesiosaurus plicatus.* These he distinguished from other vertebrae (variously named) by their greater relative length and their flat articular faces. Three years later, Seeley (1874*a*) described a postcranial skeleton then in the private collection of A. N. Leeds (now specimen R.2421), naming it *Muraenosaurus leedsii.* This specimen, which is an 'adult', has relatively elongate centra and an ossified scapulocoracoid bar. The dermal elements of the pectoral girdle are missing.

Lydekker (1888) visited the Leeds Collection, taking with him the type vertebrae of *P. plicatus* Phillips. He found that these were indistinguishable from vertebrae of the holotype of *M. leedsii*, whereupon he referred Seeley's specimen to *P. plicatus.* In 1889 this species was included in the genus *Cimoliasaurus.*

In 1889, Lydekker mentioned a further Leeds Collection specimen (now R.2428, which is a 'juvenile') for which he proposed the new name *Cimoliasaurus durobrivensis*; this he distinguished from *C. plicatus* on account of its slightly shorter vertebrae and the absence of an ossified scapulocoracoid bar. Andrews (1895*c*) examined several Leeds Collection specimens including the types of *C. durobrivensis* and *M. leedsii*, and found that the only differences were variations in size and in the extent of ossification. These he correctly ascribed to age differences (and perhaps sexual dimorphism) and referred all specimens to *Muraenosaurus plicatus.*

In 1892, Seeley described under the new name *M. platyclis* a further Leeds Collection specimen (now R.2678) which he distinguished from *M. beloclis* (herein a distinct species) and *M. (Cryptoclidus) platymerus* (herein a junior synonym of *Cryptoclidus eurymerus*) on the form of the dermal elements of the pectoral girdle. He did not attempt to distinguish the specimen from the types of *M. leedsii* and *C. durobrivensis* in which at that time no dermal pectoral elements had been recognized.

In 1909, Andrews reversed his earlier opinion by recognizing *M. leedsii, M. platyclis* and *C. durobrivensis* as discrete congeneric species. In 1910 he published distinguishing diagnoses, using as his criteria comparative size, comparative proportions and superficial features of the cervical vertebrae, proportions of the humerus and the structure of the dermal elements of the pectoral girdle. It is argued below that his characters involving comparative

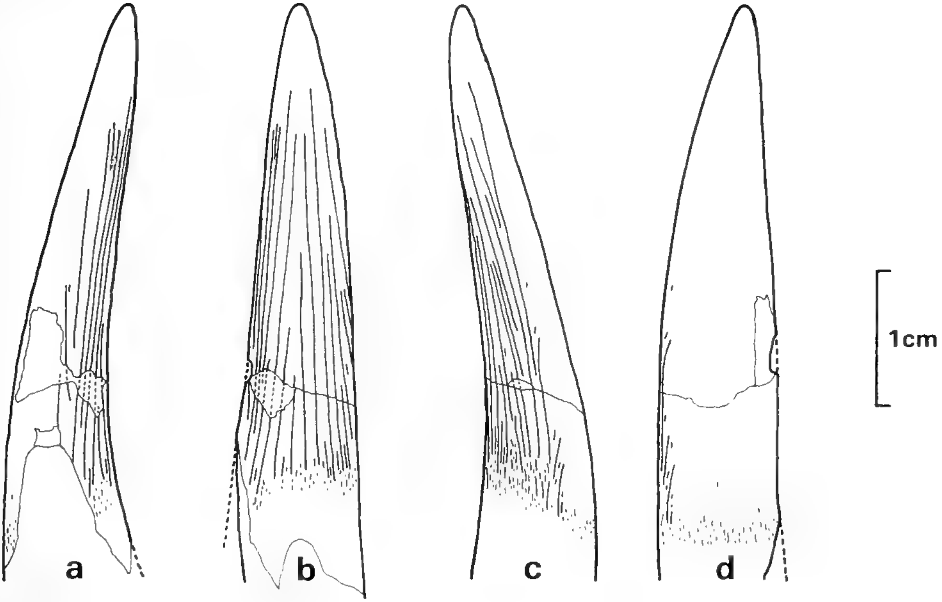


Fig. 19 *Muraenosaurus leedsii* Seeley, R.2861. Tooth showing ornamental ridges: a and c, axial; b, lingual; d, buccal aspect.

size and the proportions of vertebrae and humeri are of ontogenetic significance only. The recognition of an interclavicle associated with *M. durobrivensis* together with a reinterpretation of this element in *M. platyclis* shows the structure of the pectoral girdles to be the same.

Isolated vertebrae of the present species and of *M. beloclis* cannot be distinguished; the size differences between the species is inapplicable since posterior cervicals of *M. beloclis* (the smaller species) are considerably larger than anterior cervicals of *M. leedsii*. The type specimens of *P. plicatus* (cervical vertebrae) are therefore not diagnostic, and this name must be regarded as a *nomen dubium*. The earliest name applied to diagnostic material is *Muraenosaurus leedsii* Seeley, which is the valid name for this species.

Description of material

The description given by Andrews (1910) is extensive and largely accurate. He noted much variation in the size and ossification of individuals, interpreting this in terms of taxonomic characters by which he distinguished three species (see above). This variation is now reinterpreted as of solely ontogenetic significance.

The skull. Cranial material is preserved with several specimens, the most complete skull being that of R.2678. It was largely upon this skull that Andrews (1910 : text-figs 47, 48) based his description and reconstruction. Unfortunately this specimen has since been set in plaster for exhibition and could only be examined superficially.

JAWS AND TEETH. Parts of the jaws and teeth are preserved with specimens R.2421, R.2422, R.2427, R.2678, R.2861, R.2863 and R.2864. The teeth (Fig. 19) resemble those of Lower Jurassic plesiosauroids and Cretaceous elasmosaurs rather than those of *Cryptoclidus*. They are ornamented by numerous longitudinal ridges which are most prominent lingually, and in this aspect about 20 ridges are simultaneously visible. Several ridges may rise almost to the apex, but the prominent axial ridges characteristic of *Cryptoclidus* are lacking. The buccal aspect is ridged, though here the ridges are fewer especially in younger specimens, and may be confined largely to the basal half of the crown.

Very few whole teeth are preserved *in situ*; nevertheless, the relative sizes of teeth may be estimated from the diameter of empty sockets or the broken tooth bases. There are five premaxillary teeth, of which the 1st (most anterior) is very small; the left and right 1st sockets may be confluent, as in R.2421. The 2nd, 3rd and 4th upper teeth are large, and the 5th is usually much smaller. Behind the maxillo-premaxillary suture the 6th and 7th upper teeth (1st and 2nd maxillary teeth) are small and are of similar size to the 5th. Posterior to these the 8th and 9th upper teeth are very large, and the 10th is enlarged, but to a lesser extent. Thereafter the upper teeth decrease posteriorly forming a more or less evenly graded series. Complete maxillary toothrows are preserved in specimens R.2422 and R.2678, in both of which the maxilla bore 16 teeth, making a total of 21 teeth in the upper jaw. In the holotype (R.2421) the maxillae are less complete, the best being the right in which the most anterior 11 maxillary sockets are preserved.

The toothrow of the lower jaw is complete on at least one side in four specimens; the lower teeth number 19 in specimen R.2678, 20 in R.2422, 21 in R.2421, and in R.2861 there are 21 teeth on the left ramus and 22 on the right. In all cases the 1st (most anterior) lower tooth is of medium size, and the 2nd to 6th are very large, being equal in size to the upper 8th and 9th teeth. The lower 7th tooth is of medium size, about equalling the 1st, and the 8th is smaller. From here backwards the lower teeth form an even series, gradually decreasing in size.

The jaws of specimen R.2678 are virtually undistorted, and it is possible to superimpose them and to observe their occlusion. As in *Cryptoclidus*, the upper 1st teeth bit in advance of and between the lower 1st teeth, and from here backwards to the 7th teeth the upper and lower teeth interlocked in a one-to-one fashion. Behind the 7th teeth the width of the lower jaw decreases slightly whereas the width across the maxillae increases. This structural arrangement carries the sockets for the enlarged upper 8th and 9th teeth laterally such that they project completely clear of the lower teeth. Thus the upper 8th and 9th teeth form fangs which bit outside the smaller lower teeth, resulting in an overlapping occlusion at this point. Behind the fangs the bone outlines of the upper and lower jaws again coincide, and the more usual interlocking occlusion is resumed.

It may be noted that where Welles (1943, 1949, 1952, 1962) gives details of relative size of teeth in Cretaceous elasmosaurs, he indicates that the first one or two maxillary teeth are small and 'peg-like', and these are followed by two or three which are large and 'caniniform'; in the lower jaw the largest teeth are those beneath the premaxillae. It therefore appears that *Muraenosaurus* shows the same general pattern of dentition as that of Cretaceous elasmosaurs.

The structure of the lower jaw is essentially the same as in *Cryptoclidus*. Parts of the splenials (poorly known in that genus) are preserved in several specimens and are especially clear in R.2421, in which they fuse anteriorly in the symphysis, and extend posteriorly between the angular and surangular to reach the position of the 16th tooth socket. In specimen R.2678 the element labelled 'splenial' by Andrews (1910 : text-fig. 48) is not that element but is a part of the dentary.

NEUROCRANIUM. The general form of the braincase was described by Andrews (1910), and is very similar to that of *Cryptoclidus* except for the structure of the occipital condyle and the proportions of the paroccipital processes. The occipital condyle resembles that of *Tricleidus* and also of all Cretaceous elasmosaurs in that it is formed entirely from the basioccipital without any participation by the exoccipitals. The articular surface of the condyle is hemispherical, without a median pit, and is ringed by a constricting groove which separates it from the basioccipital-exoccipital sutures. This groove is developed to its fullest extent in 'old adults' (e.g. R.2422; see Andrews 1910 : text-fig. 44). The paroccipital process resembles *Tricleidus* closely, and is proportionally longer and slimmer than *Cryptoclidus* (Figs 2 & 23).

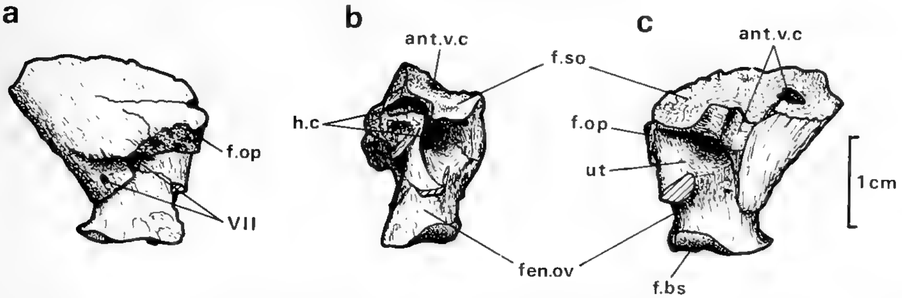


Fig. 20 *Muraenosaurus leedsii* Seeley, R.2422. Left prootic: a, lateral; b, posterior; c, medial aspect. ant.v.c, anterior vertical semicircular canal; f.bs, facet for basisphenoid; f.op, facet for opisthotic; VII, foramina for facial nerve. Other abbreviations as in Fig. 36, p 311.

In the 'old adult' specimen R.2422 the basioccipital and basisphenoid have largely fused, but a dorsal median pit, probably marking the embryonic basicranial fenestra, is present in this suture and was traced vertically downwards to a smaller median opening between these elements on the ventral surface.

The prootics (which are not known in *Cryptoclidus*) have not hitherto been described for any plesiosaur. Both are preserved with specimen R.2422, of which the left element (Fig. 20) is the most complete. This bone has been crushed and 'telescoped' somewhat, but its original shape may be perceived. It is essentially four-sided in lateral view, but with the lower posterior corner hollowed out into a short concave fifth side which forms the upper anterior margin of the fenestra ovalis. The ventral surface is a horizontal facet for union with the basisphenoid, and above the fenestra ovalis is a short and almost vertical facet for suture with the opisthotic; this is pierced by the horizontal semicircular canal. The supraoccipital facet faces upwards and backwards, and the rounded anterior margin of the prootic, the longest side, lies in the vertical plane.

The lateral surface of the prootic is convex and is marked by three small foramina, in a horizontal row, at least one of which must have been for the facial nerve. The medial surface is concave, and the posterior edge is hollowed for the utriculus which is shared equally with the opisthotic (Andrews, 1910 : text-fig. 45c, identified the opisthotic half of the utriculus cavity as the ampulla of the posterior semicircular canal). The prootic also houses the anterior half of the horizontal semicircular canal and the ventral half of the anterior vertical semicircular canal; these many be traced through the bones from the utriculus. There is no evidence of ossification around the cochlea, and so this must have been encased in cartilage.

Welles (1962), in his diagnosis of the 'suborder' Plesiosauria, stated that the fenestra ovalis and stapes are absent in the group. However, when the neurocranial elements of R.2422 are assembled the fenestra ovalis becomes at once apparent. It has the form of a short duct of circular section, its walls being formed in approximately equal thirds by the prootic, the opisthotic and the combined basioccipital and basisphenoid. There is no evidence for the existence of a stapes, but in view of the well-developed state of the fenestra ovalis its total absence may not be assumed.

Skull roof and palate. The remaining parts of the skull are less completely preserved in *Cryptoclidus* than in *Muraenosaurus leedsii*, but in so far as the former is known, they appear to differ only in details of the toothrow (described above). The postorbital bar, the jugal and the complete palate are known only for the present species, being preserved in R.2678. The palate was described fully and figured by Andrews (1910 : text-fig. 46a), with the postorbital bar and jugal receiving lesser notice but being included in the lateral reconstruction of the skull (1910 : text-fig. 46b).

In R.2678 the postfrontal elements are well preserved on both sides; they are orientated in an almost horizontal plane, and they sutured posterolaterally with the postorbitals. Only the left postorbital and jugal are preserved, and form part of a much crushed fragment which includes also the major part of the squamosal. The sutures of these latter elements are largely obscured by plaster or bad preservation and cannot be restored reliably. Moreover, the ventral part of the jugal, which Andrews (1910 : text-fig. 46b) united with the posterior end of the maxilla, is definitely not preserved.

In none of the plesiosauroid species here considered does the tapering posterior termination of the maxilla show any indications of a posterodorsal suture with the jugal such as was suggested by Andrews in his reconstruction of *Muraenosaurus leedsii.* Close inspection of specimen R.2678 indicates that the structural link between the jugal and the upper jaw was achieved not by direct union with the maxilla but instead through the ectopterygoid. This element is small but strongly constructed, and sutures anteriorly with the palatine, proximally with the pterygoid and distally with the posterior part of the medial margin of the maxilla. The dorsal surface of the left ectopterygoid is visible, and bore a thick and strong posterodorsal process, the broken section of which is oval with diameters of 1 cm (lateral axis) and 0·5 cm (anteroposterior axis). This process almost certainly provided the mechanical link to the temporal and postorbital bars.

Judged from the comparative length of the toothrow and the number of teeth, the snout of *M. leedsii* was proportionally shorter than in *Cryptoclidus* and slightly longer than *Tricleidus.* The jaws are distinguished further from the former and to a lesser extent from the latter genus by the great development of the upper 8th and 9th teeth. With the exception of these details, the shapes and proportions of the skull elements do not differ substantially from those of *Cryptoclidus* and *Tricleidus*, both of which are reconstructed here (Figs 1, 22). The overall length of the skull of 'adult' specimens is about 40 cm.

The postcranial skeleton. Postcranial material of this species is plentiful, and all growth stages are well represented. The description given by Andrews (1910) is extensive and largely accurate with regard to morphology, but differences in the osteological development of individuals are interpreted as of taxonomic rather than ontogenetic significance. Andrews took three individuals which differ in extent of osteological development (and which had been described previously by other authors, without cross-reference, as the type specimens of distinct species) and then attempted to group the remaining individuals around them. His diagnoses were based entirely upon characters of the postcranial skeleton, and he assigned all three species to the genus *Muraenosaurus.* The three type specimens are now interpreted as belonging to the single species *M. leedsii*, as follows:

(i) R.2428 (holotype of *Cimoliasaurus durobrivensis* Lydekker) has free neural arches and centra and an incompletely ossified pectoral girdle, and is therefore a 'juvenile'. By comparison with other 'juvenile' specimens (the most complete being R.2424 and R.2863) it is typical and representative of this growth stage, and is slightly smaller than the smallest 'adult' specimens.

(ii) R.2421 (holotype of *Muraenosaurus leedsii* Seeley) has the neural arches fused to the centra, and the elements of the pectoral girdle are fully formed yet still free. It is larger than all 'juvenile' forms but smaller than several other 'adult' specimens, and is therefore a relatively small 'adult'.

(iii) R.2678 (holotype of *M. platyclis* Seeley) is also an 'adult' and is one of the largest specimens, being about 10% larger than R.2421. By comparison with the two most complete 'old adult' specimens (in which the elements of the pectoral girdle are fused) it is slightly larger than R.3704 and is about the same size as R.2426 (misprinted R.2456 in Andrews 1910).

AXIAL SKELETON. A total of 66 presacral vertebrae are preserved in three specimens (R.2421, R.2863 and R.2864), and this appears to be the full complement for the species. As in *Cryptoclidus*, there is slight variation in the position of the pectoral vertebrae, there being 44 cervicals, 3 pectorals and 19 dorsals in R.2421 and R.2864, and 43 cervicals, 3 pectorals and 20 dorsals in R.2863. Four sacrals are preserved in specimens R.2421 and R.2863, and the tail is complete in R.2422 with a total of 24 caudal vertebrae.

In the holotype (R.2421) the vertebral column is complete from the atlas-axis to the 8th caudal, and the centra have been mounted with small intervening gaps amounting to rather less than the space required for intervertebral discs. The length of the series as mounted is 3·78 m; by comparison with R.2422 the missing portion of the tail would have measured approximately 0·5 m and the length of the skull of R.2421 is 0·37 m. Thus the total overall length of this small 'adult' specimen was at least 4·65 m. Comparative measurements of R.2678, the largest individual, indicate an approximate overall length of 5·2 m for this specimen.

As in *Cryptoclidus*, the centrum width is always greater than the height, but in *M. leedsii* the length of the cervical centra always exceeds the height and generally also the width in the most anterior cervicals, giving a vertebral length index in excess of 100%. In 'juveniles' the index reaches 105% in the anterior third of the neck, and in 'adults' an index of 110% or slightly more is commonly reached in the region of the 10th to 15th cervical vertebrae. Proportional length of the centra decreases posteriorly, the index dropping to about 80% at the pectorals. Thereafter, the dorsal vertebrae are very slightly longer and the caudals proportionally slightly shorter than in *Cryptoclidus.*

The neck is proportionally almost twice as long as in *Cryptoclidus.* This length is achieved both by development of a larger number of vertebrae and by the proportional lengthening of each centrum. Conversely, the tail of *M. leedsii* is proportionally slightly shorter since there are fewer caudal vertebrae (about 24 compared with about 30) and these are each proportionally shorter.

The articular faces of the vertebrae differ in shape from those of *Cryptoclidus*, and have been described as 'flat' rather than 'concave' (Andrews 1910). These terms are misleading, since vertebrae of *M. leedsii* become increasingly concave with age, and the real difference lies in the outline of a longitudinal section across the articular face. In *Cryptoclidus* this is a double sigmoid curve, the centre of the face being concave whilst the borders are convex and continue fairly smoothly into the sides of the centrum. In *M. leedsii*, on the other hand, the whole outline is concave or a very open V-shape, the borders of the face forming an abrupt angle with the centrum sides.

In 'adults' a longitudinal crest is developed on the sides of the cervical centra especially in the anterior half of the neck, and lies midway between the facets or sutures for the rib and the neural arch. Such a crest is absent in the shorter-necked forms *Cryptoclidus* and *Tricleidus* but is found in Cretaceous elasmosaurs (Welles 1943, 1952, 1962) and perhaps functioned to assist the neck muscles and ligaments in their role of supporting a very long neck when held out of the water. It is generally absent in 'juveniles' in which the neck is not so long.

In 'juveniles' and smaller 'adults' the centra are ornamented with small, closely-spaced longitudinal ridges, which occur in bands on the sides and ventral surface immediately adjacent to the articular faces. Andrews (1910) used the term 'plications' for this ornament, which is shown clearly in his plate 5, figs 2 and 3. In the largest 'adults' and 'old adults' the plications become further ossified into bands of irregular rugosities, losing the neat appearance which is characteristic of younger specimens. The ornament is strongly developed in the cervical vertebrae and continues backwards onto the dorsals with decreasing prominence, eventually to disappear before the sacrals. It was presumably associated with the insertion of longitudinal ligaments.

Andrews used comparative size, the proportional length of the centrum, the presence of a longitudinal ridge on cervicals and the development of plications as characters in the diagnoses of his three species. The differences which he noted relate entirely to the differences in the relative age and ossification of the three type specimens.

The ribs and chevrons do not differ in any respect from those of *Cryptoclidus*. The development of an anterior flange on the cervical ribs is irregular and is seldom strongly developed; in this respect the present species appears to differ from *M. beloclis*.

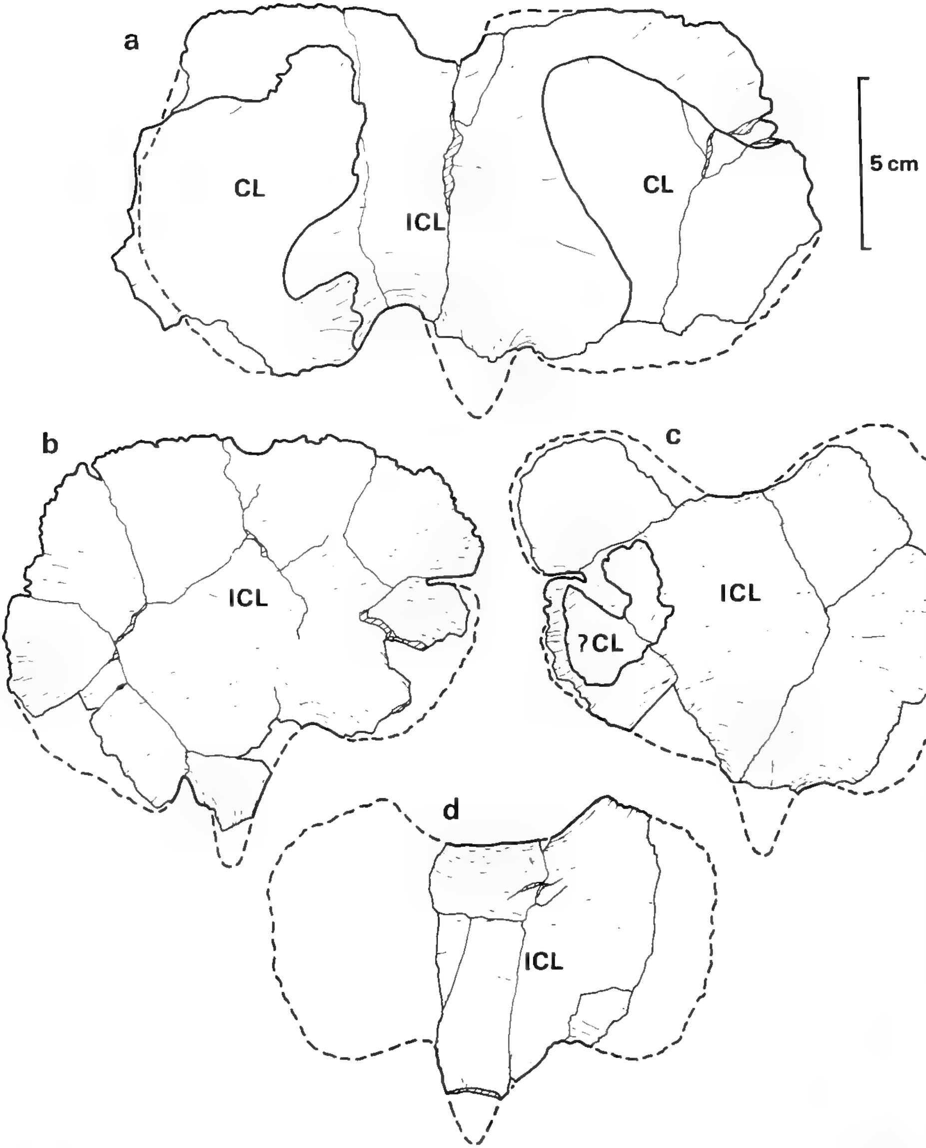


Fig. 21 *Muraenosaurus leedsii* Seeley, interclavicles and clavicles in dorsal view: a, R.2678; b, R.3704; c, R.2426; d, R.2428. Missing outlines restored with broken lines. CL, clavicle; ICL, interclavicle.

The isolated gastralial elements are identical to those of *Cryptoclidus*, suggesting a similar arrangement, but the number of rows in the complete basket is not known. Specimens of the forked posterior element which is present in *C. eurymerus* have not been seen in any other species.

APPENDICULAR SKELETON. The pelvic girdle and the distal portions of the limbs (mesopodials and phalanges) are indistinguishable from those of *Cryptoclidus*; whereas the pectoral girdle differs in several important respects, and the propodials and epipodials are also distinct.

The scapulae resemble those of *Cryptoclidus* except for the structure of the ventral rami. In 'juvenile' specimens (e.g. R.2428; see Andrews 1910 : text-fig. 67) these first contact just in advance of the developing scapulocoracoid bar, and anteriorly are separated by a V-shaped space. Ossification in a posterior direction then produces the scapulocoracoid bar typifying the 'adult' stage, as in *Cryptoclidus*; but anteriorly the ventral rami fail to contact along their entire length, being instead separated by an elongated U-shaped notch which persists in all 'adult' and 'old adult' specimens. Posteriorly this notch forms part of a foramen (interscapular foramen of Andrews) which is enclosed by the scapulae and the overlying interclavicle.

The coracoids differ from those of *Cryptoclidus* in the development of the posterior cornua. In the 'adult' and 'old adult' these are equal to or only just in excess of the interglenoid width, and they are therefore much less prominent than in that genus (cf. Figs 43a and 43b, p. 331).

The interclavicle is well developed in the present species. Andrews (1910) was confused about its structure, and used supposed differences of structure in the diagnoses of his three species. He correctly described the element in his '*M. leedsi*' from specimen R.3704 (1910 : text-fig. 62; pl. 6 figs 6, 6a), but in his description of *M. durobrivensis* he described and figured as an interclavicle a non-plesiosaurian bone accidentally associated with specimen R.2863 (1910 : pl. 5 fig. 10); this in turn led him to misinterpret the structure of the interclavicle of R.2678 (holotype of *M. platyclis*). Further to this confusion, and relying on the accuracy of Andrews' descriptions, White (1940) produced a classification of plesiosaurs based entirely on characters of the pectoral girdle, in which he made *M. platyclis* the type species of a new genus *Tremamesacleis* and founded the new family Tremamesacleididae for its reception.

The interclavicle is now known from four good specimens (see Fig. 21) and a further fragment is preserved with R.2427. These show considerable variation in size, but the basic structure is the same. The element forms an irregular oval plate, the longest axis being lateral, the ventral surface convex and the dorsal surface flat or concave. The bone is thickest in the centre, and towards the edges it becomes very thin with a ragged margin. In the anterior margin of all specimens there is a median notch, of varying size, bordering which the bone is smooth and rounded. Posteriorly there is developed a median peg-like process which is frequently triangular in section, the apex of the triangle being ventral. On either side of this process are small clefts or notches which are irregular in size and frequently asymmetrical, as in R.2678 (Andrews overlooked the broken base of the posterior process in this specimen, and interpreted the notch to its left as a median notch). The interclavicle lay dorsal to the ventral rami of the scapulae, and both elements bear rugosities marking the insertions of connecting ligaments.

The clavicles are best preserved in specimen R.2424 (see Seeley 1892 : fig. 8). They are irregularly triradiate in form, and from their shape it is evident that they did not meet in a median symphysis, but instead sutured squamously with the interclavicle (not preserved with that specimen). Parts of the clavicles are also preserved with R.2678 but here they are much thinner and have fused to the dorsal surface of the interclavicle (Fig. 21a). They are broken posterolaterally and their original outline cannot be reconstructed, but the shape of the preserved anterior portions conforms with these parts in R.2424. A fragmentary scale of bone compressed onto the left dorsal surface of the interclavicle of R.2426 (Fig. 21c) may possibly represent another clavicle.

There is a tendency towards fusion of the elements of the pectoral girdle in 'old adults', as in *Cryptoclidus*. In specimen R.2426 the left and right coracoids are fused, and in R.3704 the coracoids and scapulae are fused in the midline, and are also fused to each other at the glenoid. In both specimens this fusion involves only the ventral parts of the sutures, which remain open dorsally. In neither of these 'old adult' specimens is the interclavicle involved in fusion with the scapulae.

The humerus is indistinguishable (amongst English forms) from that of *Cryptoclidus richardsoni*, and also from that of *M. beloclis* except by superior size (Fig. 44). It thereby differs appreciably from the humerus of *C. eurymerus*. Likewise, the radius and ulna differ from these elements in *C. eurymerus* and resemble closely those of *C. richardsoni* and many Cretaceous plesiosauroids. The radius is nearly square in shape, the facet for the ulna being rather shorter than the anterior border and the facets for the humerus and radiale. Between the ulnal and radialial facets is a very small oblique facet for the intermedium; this serves to distinguish the element from the radius of *M. beloclis*, in which the intermedial facet is much larger and is equal to the intermedial facet of the ulna.

The ulna is a pentagonal bone, the longest side being the humeral facet. The thin posterior edge usually remains cartilage-covered; a small pisiform element articulates with it in the left forelimb of R.2864 (Andrews 1910 : text-fig. 63). Distally there are two facets of equal size, one facing obliquely posteriorly for articulation with the ulnare, the second facing slightly to the anterior for union with the intermedium. The anterior margin of the ulna meets the radius proximally and distally; interposed between these elements is a foramen which, unlike this structure in *Cryptoclidus*, is detectable in even the youngest individuals.

The femur of 'adults' is indistinguishable from that of *C. richardsoni* and closely similar to that of *C. eurymerus*. In 'old adults' the tibia and fibula are identical to those of *Cryptoclidus*, but in younger specimens they may be distinguished since the interposed foramen is always discernible.

The distal elements of the limbs are indistinguishable from those of *Cryptoclidus*. The left limbs of R.2864 are almost complete, and have phalangeal formulae of 6 : 12 : 14 : 13 : 8 (forelimb) and 6 : 13 : 15 : 13 : 9 (hindlimb). The hindlimb is very slightly smaller than the forelimb, as is usual in plesiosauroids. The 5th metacarpals have moved proximally only half their length into the distal carpal rows; this represents an intermediate stage between Lower Jurassic plesiosaurs (such as *Plesiosaurus dolichodeirus*) in which they are entirely level with the metacarpals, and Cretaceous forms in which these elements lie entirely in the distal carpal row.

Muraenosaurus beloclis Seeley, 1892
(Figs 43c, 44d)

1892 *Muraenosaurus beloclis* Seeley: 143, figs 10–12.
1909 *Picrocleidus beloclis* (Seeley) Andrews: 421, fig. 3.
1910 *Picrocleidus beloclis* (Seeley); Andrews: 140, fig. 70; pl. 7.
1962 *Picrocleidus beloclis* (Seeley); Welles: 9; table 1.
1963 *Picrocleidus beloclis* (Seeley); Persson: 24.
1964 *Picrocleidus beloclis* (Seeley); Novozhilov: fig. 305.

HOLOTYPE. The Leeds Collection specimen R.1965, an incomplete postcranial skeleton consisting of 6 cervical and 2 dorsal vertebrae, fragments of ribs, the pectoral girdle, both humeri and ulnae and one radius. It was described and figured by Seeley (1892 : figs 10–12) and Andrews (1910 : text-fig. 70; pl. 7 figs 2–4; note that pl. 7 fig. 1, which represents part of a lower jaw, was labelled incorrectly as associated with R.1965 but was described correctly in the text as belonging with R.3698).

TYPE LOCALITY AND HORIZON. An unspecified brick-pit near Peterborough, England; Upper

Jurassic, Callovian Stage. From the lowest deposits of the Oxford Clay, which includes the ammonite zones of *Kosmoceras jason, Erymnoceras coronatum* and *Peltoceras athleta* (see Andrews 1910 : vii).

DIAGNOSIS. Members of the genus *Muraenosaurus* in which the anterior cervical ribs normally develop a very prominent anterior flange; the interclavicle is small and lanceolate; in the manus the intermedium articulates equally with the radius and the ulna; the overall length of the 'adult' is about 2·5 m.

DISTRIBUTION AND RANGE. Diagnostic material is known only from the type locality. Upper Jurassic, Callovian Stage only.

REFERRED SPECIMENS. All the following are from the Oxford Clay of the Peterborough area.

R.2739. Incomplete 'adult' skeleton. Neurocranium figured by Andrews (1910 : text-fig. 71) as *Picrocleidus*, sp.

R.3698. Incomplete 'adult' skeleton. Lower jaw fragment figured by Andrews (1910 : pl. 7 fig. 1) as *Picrocleidus beloclis*.

R.2429. Incomplete postcranial skeleton of an 'old adult'.

DESCRIPTION OF MATERIAL. Andrews (1910) believed the holotype and the three referred specimens to represent two species of a distinct genus *Picrocleidus* (the second species was not named). However, similarities in the structure of the occipital condyle, tooth ornament, vertebral structure and numbers, development of the elements of the pectoral girdle and the form of the forelimb indicate that *M. beloclis* and *M. leedsii* are congeneric. They may be distinguished only by the four characters listed in the diagnosis.

The skull is very poorly known. A fragment of the right lower jaw ramus of R.3698 contains the broken stumps of several teeth, from which it is clear that their ornament consisted of many longitudinal ridges occurring all round the tooth. The basioccipital is preserved in R.3698 and R.2739 and forms the entire condyle, which is ringed by a groove. Fragments of an exoccipital-opisthotic, a quadrate and a squamosal are preserved with R.3698, and also part of the basisphenoid and parasphenoid with R.2739, these differing only in their smaller size from the corresponding elements of *M. leedsii*.

The most complete vertebral column is that of R.3698. Including the fused atlas-axis, 37 cervical vertebrae are preserved, and the most posterior of these is by no means the last as the facets for the cervical ribs have not begun to rise up the side of the centrum. It is therefore possible that the neck was of similar construction to that of *M. leedsii* in which 43 or 44 cervical vertebrae are found. In specimen R.2429 a sequence of ten vertebrae are preserved, these being 6 posterior cervicals, 3 pectorals and the most anterior dorsal. The dorsal vertebrae are inadequately known, and the largest number of sacrals preserved in a single specimen is two (in R.2739). In specimen R.3698 the tail is complete from the last sacral to the penultimate caudal, there being 22 caudal centra preserved. Posterior chevron facets begin on the 5th caudal and anterior facets on the 6th. In the posterior caudal vertebrae a sizeable projection develops ventrolaterally on each side of the centrum. These coexist with chevron facets and therefore cannot be fused chevrons. Such projections have never been noted in other plesiosaurs and may perhaps be an oddity of the specimen rather than typical of this species.

The overall length of the 'adult' (about 2·5 m) was calculated by comparing the length of the first 37 cervical vertebrae of specimen R.3698 with those of R.2421 (the holotype of *M. leedsii*, estimated overall length 4·65 m), and assuming similar vertebral numbers and proportions in the two species.

The vertebrae resemble those of *M. leedsii* in the shape of the articular facets, the development of the lateral longitudinal crest on anterior cervicals, and in the proportional length of the centra; in R.3698 the vertebral length index again rises over 100% in anterior cervicals, and reaches a maximum of 106% at the 16th cervical vertebra.

The development of a prominent flange to the anterior cervical ribs is most evident in specimen R.3698 and is seen to a lesser extent in R.2739. Lack of anterior cervical vertebrae and ribs with the holotype (R.1965) makes the taxonomic importance of this character somewhat dubious; it was used by Andrews (1910) and is included with reservations in the present diagnosis.

The scapulae and coracoids are preserved with specimens R.1965 and R.2429. The scapulae are indistinguishable (except by their smaller size) from those of *M. leedsii*, with an identical development of the interscapular foramen, and the coracoids differ only in being proportionally rather narrower midway between the glenoids and the cornua. Specimen R.2429 is an 'old adult' in which these elements are partially fused with their opposites in the midline, and fused to each other at the glenoid.

The interclavicle is preserved only in R.1965 (Fig. 43c), and at first sight it appears to differ widely from that of *M. leedsii*; it is lanceolate and triangular in section, with the apex of the triangle ventral. However, its wider anterior end is marked by a median notch with smooth edges, whereas the posterior end is developed into a stout and cylindrical process which may have terminated in cartilage; this structure could easily be derived from that of *M. leedsii* by the loss of the thin plate-like lateral sections of that species.

The humerus, femur, tibia and fibula are indistinguishable in shape from those of *M. leedsii*, but the radius is distinctive since it has a considerably larger facet for the intermedium and consequently a more elongated shape. Posteriorly it meets the ulna, enclosing between these elements the usual foramen. In R.3698 the ulna resembles closely the typical form of this element in *M. leedsii*, whereas in R.1965 it has a small facet facing obliquely posteriorly and proximally for articulation with an accessory ossicle. The distal parts of the limbs of *M. beloclis* are not known.

Genus ***TRICLEIDUS*** Andrews, 1909

TYPE SPECIES. *Tricleidus seeleyi* Andrews, 1909.

DIAGNOSIS. As for type species (monotypic genus).

Tricleidus seeleyi Andrews, 1909

(Figs 22–25, 43d, 44e)

1909 *Tricleidus seeleyi* Andrews: 419, figs 1, 2.
1910 *Tricleidus seeleyi* Andrews; Andrews: 149, text-figs 72–77; pl. 8.
1962 *Tricleidus seeleyi* Andrews; Welles: table 1.
1963 *Tricleidus seeleyi* Andrews; Persson: 24.
1964 *Tricleidus seeley* 'Andrews'; Novozhilov: fig. 305 (lapsus).

HOLOTYPE. The Leeds Collection specimen R.3539, consisting of disarticulated elements representing most of the skull together with about half the postcranial skeleton. It was described and figured by Andrews (1909 : figs 1, 2; 1910 : text-figs 72–77; pl. 8).

TYPE LOCALITY AND HORIZON. 'From the pit worked by Messrs Hicks and Gardner immediately across the lane from Woodston Lodge' (Leeds 1956), at Fletton, near Peterborough, England. Upper Jurassic, Callovian Stage. From the lowest deposits of the Oxford Clay, which includes the zones of *Kosmoceras jason*, *Erymnoceras coronatum* and *Peltoceras athleta* (see Andrews 1910 : vii).

DIAGNOSIS. Plesiosauroids in which the teeth are ornamented by many longitudinal ridges; the dentary bears 17 teeth on each ramus; the premaxillae bear 5 teeth each, of which the 1st and 5th are small and the 2nd to 4th are large; the most anterior maxillary tooth (6th upper tooth) is small and the 8th and 9th upper teeth are large; the parietals form a sagittal crest; the quadrate overlaps the quadrate ramus of the pterygoid posteromedially; the paroccipital process of the exoccipital-opisthotic is relatively long and slender; the pterygoid bears a process for union with the basisphenoid; the occipital condyle is ringed by a groove, and is formed from the basioccipital only; there are at least 26 and possibly slightly more cervical vertebrae with relatively amphicoelous centra, the length of which only slightly exceeds the height (but never the width) in the most anterior vertebrae; the clavicles are triangular and well developed, and lie visceral to the interclavicle which separates them in the midline; the interclavicle is well developed and plate-like; the coracoids meet the scapulae in the midline in 'adults'; the width across the posterior cornua of the coracoids exceeds the interglenoid width in 'adults'; the humerus is not greatly expanded distally, and articulates with four epipodials.

Distribution and range. Diagnostic material is known only from the Peterborough area. Upper Jurassic, Callovian Stage, type horizon only.

Referred specimens. Both from the Oxford Clay of the Peterborough area.
N.M.W. 19.96.G7 (Figs 25b, 25d). The pectoral girdle and humeri of an 'adult'.
H.M.G. V.1800. The right humerus of an 'adult'.

Description of material

The skull. Cranial material is preserved only with the holotype (R.3539). Andrews (1910) described and figured the neurocranium extensively, but the remainder of the skull received brief attention and no reconstruction was attempted.

The skull of R.3539 is disarticulated, and the separate parts are almost entirely without distortion or crushing. In consequence, the elements may be placed together and their combined shape deduced with the minimum of restoration. The skull reconstructions (Figs 22, 23) were produced by combining a large number of scale photographs of isolated or grouped elements. The dorsal midline is preserved from the parietals to the tip of the snout; a further anteroposterior line is preserved from the maxillae through the vomers and pterygoids to the right quadrate; the interlock of the teeth can be observed directly by superimposing the jaws; the lower jaw is entire, and only the absence of the supraoccipital prevents this from being linked back to the parietals.

The toothrow of the premaxillae and maxillae resembles closely that of *Muraenosaurus*: each premaxilla bears 5 tooth sockets, the 2nd to 4th being much larger than the 1st and 5th; and the maxillae bear sockets for 15 teeth each (6th to 20th upper teeth), that for the 6th upper tooth being small and those for the 8th and 9th teeth being large. The border of the external naris is fully preserved in the left premaxilla, but the posterior edge of that element is missing. Here the bone is extremely thin, and a series of ridges and grooves on the ventral surface of the premaxilla, also seen on the dorsal surface of the anterior part of the frontal, suggests an extensive area of squamous overlap. The internal surface of the premaxilla is divided by a ridge which runs from the tip of the snout to the midline of the maxillo-premaxillary suture and which indicates the line of union with the vomers.

In the left maxilla are preserved a part of the margin of the external naris and all the orbital margin of that element. As in *Cryptoclidus* and *Muraenosaurus*, there is no evidence for the presence of a lacrimal or prefrontal (a part of the frontal remains *in situ* suturing with the antorbital process), and likewise no evidence for suture of the posterior part of the maxilla with the jugal. There may therefore have been a link to the jugal through the ectopterygoid as is suggested above for *M. leedsii.*

The frontals and parietals resemble closely these elements in *Cryptoclidus* and *Muraenosaurus.* Most of the right frontal is preserved, and remains sutured posteriorly to the parietals; its broken anterior end retains a part of the border of the naris and fits exactly against a similarly broken edge on the posterior part of the right premaxilla, thus permitting the reconstruction of the dorsal midline. The pineal foramen lies almost entirely between the fused parietals, being just contacted by the frontals. The parietals form a high sagittal crest, the vertex of which is now broken away; the arrangement of the parietal-squamosal sutures shown in Fig. 22 was assumed to be as in *Cryptoclidus* and *Muraenosaurus.* The suture between the parietals, obliterated by fusion on the skull roof, is still visible on the occipital surface.

The left squamosal is almost complete, and was described and figured as two pieces by

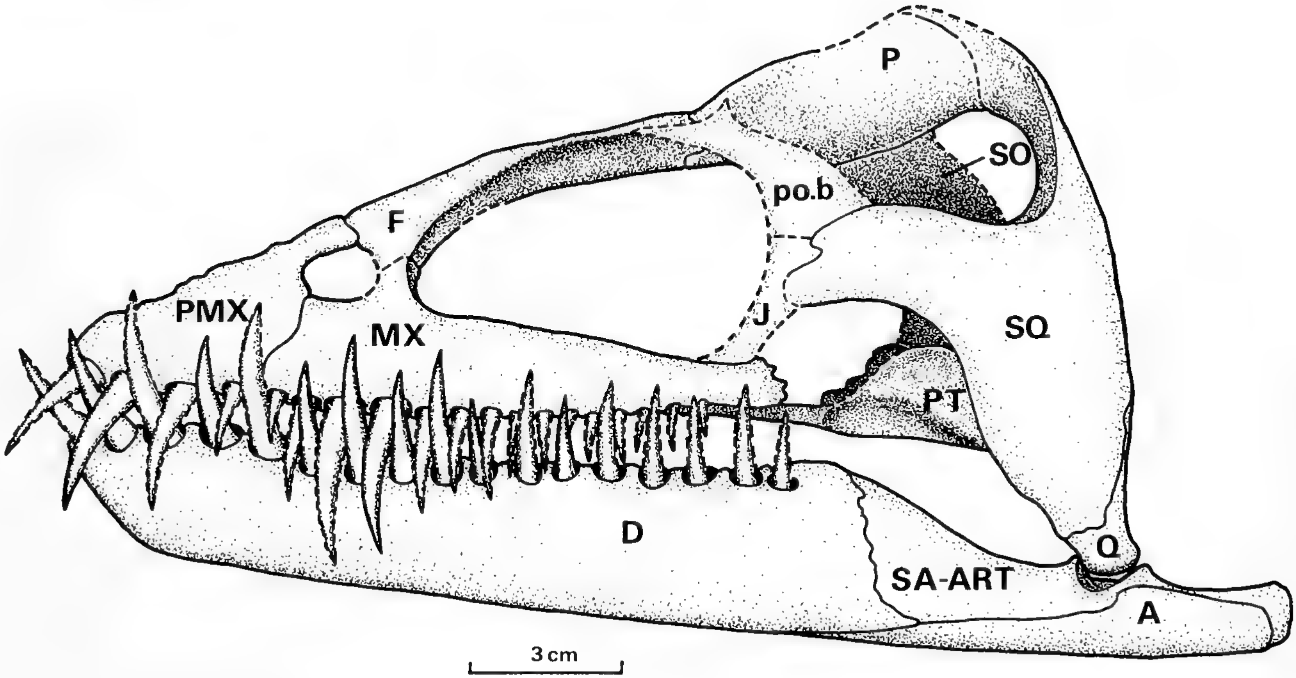


Fig. 22 *Tricleidus seeleyi* Andrews, reconstruction of skull of holotype R.3539 in lateral view. Abbreviations as in Fig. 1, p. 259.

Andrews (1910 : text-fig. 75), who labelled these sq. and sq′. The pieces, however, were separated by a natural break, not a suture, and this has now been repaired. The element is triradiate, and resembles closely that of *Cryptoclidus* and *Muraenosaurus*. No parts of the jugal or postorbital bar are preserved.

Andrews (1910) described the 'left' quadrate as consisting of two elements or fractions which he labelled q. and q′. (1910 : text-fig. 75), and the 'right' was said to be of similar construction. He suggested that either the elements were symmetrically fractured or his q. represented the quadratojugal and his q′. the true quadrate. Upon dissolving the glue binding the portions of each quadrate the adjoining surfaces were found to be covered in part with matrix. This was removed with an 'Airbrasive' machine, and the four fragments were then fitted together exactly, but with q′. belonging to the right quadrate and q. to the left.

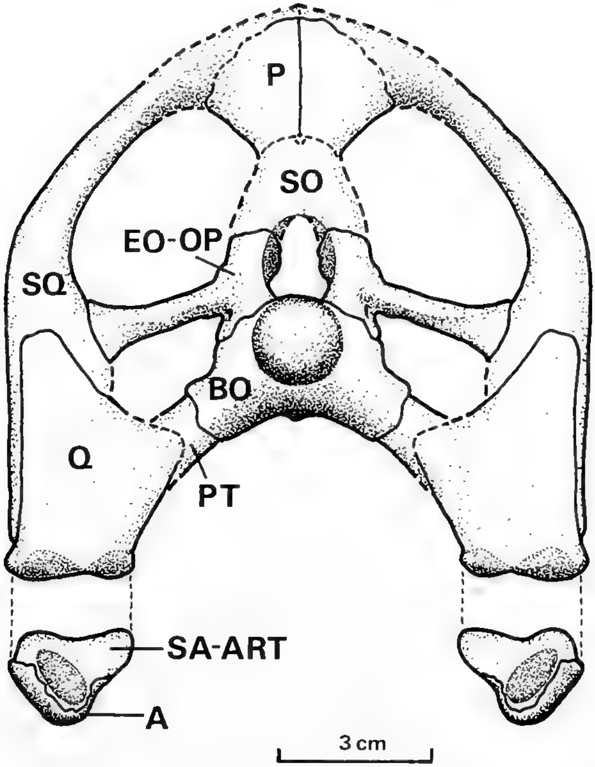


Fig. 23 *Tricleidus seeleyi* Andrews, reconstruction of skull of holotype R.3539 in occipital view. Abbreviations as in Fig. 2, p. 259.

As now assembled, the quadrates are closely similar to those of *Cryptoclidus* and *Muraenosaurus*. Pits and ridges on the anteromedial surface of the right quadrate and the posterior surface of the pterygoid show that these elements were arranged with the pterygoid in advance of the quadrate, the latter obscuring the posterior tip of the pterygoid in occipital view (Fig. 23). This arrangement is also found in *Muraenosaurus* as witnessed by the structure of the pterygoids, but differs from *Kimmerosaurus* (p. 309). The arrangement in *Cryptoclidus* is not known.

The form of the pterygoids was described accurately and figured by Andrews (1910 : text-fig. 74). They differ from all other described plesiosauroid pterygoids in the development of a

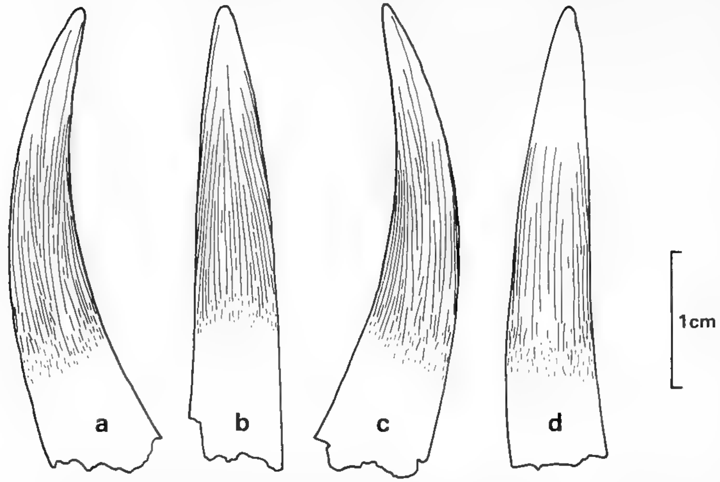


Fig. 24 *Tricleidus seeleyi* Andrews, tooth of holotype R.3539 showing ornamental ridges: a and c, axial; b, lingual; d, buccal aspect.

special process for articulation with the basisphenoid (labelled pt.f′. by Andrews). They also differ from the pterygoids of *Muraenosaurus* in that there is no prolonged process for contact with the ectopterygoid, and it must be assumed that the missing ectopterygoid in the present species was proportionally larger than in that genus.

The vomers are fused to form a single median element which has the shape of an arrowhead and resembles closely that of *Muraenosaurus*. Welles (1952 : 98) misidentified this bone as the nasals, which are not known as separate elements in Jurassic plesiosaurs.

The preserved elements of the braincase were described and figured fully by Andrews (1910). The form of the occipital condyle and the paroccipital processes are as in *Muraenosaurus*, and thereby differ from those of *Cryptoclidus* (cf. Figs 23 and 2).

The lower jaw (Andrews 1910 : pl. 8) differs from that of *Muraenosaurus* (which it otherwise resembles closely) by having only 17 tooth sockets on each ramus. Of these the 2nd to 8th are the largest, but the size does not greatly diminish posteriorly, and the most posterior may be described as of medium size. The fine state of preservation permits the orientation of the teeth to be assessed; this was just as in *C. eurymerus*, specimen R.8621 (pp. 262–3).

The right ramus of the lower jaw contains *in situ* eight complete teeth, and in addition several isolated teeth are preserved (Fig. 24). These are ornamented with many longitudinal ridges which, as in *Muraenosaurus*, are found all round the teeth and especially on their lingual sides.

By comparison with *Cryptoclidus* (Fig. 1) the skull of *Tricleidus* (Fig. 22) is relatively short in the snout region, relatively high posteriorly, and has fewer teeth. It therefore resembles more closely reconstructions by Welles (1943, 1952) of the skulls of Cretaceous elasmosaurs.

The postcranial skeleton. The axial skeleton was described and figured by Andrews (1910). It is incompletely known, and is preserved only in the holotype (R.3539). Leeds (1956) recorded that his father found this specimen disarticulated and scattered over an unusually large area, and that although he took great pains to collect as much as possible, especially of the skull, inevitably some parts were lost. It follows that the apparently complete series of 26 cervical and 3 pectoral vertebrae may in fact be incomplete, with several cervicals lost at random from the column such that no obvious gaps appear in the sequence. Five dorsals and

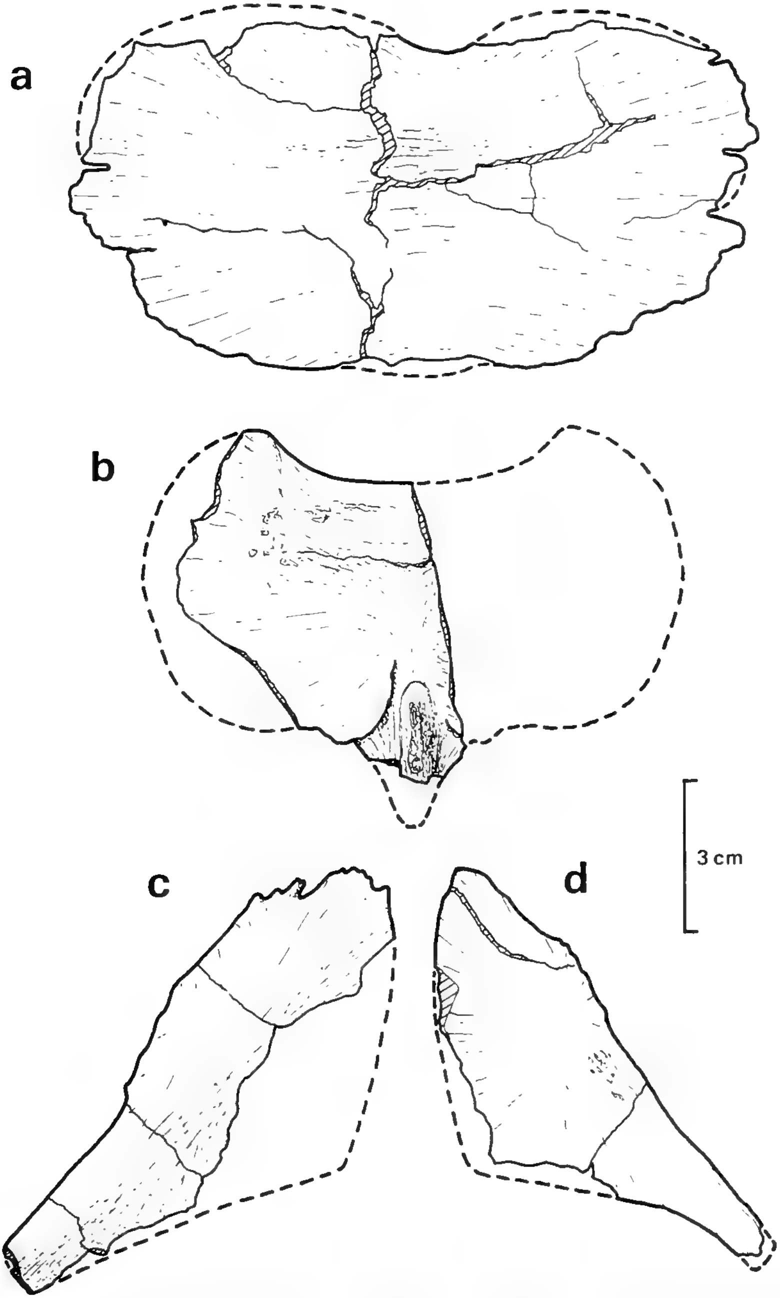


Fig. 25 *Tricleidus seeleyi* Andrews: a, interclavicle of holotype R.3539 in dorsal view; b, interclavicle of N.M.W. 19.96.G7 in ventral view; c, left clavicle of holotype R.3539 in dorsal view; d, left clavicle of N.M.W. 19.96.G7 in ventral view. Missing outlines restored with broken lines.

two caudals are also preserved, together with a few ribs and gastralia. All these parts are indistinguishable from those of 'adult' specimens of *Cryptoclidus.*

The distinctive pectoral girdle (Fig. 43d) is preserved both in R.3539 (Andrews 1909 : fig. 1; 1910 : text-fig. 76; pl. 8) and in N.M.W. 19.96.G7 (newly identified). The scapulae resemble those of *Muraenosaurus*; the ventral rami remain separated anteriorly, but the gap between them is V-shaped rather than U-shaped as in that genus. The structure of the coracoids is midway between those of *Cryptoclidus* and *Muraenosaurus*, the posterior cornua extending laterally beyond the level of the glenoids, but not to the extent seen in *Cryptoclidus.*

The dermal elements of the pectoral girdle are well developed. In R.3539 (Fig. 25a) the interclavicle is very large and plate-like, but most of its area is only thin. There is a small anterior notch as in *Muraenosaurus*, and the central part is strengthened by a T-shaped thickened area consisting of an anterior transverse bar and a median longitudinal bar. A small portion of the interclavicle of 19.96.G7 is preserved (Fig. 25b) and includes part of the anterior notch (which is wider than in R.3539) and part of the median thickening. In this specimen the interclavicle was structurally similar to that of *M. leedsii*, the median longitudinal thickening continuing posteriorly as a peg which was triangular in section. The interclavicle of 19.96.G7 was evidently smaller than that of R.3539, indicating considerable variation of the element as in *Muraenosaurus.*

The clavicles are elongated bones with a thickened anterolateral axis: the left clavicle of 19.96.G7 is almost complete and enables the form of the entire element to be restored (Fig. 25d). The posterolateral corner consists of the thickened part of the bone only, and is roughened ventrally for attachment to the scapula. The thickened axis continues anteromedially, and on the posteromedial side and to a lesser extent the anterolateral side there are developed thin expansions, such that the final shape of the bone is triangular with a concave posterior border. The ventral surface is almost flat, the dorsal surface convex. The preserved parts of the clavicles of R.3539 (Fig. 25c) agree closely in form with those of 19.96.G7.

The humerus (Fig. 44e) is relatively short and stout, and has a characteristic shape because it articulates distally with four elements. The radial facet is the largest, and faces obliquely anterodistally. The ulnal facet is distally orientated, and behind this is a small facet for the pisiform which faces obliquely posterodistally. The fourth facet, for a postaxial accessory ossicle, is about as large as the ulnal facet and faces posteriorly. The rugosities for muscle insertion are arranged as in *Cryptoclidus* and are strongly developed, this giving the bone an especially well-ossified appearance.

Distal elements of the forelimb are preserved only with R.3539, and were described and figured in articulation with the humerus by Andrews (1910 : text-fig. 77). The distal carpal row contains three small carpals together with the fifth metacarpal, which has shifted proximally for almost its entire length, as in *Cryptoclidus.* The phalanges are not known.

Of the pelvic girdle only the pubis is known, associated with R.3539. Except for its slightly smaller size, this is indistinguishable from pubes of *C. eurymerus* and *M. leedsii.*

The hind limb is represented only in R.3539 by the femur, tibia, fibula, intermedium and tibiale, which were described and figured by Andrews (1910 : pl. 8). These elements are indistinguishable from those of *Muraenosaurus* and are of the same size as in *M. beloclis.* The femur is slightly longer than the humerus and has a slimmer and less massive appearance.

Genus ***KIMMEROSAURUS*** nov.

NAME. From the stratigraphical horizon of the type species (Kimmeridgian Stage, Kimmeridge Clay).

TYPE SPECIES. *Kimmerosaurus langhami* n. sp.

DIAGNOSIS. As for the type species (monotypic genus).

Kimmerosaurus langhami sp. nov.
(Figs 26–39)

NAME. In honour of R. A. Langham, Esq., of Reading, Berkshire, who found the holotype skull in 1967 and presented it to the British Museum (Natural History) the following year.

HOLOTYPE. R.8431, a disarticulated incomplete skull consisting of the frontals, parietals, squamosals and pterygoids; the right postfrontal, postorbital and fused exoccipital-opisthotic; the left quadrate; the basioccipital; the right angular and fused surangular-articular; the dentary and 11 isolated teeth.

TYPE LOCALITY AND HORIZON. Endcombe Bay (also known as Egmont Bay), on the coast about 5 km south of Corfe Castle, Dorset, England. Upper Jurassic, Kimmeridgian Stage. From the Kimmeridge Clay; the exposed cliff section at Endcombe Bay consists lithologically of the Crushed Ammonite Shales, which are included (Arkell 1933) in the zone of *Pavlovia rotunda*.

Fig. 26 *Kimmerosaurus langhami* gen. et sp. nov. **Holotype**, R.8431. Skull roof in ventral view, *c.* × 0·8. See Fig. 32, p. 307.

Fig. 27 *Kimmerosaurus langhami* gen. et sp. nov. **Holotype**, R.8431. Dentary in dorsal view, see Fig. 37, p. 312. Skull roof in dorsal view, see Fig. 31, p. 306. Basioccipital in anterior aspect (inverted), see Fig. 35c, p. 309. All *c.* × 0·6.

Fig. 28 *Kimmerosaurus langhami* gen. et sp. nov. **Holotype**, R.8431. Posterior elements of right mandible in buccal view, see Fig. 38c, p. 313. Also four teeth. All *c.* ×0·8.

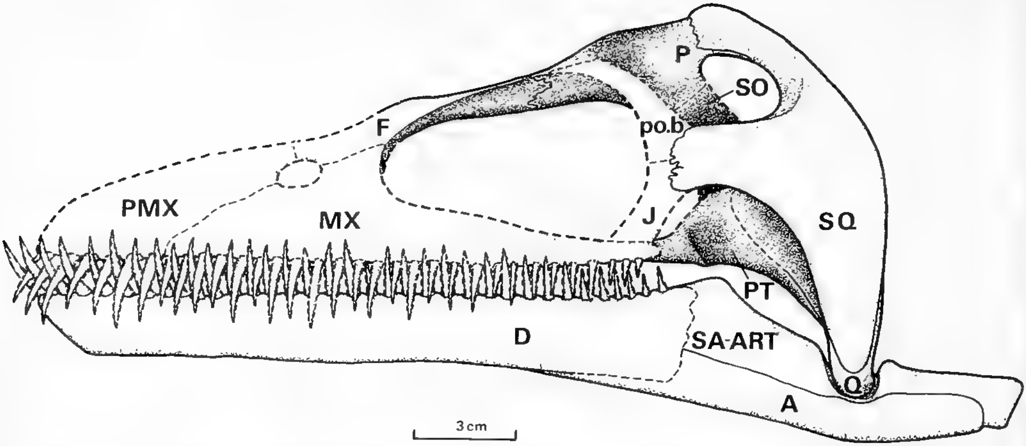


Fig. 29 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, reconstruction of skull in lateral view. Abbreviations as in Fig. 1, p. 259.

DIAGNOSIS. Plesiosauroids in which tooth ornament is absent; the teeth are greatly recurved, sharply pointed and buccolingually compressed; the premaxilla bears at least 8 teeth; the dentary bears 36 teeth on each ramus; the parietals do not form a sagittal crest; the quadrate overlaps the quadrate ramus of the pterygoid anterolaterally; the paroccipital process of the exoccipital-opisthotic is relatively short and massive; the occipital condyle is not ringed by a groove, and extends onto the pedicles of the exoccipitals. (The postcranial skeleton is not known.)

REFERRED SPECIMEN. In September 1978 R. A. and P. A. Langham exhibited at the 26th Symposium of Vertebrate Palaeontology and Comparative Anatomy, University of Reading, a second specimen of this species, consisting of a less complete skull (but including the basisphenoid) and some anterior cervical vertebrae. It is hoped that this specimen may receive description in subsequent work.

DESCRIPTION OF HOLOTYPE. Specimen R.8431 was presented almost clear of the Clay matrix, and the last traces were removed with an industrial 'Airbrasive' machine. This revealed the suture lines and surface ornament. The skull is remarkably well preserved, and consists of eight pieces with an additional nine isolated teeth. The frontals, parietals, postorbital bar and squamosals are associated in a single piece (Figs 26, 27, 31, 32) and the right angular and fused surangular-articular form a second piece (Figs 28, 38) onto which have been compressed two isolated teeth and an unidentifiable skull fragment. The remaining elements listed above are preserved completely disarticulated. A small sliver of bone compressed onto the left anterior part of the dentary appears to be a fragment of the left premaxilla.

The reconstruction of an occipital view of the skull (Fig. 30) necessitated restoration only of the missing supraoccipital, other elements being reproduced as mirror images of their opposites. From this occipital reconstruction can be determined the distance between the jaw articulations and the height from these to the skull vertex. The entire right ramus of the lower jaw is preserved, and thus the skull length can be restored; furthermore, the dorsal line of the skull is preserved almost to the anterior margin of the orbit. It was therefore possible to reconstruct a lateral view (Fig. 29), the missing outlines being restored from the reconstruction of *Cryptoclidus eurymerus* (Fig. 1).

The tooth number is known for the lower jaw from empty sockets, and their interlock was reconstructed on a one-to-one basis (approximately as in other forms) by assuming a similar

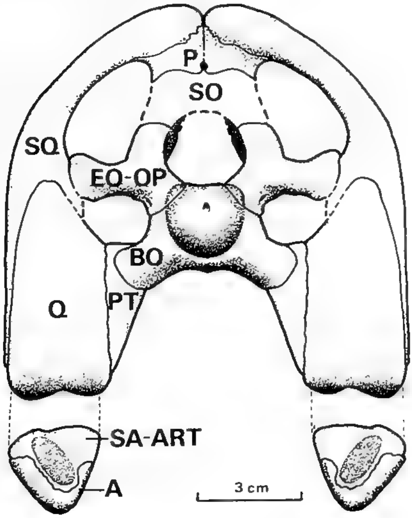


Fig. 30 *Kimmerosaurus langhami* gen. et sp. nov., R.8431. Reconstruction of skull in occipital view. Abbreviations as in Fig. 2, p. 259.

number of teeth in the upper jaw. As thus restored, the premaxilla bears 8 teeth, and this figure is upheld as a minimum number by osteological evidence (see below, p. 311).

The preserved parts of the frontals agree in general structure with those of *Cryptoclidus*. Posteriorly they unite with the parietals by complex interlaminating sutures, forming the anterior border of the pineal foramen. In advance of the foramen they suture ventrally, but dorsally they remain separated by a median groove. Judged from the shape of the orbital margins, the orbits must have been relatively large (see Fig. 29). Anteriorly the frontals are broken, and there is no evidence for the position of the nares.

A proximal portion of the postorbital bar is preserved *in situ* on the right side. It is flat and very thin, and lies in a plane which dips downwards and backwards to form an angle of about 30° with the skull table. The preserved part shows no downward curvature, and it is not possible to determine the form of its connection, if any, with elements of the cheek region. The bar is composed of the postfrontal and the postorbital; accidental breaks (now repaired with plastics soluble in chloroform) showed sections which confirmed beyond any doubt the presence of both these elements. The postfrontal is a thin lamina of bone sandwiched between a lateral flange of the parietal, upon which it rests dorsally, and the postorbital by which its posterior part is overlain. The thickest preserved part of the element is the broken anterior margin, which is 2 mm thick; when complete, the postfrontal probably met the posterolateral corner of the frontal in the region of its suture with the parietal. The postorbital is also laminate and is exceedingly thin, being only 0·5 mm in vertical section.

The parietals appear to be in the process of fusing with one another: their median suture is visible on the dorsal and occipital surfaces, but cannot be traced ventrally. Anteriorly the parietals are somewhat overlapped by the frontals, and in dorsal view the oval pineal foramen is bordered equally by both elements. Behind the foramen each parietal expands to produce a lateral flange, the plane of which curves downwards and backwards reaching a maximum angle of about 45° to the skull table. This forms the base of the postorbital bar, and together with the overlying postfrontal it forms the upper part of the orbital margin.

Behind the lateral flange, the sides of the parietals are excavated concavely for the temporal musculature. Unlike any plesiosaur described previously there is no development of a sagittal crest; instead, the temporal fossae are separated by at least 1 cm of irregularly-pitted dorsal surface, the edges of which actually overhang the excavations. In lateral view the dorsal outline of the skull is approximately linear, the parietals continuing the lines of the frontals, whereas in other plesiosaurs the sagittal crest is elevated well above this line.

Behind the smooth ventral surfaces of the lateral flanges the roof of the braincase is divided into three distinct areas (Fig. 32). In the ventral midline is a groove which widens and deepens into a roughened pit halfway along its length. The groove is surrounded by a smooth cartilage-covered area which in turn is bordered laterally by areas of roughened bone which curved ventrally to form part of the braincase walls and unite with the prootics. The posterior part of the smooth area is inclined posteroventrally at a slight angle and forms two facets, divided by a groove, for union with the supraoccipital. With the latter element in place, the groove would form a median channel leading from the occipital surface to the pit;

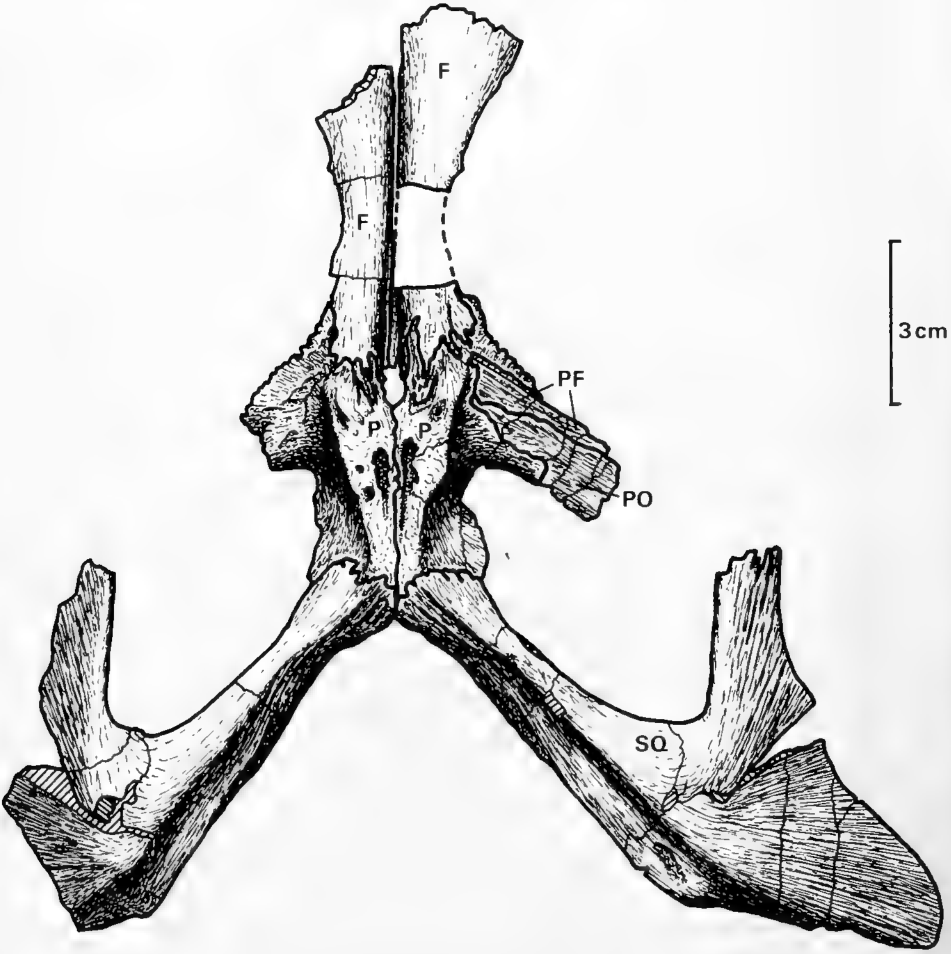


Fig. 31 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, skull roof in dorsal view. F, frontal; P, parietal; PF, postfrontal; PO, postorbital; SQ, squamosal.

as was suggested with regard to a similar structure in *Cryptoclidus eurymerus*, this may have housed the origin of a nuchal ligament. The occipital surface of the parietals is proportionally small by comparison with that of the other forms described above.

Posteriorly the parietals suture with the squamosals, beneath which they are produced into posterolateral processes which play a part in the formation of the post-temporal bar.

The squamosals are relatively large; the right element is complete and has the usual triradiate structure. Post-mortem crushing has resulted in spreading apart the ventral rami and thereby somewhat straightening the dorsal rami. The elements meet in the midline above the parietals, where the dorsal rami become unusually bulbous and form the highest part of the skull profile. In consequence, the post-temporal bar is thicker and stronger than in *Cryptoclidus*, *Muraenosaurus* and *Tricleidus*, in which genera the dorsal ramus is neatly spliced into the parietal.

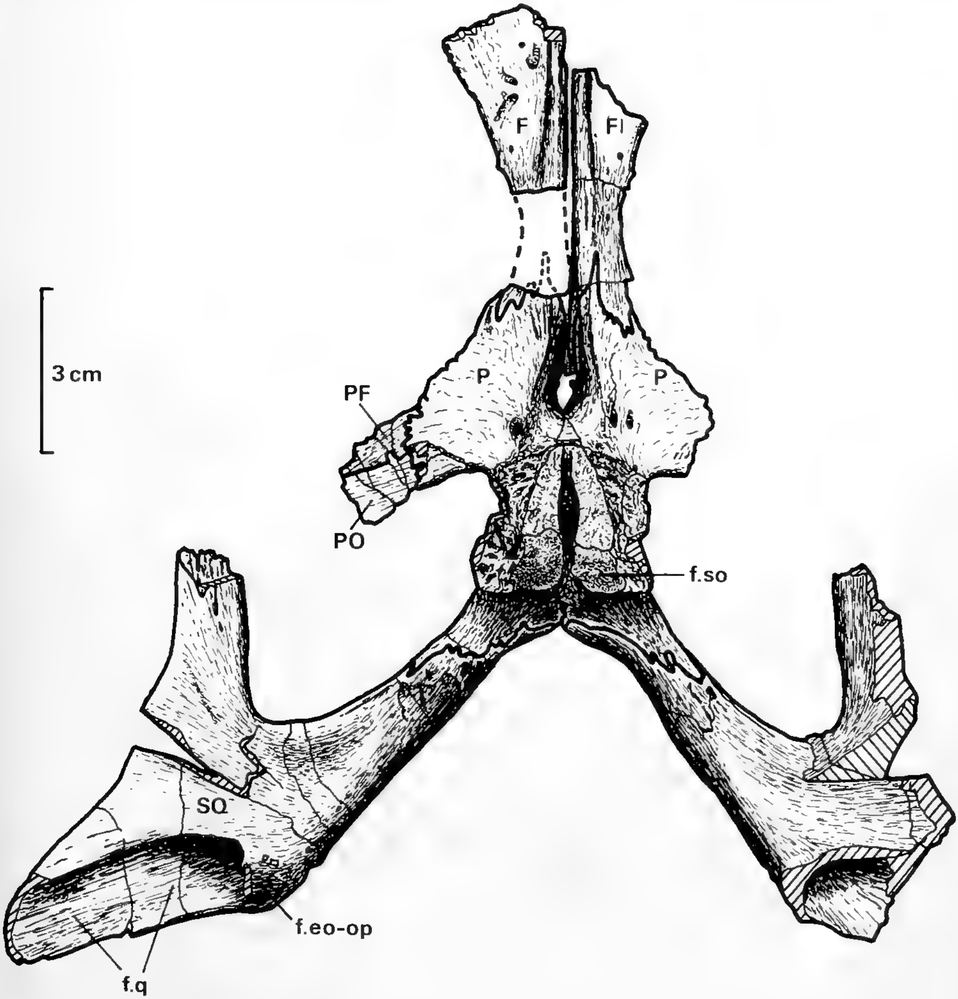


Fig. 32 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, skull roof in ventral view. f.eo–op, facet for articulation with paroccipital process of the exoccipital-opisthotic; f.q, facet for quadrate; f.so, facet for supraoccipital. Other abbreviations as in Fig. 31.

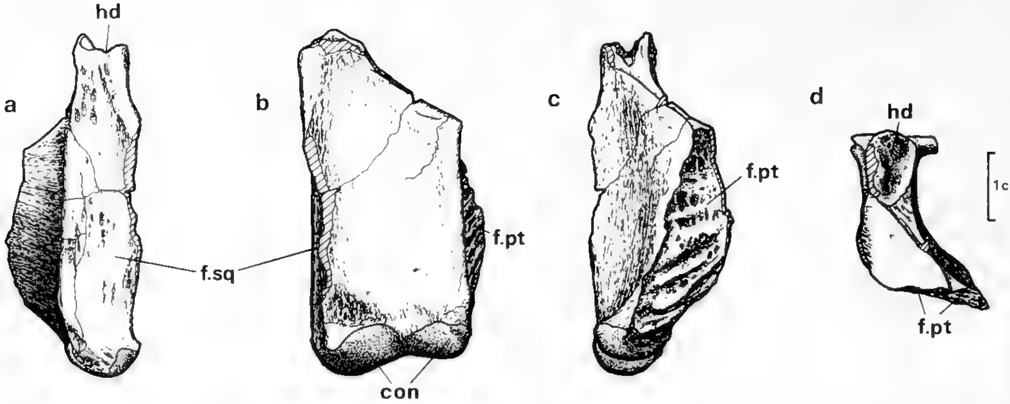


Fig. 33 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, left quadrate: a, lateral; b, posterior; c, medial; d, dorsal aspect. con, condyles for jaw articulation; f.pt, facet for pterygoid; f.sq, facet for squamosal; hd, head of quadrate.

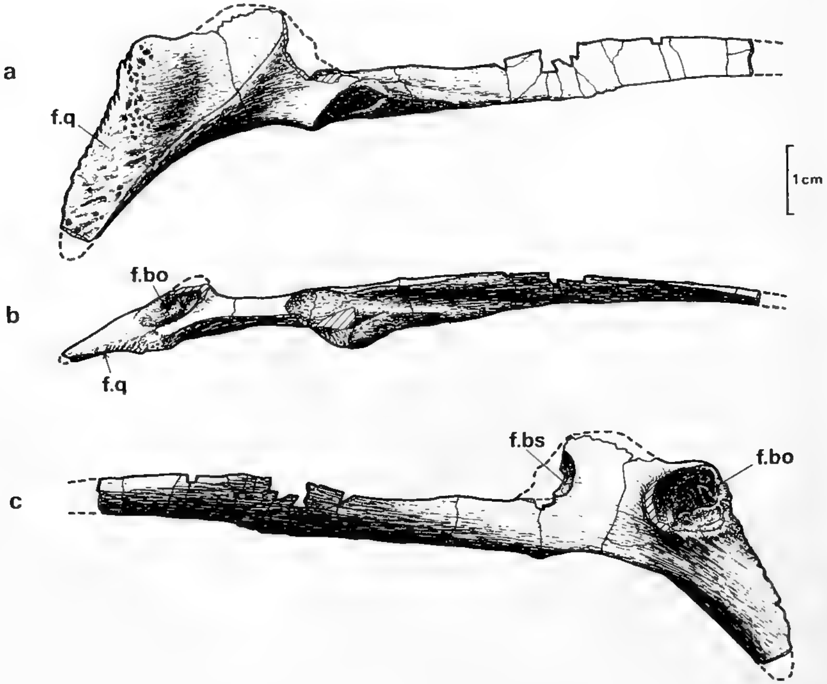


Fig. 34 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, right pterygoid: a, lateral; b, dorsal; c, medial aspect. f.bo, facet for basipterygoid process of basioccipital; f.bs, facet for basicranial process of basisphenoid; f.q, facet for quadrate.

The anterior ramus of the squamosal terminates in a large sutural surface, but there is no indication of the nature and direction of the elements with which it was united. The ventral ramus has the same structure as in *C. eurymerus*: on its medial surface is a large facet for the quadrate, above which is a small facet for the paroccipital process of the exoccipital-opisthotic.

The quadrate (Fig. 33) is relatively larger and proportionally longer than in the preceding genera. Ventrally it forms two ovoid condyles for articulation with the lower jaw, the lateral condyle being slightly larger than the medial. The large lateral facet for the squamosal is 5·7 cm long; above its dorsal end is the conical primary head, which was tipped with cartilage. From this prominence the dorsal edge of the quadrate describes an inward, forward and downward arc which terminates along the upper edge of the pterygoid facet and was continued by the pterygoid. The large pterygoid facet is vertically orientated, extends for 4·8 cm from the dorsal margin to the inner angle of the medial condyle, and faces postero-medially at *c.* 20° to the long axis of the skull; the anteromedial margin is thin and broken, and may possibly have continued as a thin film of bone further anteriorly across the lateral surface of the pterygoid, its ultimate extent being indicated by a ridge on the pterygoid. The mechanism of suture of the two elements in the present specimen, where the quadrate extensively overlaps the pterygoid anterolaterally, is the reverse of that described in *Muraenosaurus* and *Tricleidus*, where the posterior end of the pterygoid fits into an anterolateral notch in the quadrate.

Parts of both pterygoids are preserved, the right being the more complete (Fig. 34). It is an elongated element consisting of a long, thin and horizontally orientated anterior part which was involved in the formation of the palate, together with a more massive posterior part which bears facets for union with the basisphenoid, basioccipital and quadrate.

The quadrate facet is large, its surface is much pitted, and its anteroventral edge is defined

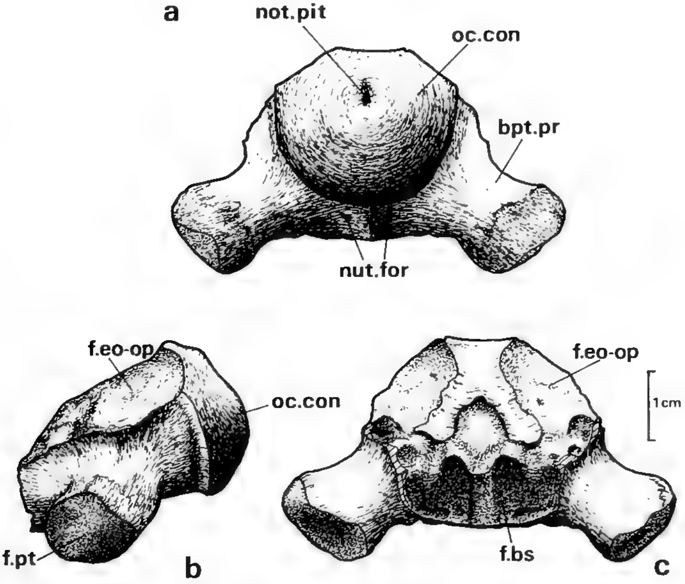


Fig. 35 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, basioccipital: a, posterior; b, left lateral; c, anterior aspect. bpt.pr, basipterygoid process; f.bs, facet for basisphenoid; f.eo–op, facet for exoccipital-opisthotic; f.pt, facet for pterygoid; not.pit, notochordal pit; nut.for, nutritive foramina; oc.con, occipital condyle.

by a prominent oblique ridge. This facet is confined to the lateral surface of the bone, the pterygoid thereby differing in form from those of *Muraenosaurus* and *Tricleidus*.

The facet for articulation with the basioccipital is a deep and oval depression on the medial surface of the pterygoid. It has a much roughened floor and an elevated rim, and it faces posteromedially. Since it is situated opposite the upper end of the quadrate facet, the basioccipital and quadrate are at this point separated only by a lamina of pterygoidal bone about 2 mm thick.

Anterior to the quadrate and basioccipital facets the dorsal edge of the pterygoid rises to form a thin crest of bone, beyond which it falls to the base of the palatal ramus. The facet for union with the basisphenoid, which is a crescentic depression with a roughened floor, lies on the medial surface just posterior to this point and about 2 cm anterior to the basioccipital facet. There is no development of a process marking a second and more posterior contact with the basisphenoid such as characterizes the pterygoid of *Tricleidus*.

Immediately in front of the basisphenoid facet the pterygoid expands to twice its width, this increase being produced on the lateral side of the bone. From here the palatal ramus extends forwards as a flattened rod. At first this is orientated to face about 45° dorsolaterally, but further forward the angle is increased by spiralling until the plane of the bone is vertical. The twist may perhaps be a result of post-mortem distortion or of cumulative small errors in repairing many breaks across the very thin bone; if this be the case, then it is likely that the present flat medial surface was once ventrally orientated and played a normal role in the formation of the palate as in other plesiosaurs. It is not possible, however, to judge how this anterior part of the pterygoid might have connected with the rest of the palate. There are no facets on the preserved parts, and it is unlikely that contact was made with the parasphenoid as in *Tricleidus*.

The basioccipital (Figs 27, 35) is relatively large, and articulated with the exoccipital-opisthotics, basisphenoid, pterygoids and atlas. The dorsal surface is comprised of the large lateral facets for the exoccipital-opisthotic elements, between which lies the floor of the braincase. Posteriorly this is concave, but anteriorly it is divided by a median ridge the surface of which has not been completely ossified.

The anterior basioccipital surface is the facet for the basisphenoid. This is compressed dorsoventrally into an elliptical shape and is relatively small, barely equalling a facet for an exoccipital-opisthotic. It is marked by a median vertical groove which with the basisphenoid may have formed a small dorsoventral channel such as was noted in *Muraenosaurus*. The ventral surface of the element is marked by a gentle median ridge, on either side of which are small nutritive foramina.

On the lateral surfaces are produced the short and massive pterygoid processes. Distally these form the pterygoid facets, which are orientated anterolaterally and are isolated completely from the basisphenoid facet by finished bone surface. In the genera described previously, the pterygoid and basisphenoid facets are confluent except in fully ossified 'old adult' specimens.

The structure of the occipital condyle is unique. It is reniform in outline, being formed largely from the basioccipital with about one tenth of its area being borne on the pedicles of the exoccipitals (this character is known to be shared only with the genus *Cryptoclidus*). Furthermore, its surface is not spherical, but instead is marked by a well-developed notochordal pit which is situated a little above the centre.

The exoccipital and opisthotic are fused, as in other plesiosaurs. The right combined element is preserved (Fig. 36), in which the line of fusion of its components is indicated on the medial surface by a ridge and at the dorsal and ventral margins by notches. The exoccipital portion largely forms the facet for the basioccipital, and is pierced anteriorly by a large jugular foramen and more posteriorly by two foramina for branches of the hypoglossal nerve; it also forms a small part of the occipital condyle. The opisthotic portion largely forms the facet for the supraoccipital, and contains the posterior half of the utriculus and parts of the horizontal and posterior vertical semicircular canals. It is not clear which part formed the paroccipital process, which in this genus is comparatively shorter and more massive than in

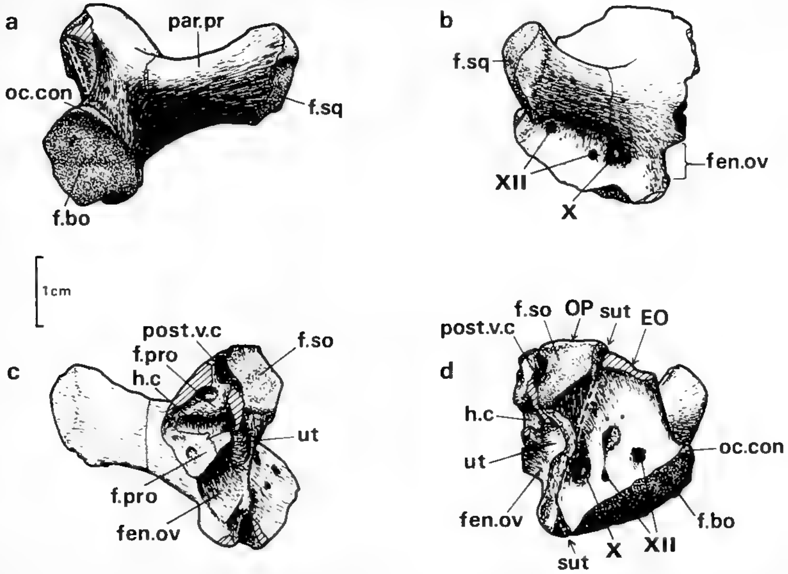


Fig. 36 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, fused right exoccipital-opisthotic: a, posterior; b, lateral; c, anterior; d, medial aspect. EO, exoccipital part; f.bo, facet for basioccipital; f.pro, facet for prootic; f.so, facet for supraoccipital; f.sq, facet for squamosal; fen.ov, position of fenestra ovalis; h.c, horizontal semicircular canal; oc.con, occipital condyle; OP, opisthotic part; par.pr, paroccipital process; post.v.c, posterior vertical semicircular canal; sut, position of fused suture between component elements; ut, depression for utriculus; X, jugular foramen; XII, foramina for branches of hypoglossal nerve.

Cryptoclidus, and considerably more so than in *Muraenosaurus* and *Tricleidus*. Distally the paroccipital process bears a facet for union with the squamosal.

The dentary (Figs 27, 37) is remarkably slender and lightly built, and in dorsal view the tooth-bearing area of spongy bone is predominant whilst the solid lamellar bone which strengthens the medial margin of the jaw ramus appears deficient by comparison with other genera (e.g. *Cryptoclidus*, cf. Figs 3 and 37). The specimen has been eroded somewhat: the dorsal portions of the tooth sockets have been lost yet the ventral parts remain, and so the sockets appear as grooves which are orientated outwards and inclined slightly upwards. There are 34 well-preserved sockets on the right ramus, the most posterior of which blends into a space large enough to have held a further two sockets, thus making a total of 36; this is probably also the total for the left ramus. No remains of splenials could be identified on the medial surface.

A small fragment of bone which represents part of the left premaxilla (judged from its position and close fit with the dentary) is compressed onto the dentary over the 3rd to 7th left tooth sockets. This fragment suggests that in life the premaxilla extended posteriorly at least to the level of the lower 7th socket. As the 1st upper tooth interlocks in advance of the 1st lower tooth in all described plesiosaurs, and as the interlock of the teeth is on a one-to-one basis at least for the length of the premaxilla, it follows that there were probably at least 8 pairs of premaxillary teeth in the present species. This figure, and also the number of dentary teeth, exceeds that recorded for all plesiosauroids except one, the South American Cretaceous form *Aristonectes parvidens* Cabrera, 1941. In that genus and species (described as 'aberrant' by Welles, 1962) there are 15 pairs of premaxillary teeth and 58 pairs of teeth on the dentary.

The angular, surangular and articular are preserved on the right side (Figs 28, 38); these

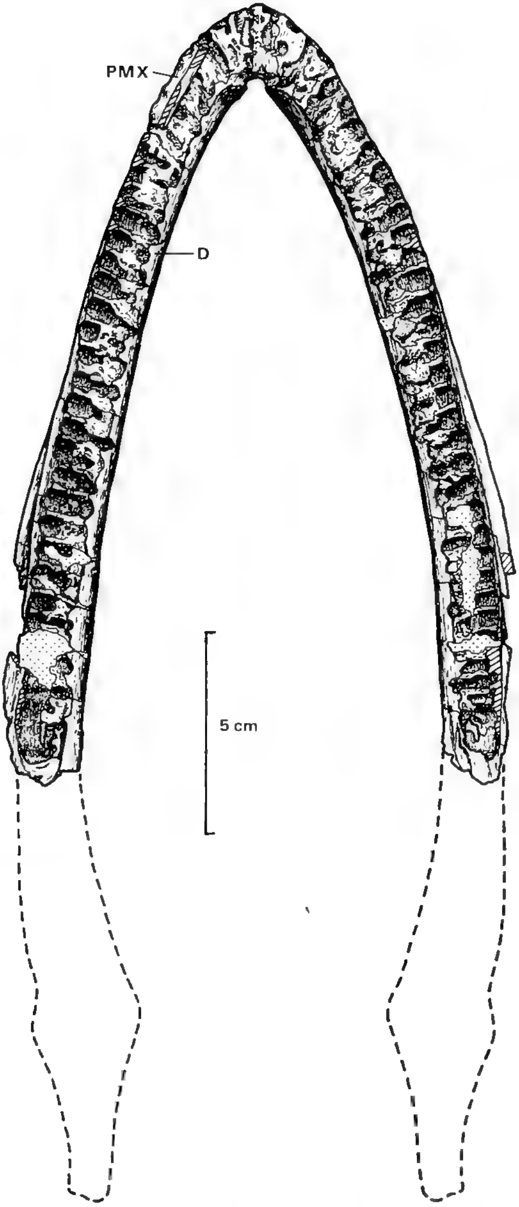


Fig. 37 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, dentary in dorsal view. Outline of posterior portions of lower jaw restored with broken lines. D, dentary; PMX, a small fragment of the left premaxilla.

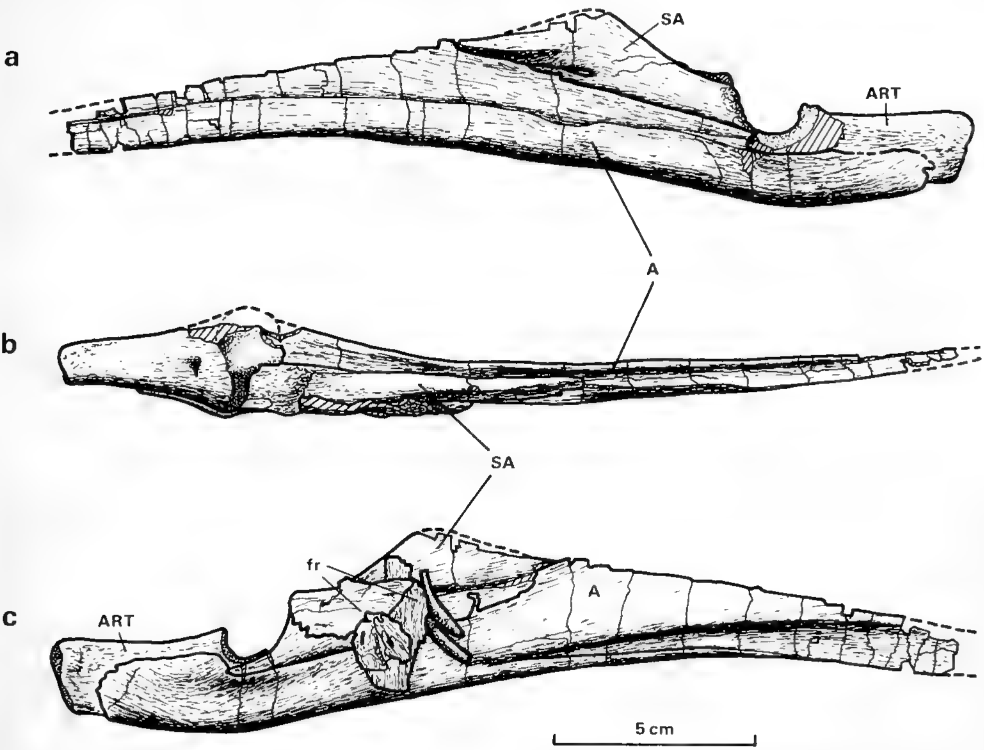


Fig. 38 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, posterior elements of right lower jaw: a, medial; b, dorsal; c, lateral aspect. fr, compressed fragments of skull and two teeth. Other abbreviations as in Fig. 4, p. 263.

are very similar to the corresponding parts of *Cryptoclidus* (cf. Fig. 4). The articular and surangular appear to be fused as in other forms, but what is probably the line of fusion may be traced across the jaw articulation. In lateral view the angular shows marked curvature in the vertical plane, with the ventral edge concave. This curvature has the effect of lowering the jaw articulation with respect to the toothrow, which also occurs to a slightly lesser extent in *Cryptoclidus* but not at all in *Tricleidus* (cf. Figs 29, 1 and 22). The lateral surfaces of the angular and surangular were overlapped by the dentary, whose posterior limit is indicated on these elements by ridges which are partly overlain by compressed unidentifiable debris and two teeth. The extent of this overlap is shown in Fig. 29.

The teeth (Figs 28, 39) are unique amongst plesiosaurs in three respects: they are completely lacking in longitudinal ornamental ridges; they are greatly recurved, the crowns curving through an arc of up to 75°; and in section the distal parts of the crowns are not circular but elliptical, being buccolingually compressed. They are very sharply pointed, and it is notable that even the largest teeth show no signs of attrition. Some large specimens show facets resulting from resorbtion of the root in advance of an approaching replacement tooth.

With regard to the proportional length of the snout and the dentition, the present specimen is quite unlike any plesiosaur reconstructed previously. Several characters (including increase in numbers of teeth, reduction in dental ornament, form of the occipital condyle, reduction in length of the paroccipital process and curvature of the angular) suggest an affinity closer to *Cryptoclidus* than to *Muraenosaurus* or *Tricleidus*.

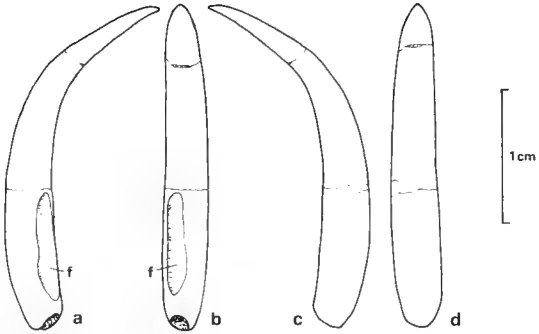


Fig. 39 *Kimmerosaurus langhami* gen. et sp. nov. R.8431, tooth: a and c, axial: b, lingual; d, buccal aspect. Note absence of ornamental ridges. f, resorbtion facet on root.

Genus ***COLYMBOSAURUS*** Seeley, 1874

TYPE SPECIES. *Plesiosaurus trochanterius* Owen, 1840.

DIAGNOSIS. As for the type species (monotypic genus).

Colymbosaurus trochanterius (Owen, 1840)
(Figs 40, 43e, 44f)

1840 *Plesiosaurus trochanterius* Owen: 85.
1841 *Plesiosaurus (Pliosaurus) trochanterius* Owen; Owen: 64.
1869 *Pliosaurus trochanterius* (Owen) Owen: 7 (name only).
1869 *Pliosaurus portlandicus* Owen: 8; pl. 4.
1869 *Plesiosaurus megadeirus* Seeley: xx.
1869 *Plesiosaurus macrodeirus* Seeley: 143 (alternative original spelling for *P. megadeirus*, rejected Lydekker 1889 : 190).
1870 *Plesiosaurus manselii* Hulke: 612; pl. 41 figs 1–6.
1870 *Plesiosaurus megadeirus* Seeley; Hulke: 618.
1870 *Plesiosaurus trochanterius* Owen; Hulke: 620.
1870 *Pliosaurus portlandicus* Owen; Hulke: 620.
1871 *Plesiosaurus trochanterius* Owen; Phillips: 316, fig. 162.
1871 *Pliosaurus portlandicus* Owen; Seeley: 181.
1871 *Plesiosaurus megadeirus* Seeley; Seeley: 184.
1874*b* *Colymbosaurus megadeirus* (Seeley) Seeley: 445, fig. 12.
1874*b* *Muraenosaurus mansellii* ('Hulke') Seeley: 448 (mis-spelling).
1879*a* *Muraenosaurus manselii* (Hulke); Sauvage: 1.
1879*a* *Muraenosaurus manselii* (Hulke); Sauvage: 1.
1883 *Plesiosaurus manseli* 'Hulke'; Hulke (mis-spelling).
1888 *Plesiosaurus trochanterius* Owen; Lydekker: 353, fig. 2.
1888 *Plesiosaurus megadirus* 'Seeley'; Lydekker: 353 (mis-spelling).
1888 *Plesiosaurus manseli* 'Hulke'; Lydekker: 354.
1889 *Cimoliosaurus trochanterius* (Owen) Lydekker: 190, figs 59, 62–65 (mis-spelling for *Cimoliasaurus* Leidy, 1852).
1889 *Muraenosaurus manseli* ('Hulke'); Lydekker: 190 (cited in synonymy).
1889 *Plesiosaurus macrodirus* 'Seeley'; Lydekker: 190 (mis-spelling cited in synonymy).
1889 *Colymbosaurus megadirus* ('Seeley'); Lydekker: 190 (cited in synonymy).
1889 *Cimoliosaurus portlandicus* (Owen) Lydekker: 227, fig. 70.
1892 *Colymbosaurus megadeirus* (Seeley); Seeley: 138.
1892 *Colymbosaurus mansellii* ('Hulke') Seeley: 138.
1892 *Colymbosaurus portlandicus* (Owen) Seeley: 147.
1895*c* *Muraenosaurus mansellii* ('Hulke'); Andrews: 432.

1911 *Cryptocleidus trochanterius* (Owen) Sauvage: 186–215 (mis-spelling for *Cryptoclidus* Seeley, 1892).
1924 *Colymbosaurus manselli* ('Hulke'); Watson: 902.
1959 *Colymbosaurus portlandicus* (Owen); Delair: 62.
1959 *Colymbosaurus manseli* ('Hulke'); Delair: 63.
1959 *Colymbosaurus trochanterius* (Owen) Delair: 64.
1963 *Colymbosaurus megadeirus* (Seeley); Persson: 24.
1963 *Colymbosaurus manseli* ('Hulke'); Persson: 24.
1963 *Colymbosaurus portlandicus* (Owen); Persson: 24.
1963 *Colymbosaurus trochanterius* (Owen); Persson: 24.
1964 *Colymbosaurus megadeirus* (Seeley); Novozhilov: 321, fig. 305.

HOLOTYPE. Specimen 31787, the right humerus of a large 'old adult' individual. It was collected by Viscount Cole (later 3rd Earl of Enniskillen), described by Owen (1840) and figured from a plaster cast in the Oxford Museum by Phillips (1871 : fig. 162).

TYPE LOCALITY AND HORIZON. From the Kimmeridge Clay of Shotover Hill, Oxfordshire, according to Owen (1840). Phillips (1871) recorded the dissent of the Earl of Enniskillen, who claimed that although several specimens similar to the type had been collected by him from Shotover Hill, the holotype itself was taken from the Oxford Clay of Christian Malford, Wiltshire. Lydekker (1889) cited the horizon and locality as the Kimmeridge Clay of Wiltshire; this is an unsatisfactory compromise. In view of the fact that many specimens similar to 31787 are known, all of which are from Kimmeridge Clay, it seems more reasonable to accept Owen's account rather than to trust the Earl's memory thirty years after that publication.

DIAGNOSIS. Plesiosauroids in which there are 42 cervical vertebrae with amphicoelous centra, the length of which never exceeds the height; the ventral ramus of the scapula is relatively large and plate-like, and has a convex anterior margin; the coracoids meet the scapulae in the midline in 'adults'; the width across the posterior cornua of the coracoids slightly exceeds the interglenoid width in 'adults'; the humerus and to a lesser extent the femur are expanded posterodistally, both forming three distal articular facets; there are three epipodials in both the manus and the pes; the overall length of the 'adult' is 5·0 to 6·6 m. (The skull and dermal elements of the pectoral girdle are unknown in this genus and species.)

DISTRIBUTION AND RANGE. Diagnostic material is known from several English localities ranging from Kimmeridge Bay, Dorset, through Oxfordshire and Cambridgeshire to Downham Market, Norfolk. Upper Jurassic, Kimmeridgian and Portlandian Stages. Two referred specimens may be accurately placed: 40106 is from the cliffs to the east of Clavell's Tower, Kimmeridge Bay, Dorset (Hulke 1870), and therefore from the zone of *Pectinatites pectinatus*, Upper Kimmeridgian Stage (Arkell 1933); 40640 is from the Portland Stone of Portland Island, Dorset (Owen 1869) and therefore from the zone of *Titanites giganteus*, Portlandian Stage (Arkell 1933).

REFERRED SPECIMENS. The following specimens are diagnostic; those with numbers without prefixed letters are in the collection of the British Museum (Natural History) (see p. 254).

31785. An 'adult' left femur from the Kimmeridge Clay of Shotover, Oxfordshire.

31795. An 'adult' left humerus from the Kimmeridge Clay of Shotover, Oxfordshire.

40106. Incomplete 'adult' postcranial skeleton from the Kimmeridge Clay (*Pectinatites pectinatus* Zone) of Kimmeridge Bay, Dorset. Described and partly figured by Hulke (1870) as the holotype of *Plesiosaurus manselii* Hulke. Originally catalogued (Lydekker 1889) under the numbers 40106, 40107a, 40107b, 40108a, 42496 and 42496a.

40107. An 'adult' left femur from the Kimmeridge Clay of Kimmeridge Bay, Dorset.

40640. A 'juvenile' right femur and associated epipodials, tarsals and proximal phalanges from the Portland Stone (*Titanites giganteus* Zone) of Portland Island, Dorset. Figured by Owen (1869 : pl. 4) and by Hulke (1883 : fig. 8) as the holotype of *Pliosaurus portlandicus* Owen.

46479. A 'juvenile' right humerus from the Kimmeridge Clay (locality unknown). A figure by Lydekker (1889 : fig. 62), alleged to be of this specimen, is not representative.

C.M.N. 15.72(2) (Fig. 40). An 'adult' left femur, tibia, fibula, two distal tarsals and several phalanges (on display), and a right femur. Collected from the Kimmeridge Clay of Downham Market, Norfolk, by C. B. Rose.

M.M. LL.5513–8. An incomplete 'adult' postcranial skeleton consisting of the right humerus (LL.5513), left humerus (LL.5514), left scapula (LL.5515), both coracoids (LL.5516–7) and two ulnae, one ulnare and a carpal (LL.5518a–d) from the Kimmeridge Clay of Coppock's Pit, Shotover, Oxford. Figured by Watson (1924 : figs 8, 10d).

S.M.C. J.29596 etc. Incomplete 'adult' postcranial skeleton collected from the Kimmeridge Clay of Ely by Stead Jones. Catalogued and made a syntype of *Plesiosaurus megadeirus* by Seeley (1869). Each bone is numbered separately: coracoids J.29596–7; vertebrae J.29598–653; left hindlimb J.29654–91, and the right hindlimb J.59736–43.

S.M.C. J.63919. Incomplete 'adult' vertebral column from the Kimmeridge Clay of Haddenham. Catalogued and made a syntype of *Plesiosaurus megadeirus* by Seeley (1869).

Discussion of synonymy

Owen (1840) described the holotype (31787) as a 'limb bone'. It was identified correctly by Phillips (1871) as a humerus, but was misidentified as a femur by Hulke (1870, 1883) and by Lydekker (1889). Hulke also mistook it for the type specimen of *Pliosaurus brachydeirus* Owen, apparently because it was incorrectly labelled (Lydekker 1889), and misidentified specimen 31795 as the type of the present species. Fortunately, specimen 31787 shows several distinguishing features which were described by Owen and Phillips. Much confusion exists in the literature, but happily not in the type material.

Seeley (1869) listed two specimens (now J.29596 etc. and J.63919) in the Sedgwick ('Woodwardian') Museum, Cambridge, under the new name *Plesiosaurus megadeirus*. He merely listed the bones present, this leading Lydekker (1888, 1889) to regard the name as not established. However, Seeley's listing revealed that the neck consists of 42 cervical vertebrae (in J.29596 etc.); this is still used as a distinguishing taxonomic character, and so *P. megadeirus* is an available name.

Owen (1869) described a small right femur and associated paddle bones of a 'juvenile' specimen (40640) under the new name *Pliosaurus portlandicus*. A character shown by this limb (in which the elements are preserved *in situ*) is that the distal end of the femur articulates with three epipodials.

In 1870, Hulke described and figured a large 'adult' postcranial skeleton (specimen 40106) under the new name *Plesiosaurus manselii*. This specimen includes most of the vertebral column and proximal parts of both left limbs including the humerus and the femur (which were confused by Hulke). An important observable character is the form of the humerus ('femur' of Hulke) which, like the femur ('humerus') articulates distally with three epipodials.

Hulke commented on the apparent similarity of his specimen to the syntypes of *P. megadeirus*, but was prevented from making a detailed comparison by the lack of adequate description of the latter specimens. He also noted a strong similarity between the humerus ('femur') of *P. manselii* and the type humerus ('femur') of *P. trochanterius* ('*Pliosaurus brachydeirus*'). Finally he engaged upon a comparison between them and the type specimen of *Pliosaurus portlandicus* (which is truly a hind limb) and came very close to invalidating his new name through synonymy. Lydekker (1888, 1889) formally synonymized *P. manselii* and *P. megadeirus* with *P. trochanterius* and transferred the species to the genus *Cimoliasaurus* (a *nomen dubium*, see Welles 1962).

Seeley (1874*b*) distinguished several English genera of plesiosaurs using as his principal criterion the structure of the pectoral girdle. He introduced the new generic name *Colymbosaurus*, and indicated *P. megadeirus* as the type species. He later modified the diagnosis (Seeley 1892) to enable *Colymbosaurus* to be distinguished from *Muraenosaurus*, this time using the comparative form of the vertebrae and propodials and the presence of at least three epipodials in each paddle in *Colymbosaurus*. Three species were referred to the genus (*C. megadeirus*, *C. manselii* and *C. portlandicus*), Seeley believing that these could be distinguished by the comparative form and number of epipodials (he misinterpreted *C. manselii* as having four epipodials, and separated *C. portlandicus* by characters which are typical of 'juvenile' individuals).

It is now argued that the material described under the names *Plesiosaurus trochanterius, P. megadeirus, P. manselii* and *Pliosaurus portlandicus* represents a single species, the valid name for which is *Colymbosaurus trochanterius* (Owen). The taxon is distinguished by characters of the cervical vertebrae, scapula, humerus, femur and epipodials, yet the holotype consists only of an isolated humerus and even the most complete specimens (40106 and J.29596 etc.) do not display all the characters. The diagnosis depends upon the overlap of several specimens which together show all characters. In 40106 are preserved distinctive cervical vertebrae, a humerus with epipodials and a femur. The humerus is of the same kind as the holotype (31787) and also of LL.5513–8; with the latter is preserved a pectoral girdle including the characteristic scapula. The femur of 40106 is of the same kind as those of 40640 and 15.72(2), in which epipodials are preserved, and also J.29596 etc. in which is preserved the full complement of cervical vertebrae.

Description of material

Colymbosaurus trochanterius is the largest and longest of the English Upper Jurassic plesiosauroids. The preserved vertebral columns of specimens 40106 and J.29596 etc. are incomplete but complementary, and it was possible to deduce the composition of the entire column in this species, and hence to estimate the postcranial length of each specimen. Allowing 10% for intervertebral cartilage, the postcranial length estimate for 40106 is 5·7 m. If the skull-length to postcranial-length ratio was as in *Muraenosaurus*, then the skull might have been 0·45 m long, and the total length about 6·15 m. A similar procedure with specimen J.29596 etc. gives an estimated length of 5·0 m. The holotype (31787) is the largest known humerus, with a total actual length (discounting plaster involved in a repair to the shaft) of 0·57 m. Comparative measurements of the humeri of 40106 and 31787 indicate that the total overall length of the latter individual may have been as great as 6·6 m.

The vertebral column of J.29596 etc. is apparently complete from the fused atlas-axis to the middle of the dorsal series, and comprises 42 cervical vertebrae, 3 pectorals and 11 dorsals. In 40106 is preserved the axis-atlas, behind which is a gap (large enough for 10 vertebrae) followed by a further 30 cervicals. Distortion and damage makes many of the trunk vertebrae difficult to identify; the 32 centra probably represent 3 pectorals, 25 dorsals and 4 sacrals. Posterior to these are 20 well-preserved caudal vertebrae; between two of these is a small gap for 3 vertebrae, and a further 3 or 4 are required to complete the tip of the tail. Posterior chevron facets begin on the 4th caudal, and anterior facets on the 10th.

The shape and proportions of the vertebral centra are similar to those of *Cryptoclidus*: the outline of a longitudinal section across the articular face is a double sigmoid curve (cf. *Muraenosaurus*), and the length of the cervical centra never exceeds the height. By comparison with *Cryptoclidus*, the neck of *Colymbosaurus* is lengthened by an increase only in the number of vertebrae, without the accompanying increase in proportional length which occurs in *Muraenosaurus*.

The most complete pectoral girdle is that of LL.5513–8, in which the left scapula and both coracoids are preserved (Fig. 43e). The coracoids are similar in form to those of *Tricleidus*, the width across the posterior cornua being slightly in excess of the interglenoid width. The scapula is distinctive, and differs from other scapulae in the structure of the ventral ramus. This part ('anterior ramus' of Watson 1924) is greatly expanded anteroposteriorly, and unusually so where it meets the base of the dorsal ramus. The dorsal and ventral rami thus appear confluent; their combined anterior margin is convex and thereby differs in shape from that of contemporary genera, in which the base of the ventral ramus is constricted into a bar. The dorsal ramus is broken distally, but the proximal part has the usual structure, and there is no evidence to support the statement by Watson (1924 : 903) that in this species it was 'of very small size, being thin and weak in consonance' (*sic*).

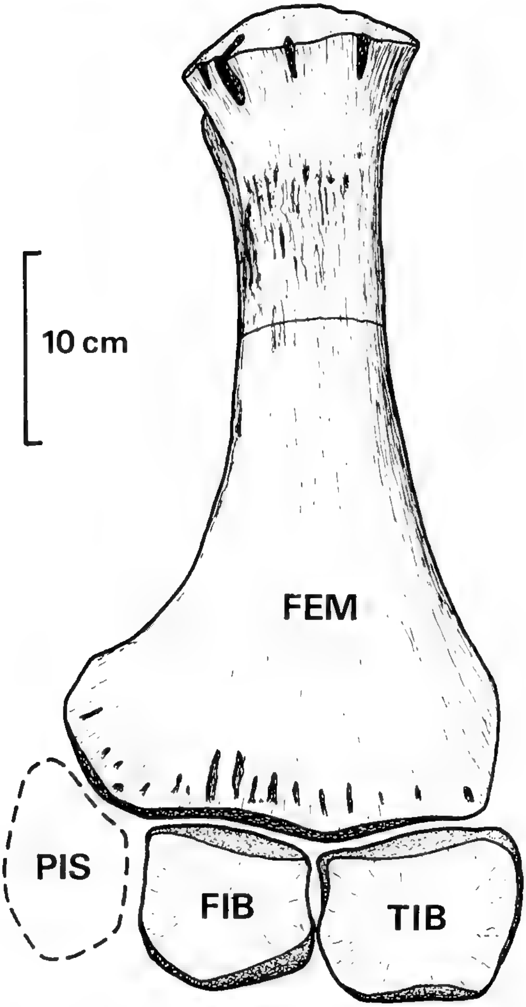


Fig. 40 *Colymbosaurus trochanterius* (Owen), left femur and epipodials of C.M.N. 15.72(2) in ventral view. FEM, femur; FIB, fibula; PIS, pisiform; TIB, tibia.

There are no indications either for or against the presence in this species of an interclavicle or clavicles. The pelvic girdle is not preserved with any specimens.

The humerus (Fig. 44f) is proportionally large and is strongly built with a cylindrical shaft. It is expanded distally, this expansion being largely posterior to the axis of the shaft as in *Muraenosaurus*. Three facets are formed for articulation with the epipodials, the anterior facet for the radius facing somewhat anterodistally and the ulnal facet somewhat posterodistally. The posterior and smaller facet for the pisiform is orientated obliquely posterodistally. The humeri of specimens LL.5513–8 and 46479 (the latter is rather small and probably 'juvenile') show the complete form of the distal facets, whereas the remaining specimens including 31787 and 40106 have the posterodistal part of the bone broken away.

Specimen 31787 was evidently part of an 'old adult': the cartilage-covered areas of the head and the tuberosity are separated by a strip of finished periosteal bone surface such as was noted above in 'old adult' specimens of *Cryptoclidus* and *Muraenosaurus*.

The three epipodials of the forelimb have been found only with specimen 40106 (a further two ulnae are preserved with LL.5513–8). Since the original description of 40106 (Hulke 1870, 1883) the specimen has suffered badly from pyritic decay, and all that now remains of the epipodials are the proximal parts of the radius and ulna. These have been fortified with cement and varnish to prevent further crumbling, but little can now be made of their structure. However, Hulke's description is detailed and the specimens were figured (Hulke 1870 : pl. 41 fig. 3; 1883 : fig. 7). Both the radius and ulna ('tibia' and 'fibula' of Hulke 1870; 'tibia' and 'intermedium' of Hulke 1883) were described as pentahedral, and the pisiform (not named by Hulke 1870; 'fibula' of Hulke 1883) was said to be five- or six-sided and approximately equal in size to the radius and ulna. The elements were evidently held *in situ* by the matrix, and from their combined shape Hulke was able to restore the original posterodistal outline of the humerus ('femur').

The femur of *C. trochanterius* is very similar to the humerus, but the propodials may be distinguished, as with all plesiosauroid propodials, by differences in the development of the humeral tuberosity and the femoral trochanter. The tuberosity is better developed than the trochanter and lies obliquely posterodistal to the head, forming a prominent posterior angle when seen in proximal view; whereas the trochanter is dorsal but never posterior to the head (see *Cryptoclidus eurymerus*, Fig. 17a and c).

Complete femora are preserved with specimens 15.72(2) (an 'adult', Fig. 40) and 40640 (a 'juvenile', figured Owen 1869 : pl. 4), and in addition the femora of 40106 and J.29596 etc. are almost entire and may be restored. The distal end is expanded only slightly less than in the humerus, and three articular facets for the epipodials are also developed and orientated as in that element.

Tibiae and fibulae are preserved with 15.72(2) (Fig. 40), with J.29596 etc. and with 40640. Both elements are five-sided, but they differ in shape, the facet on the tibia for the intermedium being less than half the length of that facet on the fibula. The fibula has a long femoral facet, short facets for the tibia and pisiform and similar distal facets for the intermedium and fibulare. The pisiform (termed 'fabella' by Owen, 1869) is known only in 40640, and there only from its external mould in the matrix. This impression is half the size of the fibula and shows that the element articulated by three almost equal facets with the femur, fibula and fibulare.

In specimen 40640 all six tarsals together with the first three metatarsals are preserved *in situ*; wide spaces for much intervening cartilage testify to the 'juvenile' nature of the individual. The fibulare bears two almost equal distal facets, one facing obliquely anterodistally and articulating with the third distal tarsal, and the second facing obliquely posterodistally, evidently for articulation with the missing fifth metatarsal, which element had therefore completed its proximal migration into the distal tarsal row in this species.

Miscellaneous additional material

ISOLATED TEETH. Three teeth in the Sedgwick Museum, Cambridge (J.30069, J.30070 and J.30071) were collected from the Kimmeridge Clay of Ely by J. Carter. J.30070 (Fig. 41) is complete almost to the tip, and its crown is approximately 3 cm long. The crown is ornamented with numerous longitudinal ridges which are confined to the lingual side, and in this it resembles teeth of 'juveniles' of *Muraenosaurus leedsii*. Another tooth in the Sedgwick Museum (J.14270a, Fig. 42) is labelled 'from the Portland Oolite', and has a cylindrical crown approximately 4 cm long. The proximal part of the crown is ornamented by numerous longitudinal ridges which are longer and more pronounced on the lingual side, but the distal third is smooth and without ornament. This tooth resembles those of *Muraenosaurus* and/or *Tricleidus* in general form except for the lack of ornament distally.

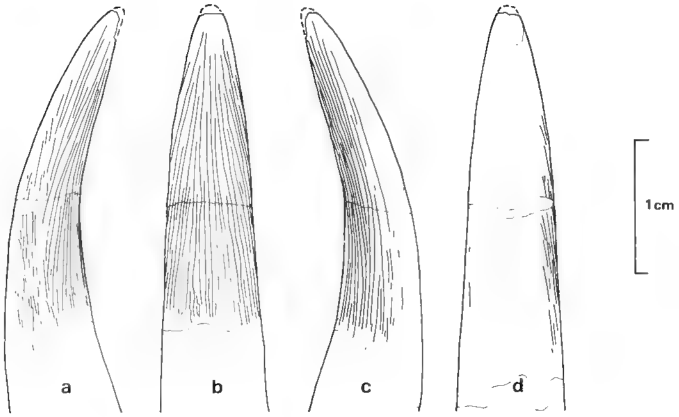


Fig. 41 S.M.C. J.30070, indeterminate tooth from Kimmeridge Clay: a and c, axial; b, lingual; d, buccal aspect.

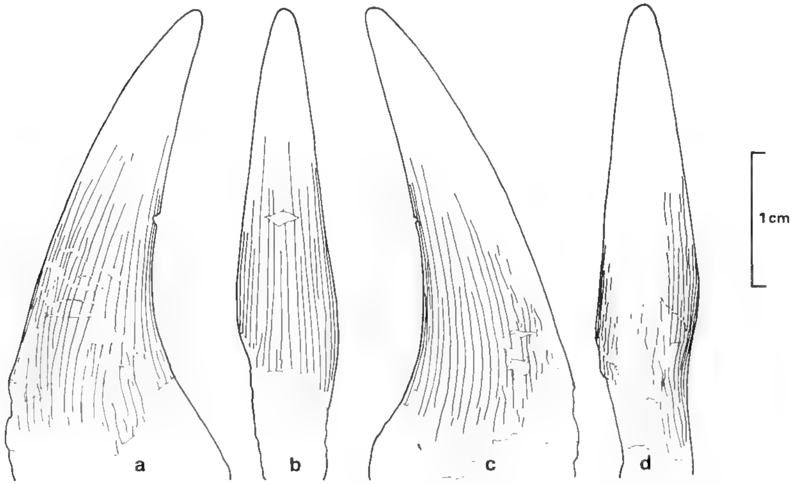


Fig. 42 S.M.C. J.14270a, indeterminate tooth from Portland Stone: a and c, axial; b, lingual; d, buccal aspect.

Both J.30070 and J.14270a may be referable to *Colymbosaurus trochanterius*, in which the teeth are unknown, or they may indicate that the ranges of the genera *Muraenosaurus* and/or *Tricleidus* extend upwards above the Callovian.

Lower jaw symphysis. Specimen L.9412 in the Manchester Museum is the anterior portion of a dentary collected from the Kimmeridge Clay by P. Manning. It consists of the symphysis together with eight tooth sockets on the right ramus and five on the left. Two immature teeth are present and are ornamented by longitudinal ridges. The specimen is indistinguishable from lower jaws of *Muraenosaurus leedsii* and *Tricleidus seeleyi*, and may indicate the extension of the ranges of either species into the Kimmeridgian.

Vertebrae. Several large vertebrae in the Castle Museum, Norwich and numbered 15.72(3)–(5) were collected from the Kimmeridge Clay of Downham Market, Norfolk, by C. B. Rose. The largest specimen, 15.72(5), is a cervical centrum of an 'adult' and has a length of 8·5 cm, a posterior height (to the neural canal) of 9·1 cm and a posterior width of 10·1 cm, and is to the best of my knowledge the largest plesiosauroid vertebra from the English Jurassic. It is distinct from the vertebrae of *Colymbosaurus trochanterius* in that it has 'flat' articular faces as in *Muraenosaurus*, and each end is ringed by an ornament of 'plications' such as are described above in 'juveniles' of *M. leedsii*. They differ from those of the latter species only in size and known geological range, but might prove to represent a distinct species were more diagnostic associated material to be found.

Several vertebrae in the Castle Museum, Norwich, and in the Sedgwick Museum, Cambridge (e.g. specimen J.29717) are recorded as from the Kimmeridge Clay, and are indistinguishable from vertebrae of the Callovian genera *Cryptoclidus* and *Tricleidus*. These may indicate that the ranges of those genera extend into the Kimmeridgian; alternatively, they may represent *Kimmerosaurus langhami*, in which species the postcranial skeleton is unknown but the skull is in several ways similar to that of *Cryptoclidus*.

Rejected names

The most frequent causes for rejection of names (below) are that they are *nomina dubia* or *nomina oblita:*

(i). A *nomen dubium* is defined (Stoll *et al.* 1964 : 151) as 'a name not certainly applicable to any known taxon', and thus covers names erected upon indeterminate type specimens. Such names were called *nomina vana* by Simpson (1945), a term which Welles (1952, 1962) used extensively with this meaning, but the term *nomen vanum* was redefined by Moore (1955) to indicate an unjustified emendation of spelling (*sensu* Stoll *et al.* 1964). Chorn & Whetstone (1978) noticed the resultant ambiguity of the *nomen vanum*, and the present work follows their recommendation that *nomen dubium* be used to indicate names erected on indeterminate type specimens or with inadequate original diagnoses.

(ii). A *nomen oblitum* is defined (Stoll *et al.* 1964 : 23, art. 23b) as a forgotten name which has 'remained unused as a senior synonym in the primary zoological literature for more than fifty years'. Such names are not to be used unless the International Commission on Zoological Nomenclature so directs. Subjective interpretation of 'the primary zoological literature' is required: in the present work the mere listing of a name in a taxonomic catalogue has been discounted, but the inclusion of any remarks indicating that the author has positive reasons for regarding that name as a senior synonym has been counted for this purpose.

For synonymies of names which are junior synonyms, see section on the senior synonym, above. Synonymies of other names are restricted to show original and subsequent combination authorship only.

Genus ***APRACTOCLEIDUS*** Smellie, 1915

TYPE SPECIES. *Apractocleidus teretipes* Smellie, 1915.

STATUS. Subjective-objective junior synonym of *Cryptoclidus* Seeley, 1892. (*Sensu* Blackwelder 1967: the synonymy of the genera is objective so long as the synonymy of their type species is subjectively maintained.)

Genus ***PICROCLEIDUS*** Andrews, 1909

TYPE SPECIES. *Muraenosaurus beloclis* Seeley, 1892

STATUS. Subjective junior synonym of *Muraenosaurus* Seeley, 1874*a*.

Genus ***TREMAMESACLEIS*** White, 1940

TYPE SPECIES. *Muraenosaurus platyclis* Seeley, 1892.

STATUS. Subjective-objective junior synonym of *Muraenosaurus* Seeley, 1874*a*.

Plesiosaurus affinis Owen, 1840

HOLOTYPE. A small propodial from the Kimmeridge Clay of Heddington pits, Oxford, and originally in the collection of Viscount Cole. Present location unknown, presumed lost.

STATUS. *Nomen dubium; nomen oblitum.*

Plesiosaurus brachistospondylus Hulke, 1870

1870 *Plesiosaurus brachistospondylus* Hulke: 611; pl. 41 figs 7–9.
1889 *Cimoliosaurus brachistospondylus* (Hulke) Lydekker: 200 (mis-spelling of *Cimoliasaurus* Leidy, 1852).
1912 *Colymbosaurus brachistospondylus* (Hulke); Bogolubov: 1–4.

HOLOTYPE. 45869, a phalanx, a carpal or tarsal, rib fragments and five axially-compressed dorsal vertebrae preserved in Kimmeridgian clay-stone from Kimmeridge Bay, Dorset.

STATUS. *Nomen dubium.*

Cimoliasaurus brevior Lydekker, 1889

1889 *Cimoliosaurus brevior* Lydekker: 243, fig. 75 (generic mis-spelling).
1911 *Muraenosaurus brevior* (Lydekker) Sauvage: 186–215.
1963 *Cimoliasaurus brevior* Lydekker; Persson: 24.

HOLOTYPE. 41955, 6 cervical centra of a 'juvenile' from the Kimmeridge Clay of Weymouth, Dorset.

STATUS. *Nomen dubium.*

Plesiosaurus brevis Owen, 1854

HOLOTYPE. R.C.S. 249, which was a cervical centrum from the Oxford Clay of Wiltshire. Destroyed by a fire in the Royal College of Surgeons Museum.

STATUS. *Nomen dubium; nomen oblitum.*

Plesiosaurus carinatus Phillips, 1871 (*non* Cuvier, 1824)

HOLOTYPE. See *Plesiosaurus phillipsi* Sauvage, 1879 (p. 323).

STATUS. Junior homonym, rejected and replaced by *P. phillipsi* Sauvage, 1879*a*.

Plesiosaurus doedicomus Owen, 1840

HOLOTYPE. R.273, a badly-eroded indeterminate bone, not of a plesiosaur.

STATUS. *Nomen dubium.* (Not plesiosaurian).

Cimoliasaurus durobrivensis Lydekker, 1889

HOLOTYPE. R.2428.

STATUS. Subjective junior synonym of *Muraenosaurus leedsii* Seeley, 1874*a* (see p. 284).

Plesiosaurus ellipsospondylus Phillips, 1871

HOLOTYPE. U.M.O. J.12083 and J.25942–9, nine associated cervical vertebrae from the Kimmeridge Clay of Shotover, Oxfordshire.

STATUS. *Nomen dubium; nomen oblitum.*

Plesiosaurus hexagonalis Phillips, 1871

Holotype. U.M.O. J.12068, a caudal centrum from the Kimmeridge Clay of Cowley Pit, Oxfordshire.

Status. *Nomen dubium; nomen oblitum.*

Plesiosaurus infraplanus Phillips, 1871

Syntypes. U.M.O. J.12069, J.12087 and J.12088, isolated single cervical centra from the Kimmeridge Clay of Stanford, Brill and Shotover (respectively), Oxfordshire.

Status. *Nomen dubium; nomen oblitum.*

Plesiosaurus levis Owen, 1854

Syntypes. R.C.S. 245 and 246, which were two dorsal vertebrae from the Kimmeridge Clay of Shotover Hill, Oxfordshire. Destroyed by fire at the Royal College of Surgeons Museum.

Status. *Nomen nudum; nomen oblitum.*

Plesiosaurus manselii Hulke, 1870

Holotype. 40106.

Status. Subjective junior synonym of *Colymbosaurus trochanterius* (Owen, 1840) (see p. 316).

Plesiosaurus megapleuron Owen, 1854

1854 *Plesiosaurus megapleuron* Owen: 60.
1959 *Colymbosaurus megapleuron* (Owen) Delair: 65.

Holotype. R.C.S. 233, which consisted of four cervical vertebrae. Destroyed by fire at the Royal College of Surgeons Museum.

Status. *Nomen nudum.*

Plesiosaurus oxoniensis Phillips, 1871

Syntypes. Phillips (1871) mentioned numerous finds of material from various Oxford Clay sites in Oxfordshire preserved in the University Museum, Oxford. These included 6 cervical vertebrae, various dorsal vertebrae, rib fragments, 8 caudal vertebrae, a pectoral girdle (described as a pelvis), a femur and several other paddle bones. These cannot now be identified amongst a mass of unlabelled plesiosauroid bones (H. P. Powell, personal communication).

Status. *Nomen dubium* (See discussion of synonymy of *Cryptoclidus eurymerus*, pp. 257–8).

Plesiosaurus phillipsi Sauvage, 1879(*a*)

Holotype or syntypes. U.M.O. J.12070 and J.25920–7, one cervical, two pectoral and six dorsal vertebrae from Quainton, Buckinghamshire.

Status. *Nomen novum* for *P. carinatus* Phillips, 1871 (*non* Cuvier, 1824); see above. *Nomen dubium*; *nomen oblitum.*

Plesiosaurus planispondylus Damon, 1860

Syntypes. 'Saurian bones' from the Oxford Clay of Dorset. These are believed to have been in the Dorset County Museum, Dorchester, but are now lost (Delair 1959).

Status. *Nomen nudum.*

Muraenosaurus platyclis Seeley, 1892

Holotype. R.2678.

Status. Subjective junior synonym of *Muraenosaurus leedsii* Seeley, 1874*a*. (see p. 284). Type species of the genus *Tremamesacleis* White, 1940.

Muraenosaurus (Cryptoclidus) platymerus Seeley, 1892

Holotype. R.2412.

Status. Subjective junior synonym of *Cryptoclidus eurymerus* (Phillips, 1871) (see p. 258); *nomen oblitum*.

Plesiosaurus plicatus Phillips, 1871

1871 *Plesiosaurus plicatus* Phillips: 313, figs 118, 119.
1889 *Cimoliosaurus plicatus* (Phillips) Lydekker: 234 (generic mis-spelling).
1895*c* *Muraenosaurus plicatus* (Phillips) Andrews: 429.

Holotype or syntypes. U.M.O. J.25929–41, 8 cervical and 5 dorsal vertebrae from the Oxford Clay of St Clements, Oxfordshire.

Status. *Nomen dubium.*

Pliosaurus portlandicus Owen, 1869

Holotype. 40640.

Status. Subjective junior synonym of *Colymbosaurus trochanterius* (Owen, 1840) (see p. 316).

Plesiosaurus subdepressus Owen, 1854

Holotype. R.C.S. 248, which was a cervical centrum from the Kimmeridge Clay of Nuneham, Oxfordshire. Destroyed by fire at the Royal College of Surgeons Museum.

Status. *Nomen nudum; nomen oblitum.*

Apractocleidus teretipes Smellie, 1915

Holotype. H.M.G. V.1091.

Status. Subjective junior synonym of *Cryptoclidus eurymerus* (Phillips, 1871) (see p. 258); type species of the genus *Apractocleidus* Smellie, 1915.

Plesiosaurus truncatus Owen, 1854

1854 *Plesiosaurus truncatus* Owen: 59.
1889 *Cimoliosaurus truncatus* (Owen) Lydekker: 230 (generic mis-spelling).
1911 *Muraenosaurus truncatus* (Owen) Sauvage: 186–215.

Holotype. R.C.S. 228, which was a cervical centrum of a 'juvenile' from the Kimmeridge Clay of Shotover, Oxfordshire. Destroyed by fire at the Royal College of Surgeons Museum.

Status. *Nomen dubium.*

Plesiosaurus validus Phillips, 1871

Syntypes. U.M.O. J.28542–56, 15 cervical vertebrae from the Kimmeridge Clay of Cumnor, Oxfordshire, together with cervical, dorsal and caudal vertebrae from other Kimmeridge Clay sites including Baldon, Oxford. These latter syntypes cannot now be distinguished from other unlabelled material in the Museum.

STATUS. *Nomen dubium; nomen oblitum.*

Plesiosaurus winspitensis Seeley, 1871

HOLOTYPE. S.M.C. J.5345–6, two associated cervical vertebrae from the Portland Stone of Winspit, Dorset. Seeley (1871) also mentioned a pectoral vertebra, but this cannot now be found.

STATUS. *Nomen dubium; nomen oblitum.*

Discussion of the phylogeny and classification of plesiosaurs

Historical review

In 1821, Conybeare proposed the generic name *Plesiosaurus* for an animal whose structure he considered to be intermediate between *Ichthyosaurus* and the crocodiles. In 1824 he named the type species *Plesiosaurus dolichodeirus* on account of its long neck.

The ordinal name Plesiosauria was proposed and defined by de Blainville (1835) to include only the plesiosaurs, and is now established by useage rather than by priority (Welles 1943) as the name for an order of the subclass Sauropterygia Owen, 1860 ('suborder' and 'order' of Welles; present ranking after Tarlo 1967).

Owen made the first major division of the order by introducing the name *Pliosaurus* (in 1841 as a subgenus, in 1861 as a genus) to include all plesiosaurs with large 'canine' teeth, a large head and a short neck. The genera *Plesiosaurus* and *Pliosaurus* are now the types of the two major superfamilies, but the significance of Owen's division was not appreciated until 1924, when Watson discussed the evolution of the group and distinguished divergent lines of long-necked and short-necked forms ranging from the Lower Jurassic to the Upper Cretaceous.

The years between 1861 and 1943 saw a host of attempts to produce classifications in the absence of an understanding of evolution. Most of these attempts were based upon isolated skeletal characters rather than upon a synthesis of characters taken from the whole skeleton. Characters so used include the relative length of the neck (Kiprianov, 1882; Seeley, 1892; Bogolubov, 1912; Nopcsa, 1928); the length of individual centra (Owen, 1865); the number of cervical rib-heads (Seeley, 1892; Williston, 1925; Woodward, 1932; Kuhn, 1935); the presence or absence of an interclavicle (Seeley, 1874*b*; Sauvage, 1879*a*) and the general structure of the pectoral girdle (White, 1940).

Of some historical importance was a classification proposed by Seeley (1892). He divided the Plesiosauria into Dicranopleura and Cercidopleura on the basis of double-headed or single-headed cervical ribs, and then subdivided the Dicranopleura into Brachydeira and Dolichodeira on the basis of a relatively short or long neck (a few intermediate forms being termed 'mesodeiran'). He overlooked the fact that his Cercidopleura also contained brachydeiran and dolichodeiran forms. Although his classification was little used, his names have remained widely employed as descriptive terms, and his emphasis on the number of cervical rib-heads has influenced several taxonomists including Welles.

In 1943, Welles emphasized the importance of basing the classification upon a synthesis of all observable characters, and compiled a list of 22 characters available for study. He recognized that several characters (including general increase in size, reduction of cervical rib-heads from two to one, shortening and broadening of epipodials and development of hyperphalangy) represent progressive evolutionary trends which apply to all lineages and are therefore of secondary importance in taxonomic subdivision. Of greater importance are those characters of opposing nature which occur simultaneously throughout the group, such as the tendencies to lengthen or shorten the neck, and to shorten or lengthen the head and the pelvis. These are the distinguishing features of Watson's (1924) phyletic lines, and from them Welles constructed his diagnoses of the superfamilies Plesiosauroidea and Pliosauroidea. He then subdivided the superfamilies into grades using characters of cervical ribs and epipodials.

In 1962 Welles modified his classification to include the Pistosauridae, but his criteria remained essentially unchanged. Thus the primitive families Plesiosauridae and Pliosauridae are dicranopleurous with elongate epipodials, and the advanced families Elasmosauridae and Dolichorhynchopidae[1] are cercidopleurous with short epidodials.

Welles' division of the superfamilies into grades on the basis of double or single-headed cervical ribs has the advantage of easy practical application; yet Welles did not trust the scheme fully, and placed the English Upper Jurassic plesiosauroid genera (all of which are cercidopleurous) in the primitive dicranopleurous family Plesiosauridae, this presumably on account of their moderate length of neck. It would seem that the precise position of the supposed 'mesodeiran' forms of Seeley (1892) was even here considered to be a problem.

Three classifications have been published subsequently: by Persson (1963), Novozhilov (1964) and Romer (1966, based largely on his work of 1956). Welles' division into the superfamilies Plesiosauroidea and Pliosauroidea has been followed in each classification; but by the use of criteria differing from both those of Welles and of each other these authors have distinguished additional families containing 'mesodeiran' forms. Thus, Persson and Romer have each divided the superfamilies into three (differing) families, and Novozhilov has distinguished four plesiosauroid and five pliosauroid families.

Unfortunately, Persson, Novozhilov and Romer have not listed consistently the state of every character for each family diagnosis. In consequence, the differences between families are not absolutely clear, nor can their classifications be compared. In practice, genera must be assigned to families because of a comparative similarity between the generic and family diagnoses, and not through an absolute conformity to the diagnosis of one family.

The most serious criticism of these three recent classifications is, however, the lack of supporting phylogenetic theory. Novozhilov and Romer did not attempt to relate their classifications to evolution, except in so far as Romer (1956) likened the branching of plesiosaurian phylogeny to that of a bush, with the main branches having a common stock. By means of a figure, Persson suggested that his three pliosauroidean families Rhomaleosauridae, Pliosauridae and Polycotylidae[2] represent grades of a single lineage, whereas in the Plesiosauroidea the Jurassic family Plesiosauridae was ancestral to the two Cretaceous families Cimoliasauridae[2] and Elasmosauridae. Persson did not support this suggestion on osteological grounds. On the contrary, he used as his principal taxonomic criterion the comparative proportions of cervical vertebrae; it is argued below that the extent of variation of such proportions, even intraspecifically, is such as to render them unsatisfactory as taxonomic characters.

It is generally agreed (Welles 1943, 1962; Romer 1956, 1966; Persson 1963; Novozhilov 1964) that the Triassic nothosaurs were ancestral to the Jurassic and Cretaceous plesiosaurs, and that the genus *Pistosaurus* and allied Triassic genera form a phylogenetic link (or links) between the suborders. Traditionally these genera were classified with the Nothosauria, but in the four most recent classifications at least some of the pistosaurs have been included in the Plesiosauria. Welles (1962) included the family Pistosauridae within the Plesiosauroidea; Persson (1963) ranked this group as a separate superfamily; and Novozhilov (1964) and Romer (1966) included within the Pistosauroidea a second Triassic family, the Cymatosauridae. A widely acceptable classification of these forms is unlikely to become available until both the nothosaurs and the Lower Jurassic plesiosaurs have received adequate revision, and their phylogenetic interrelationship is understood.

As a result of discussion of taxonomic characters and a revision of theories on the phylogeny of plesiosaurs (below), it is concluded that existing schemes for the classification of plesiosaurs are inappropriate. A new classification is therefore proposed.

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[1] The name Dolichorhynchopidae Welles, 1962, is a junior synonym of Leptocleididae Romer, 1956; *non* Leptocleididae White, 1940, which is itself a junior synonym of Rhomaleosauridae Nopcsa, 1923.

[2] The names of the family type genera *Polycotylus* and *Cimoliasaurus* were found by Welles, 1962, to be *nomina dubia.*

Characters employed in taxonomy

In 1943, Welles listed and discussed 22 skeletal features at that time known to be variable amongst plesiosaurs, and emphasized the importance of considering all of these together when compiling a classification. Modern classifications reflect this thinking, being based upon a synthesis of many characters; however, there is as yet no general agreement on a scheme of classification below the superfamily level. This situation would appear to stem from a general lack of understanding of evolution within each superfamily. This in turn has led to a widespread misunderstanding of the relevance of each character to ontogeny or phylogeny.

At the present time the best-known plesiosaur material is that in the United States, since this has been reviewed extensively by Welles (1943, 1952, 1962). Unfortunately the American species which he studied do not seem to be represented adequately by specimens of differing and intergrading developmental stages, and so he has not always been able to recognize and distinguish between ontogenetic variants and variants of real evolutionary (and hence taxonomic) significance. The same would apply to English material and its interpretation were it not for the preservation of representative populations of some species in the unique Leeds Collection. Study of this material has enabled the ontogeny of several skeletal features to be observed directly; and furthermore the interspecific variation of certain features of the skulls of these forms has provided additional characters for use in taxonomy.

A total of 38 variable features of the plesiosaurian skeleton are recognized here and are available for consideration as taxonomic characters. These are listed and discussed below.

1. GENERAL SIZE. There is a trend towards increase in size with time which is shown throughout the suborder. Most early Jurassic forms have an overall length of 3–5 m, whereas late Cretaceous forms may reach a length of 8–12 m and be proportionally more massive.

2. RELATIVE SKULL SIZE. The skull may remain relatively small (with respect to the trunk), or may show a chronological trend towards increase in size. The ratio of skull-length to neck-length has been used frequently as an index of skull size, but this is misleading, as decrease of neck length is correlated with increase of skull size in many but not all forms.

3. TOOTH FORM. Large-skulled plesiosaurs have teeth with relatively large roots and a relatively short, wide-based and slightly curving crown which may show considerable wear on its tip. Small-skulled forms have teeth with smaller roots, and with proportionally slimmer crowns which are rather more curved and show little or (usually) no wear on their tips. Crowns are usually circular in section, but may be subtriangular (in Kimmeridgian pliosaurs: Tarlo 1960), or be buccolingually compressed and show a curvature of up to 75° (in *Kimmerosaurus*).

4. TOOTH ORNAMENT. The teeth of all plesiosaurs except *Kimmerosaurus* are ornamented by numerous longitudinal ridges. The pattern of these ridges is distinctive and therefore taxonomically useful in some genera (in *Cryptoclidus*, and in Oxford Clay pliosaurs reviewed by Tarlo 1960), but since little attention has been paid to it in forms outside the Upper Jurassic, the extent of its usefulness is not known. There is some ontogenetic variation, ornamental ridges being more prominent and sometimes more numerous on the teeth of older individuals.

5. LOWER JAW SYMPHYSIS. The symphysis is generally described as either short or long. A short symphysis is a simple unexpanded median union of the rami, relates only to the first pair of teeth and is correlated with a small skull. A long symphysis shows median antero-posterior expansion, is correlated with a relatively large skull and relates to the alveoli of several pairs of teeth (the number of pairs is variable).

6. NUMBER OF PAIRS OF DENTARY TEETH. The range of variation in lower tooth numbers is much less in Lower Jurassic genera (about 24–30) than in those from the Upper Cretaceous

(about 14–58), and trends to increase or decrease the toothrow are evident. The teeth of Lower Jurassic plesiosaurs have seldom been counted accurately, but from personal observations *Plesiosaurus dolichodeirus* (small-skulled, short symphysis) has about 24 teeth each side, whereas *Macroplata longirostris* and *Rhomaleosaurus zetlandicus* (large-skulled, long symphysis) have about 30 each.

The Upper Jurassic large-skulled forms have from 25 (in *Simolestes*) to 40 (in *Peloneustes*) (Tarlo 1960), and the Upper Cretaceous genus *Dolichorhynchops* has 26 pairs (*D. osborni*) or 34 pairs (*D. willistoni*) (Welles 1962). There is therefore no trend in these forms to increase or decrease the number of lower teeth, which averages consistently about 30 pairs.

The small-skulled forms, on the other hand, show a marked trend to decrease the lower teeth from 24 pairs: the Upper Jurassic genus *Muraenosaurus* has about 22 pairs (present work), and in Upper Cretaceous forms this is reduced to between about 18 (in *Styxosaurus*) and 14 (in *Thalassomedon*) (Welles 1952). Only two genera with a short symphysis do not follow this trend: the Upper Jurassic genus *Kimmerosaurus* has 36 pairs (present work), and the South American Upper Cretaceous genus *Aristonectes* has 58 pairs of lower teeth (Cabrera 1941).

There is slight ontogenetic variation in this character, 'adults' having one or two pairs of dentary teeth more than 'juveniles'.

7. Number of pairs of premaxillary teeth. There are usually 5 teeth borne by each premaxilla, and this number is probably primitive for the group. Large-skulled forms appear always to retain this number. In the Upper Jurassic small-skulled genera *Muraenosaurus* and *Tricleidus* the most anterior tooth is reduced in size (present work), as in most Cretaceous forms, and in the Cretaceous genera *Thalassomedon* and *Styxosaurus* it is lost, reducing the count to four (Welles 1952). There are only three genera in which the premaxilla bears more than 5 teeth, these being *Cryptoclidus* and *Kimmerosaurus* with 6 and at least 8 respectively (present work), and *Aristonectes* with 15 (Cabrera 1941).

8. Regularity of dentition. Large-skulled forms (all with a long symphysis) tend to develop large 'caniniform' teeth towards the tip of the snout around the symphysis and on the premaxillae. Posterior to these the teeth are smaller and form a regularly decreasing series. Early small-skulled forms (all with a short symphysis) have a regular dentition without the precocious development of 'caniniform' teeth. Later forms showing an increase in tooth number (*Cryptoclidus*, *Kimmerosaurus* and *Aristonectes*) retain this regularity (present work; Cabrera 1941), whereas in the remaining later genera (showing a trend towards reduction in tooth number) the regularity becomes disrupted by the reduction in size of the most anterior premaxillary tooth and by increase of all other premaxillary teeth together with one or two maxillary teeth in a position beneath the anterior margin of the orbit (present work). The lower toothrow in small-skulled forms is generally regular, and the largest teeth occur beneath the maxillo-premaxillary suture.

9. Parietal crest. When Williston (1903) stated that the parietals may form a high thin crest or be without such a crest he was almost certainly referring to ontogenetic development, the sagittal crest being the last part of the parietals to ossify. However, a crest is not developed in *Kimmerosaurus*, and in this genus only are the lateral excavations of the parietals separated by at least 1 cm of finished dorsal surface (present work).

10. Pterygoid structure. Usually the pterygoid is overlapped posterolaterally by the quadrate, which develops a rough socket for its reception; but in *Kimmerosaurus* the pterygoid overlaps the quadrate posteromedially, and the quadrate produces a large flange which extends forward along the anterolateral surface of the pterygoidal quadrate ramus. The manner of contact with the braincase is variable, and the form of the facets and processes on both the pterygoid and the braincase elements differs from genus to genus. Details of pterygoidal structure are known only for English Upper Jurassic small-skulled genera (present work), and so wide-ranging conclusions cannot be drawn.

11. Paroccipital process. The relative length and thickness of the paroccipital process is variable (present work). In *Muraenosaurus* and *Tricleidus* it is long and slender and resembles those of Cretaceous genera figured by Welles (1943, 1952, 1962). In *Cryptoclidus* it is shorter, and in *Kimmerosaurus* it may reasonably be described as short and massive by comparison with most genera. This character is inadequately described for most genera, and wide-ranging conclusions cannot be drawn.

12. Occipital condyle. Welles (1962) described the occipital condyle as either 'projecting, hemispherical, marked off by a constricting groove' (in the Plesiosauroidea) or 'short and close to the skull' (in the Pliosauroidea). The constricting groove develops ontogenetically in at least the genus *Muraenosaurus* (present work), being most prominent in the oldest individuals, but its presence is indeed characteristic of small-skulled forms. The occipital condyle of almost all small-skulled genera is formed from the basioccipital only; but in *Cryptoclidus* and *Kimmerosaurus* (present work) its formation is shared by the pedicles of the exoccipitals. In these two genera the condyle is also very short, and is not ringed by a groove. A third genus with this structure might be *Aristonectes*; in this form the exoccipitals are not known, but the basioccipital part of the condyle is described as very short, without a separating groove (Cabrera 1941). The condyles of most large-skulled forms have not been described adequately, and a detailed comparison cannot be made.

13. Atlas. Linder (1913) distinguished between two types of atlas formation: 'a. Atlas centrum forms most of the support for the condyle. b. Atlas intercentrum and arches ring the centrum and may exclude it from the condyle'. However, the atlas and axis fuse in 'adults' with complete obliteration of all sutures, and in 'juveniles' the very small atlas intercentrum and neural arch are usually lost. Although apparently variable, this character is scarcely known and therefore only of dubious taxonomic value.

14. Number of cervical vertebrae. The primitive number of cervical vertebrae for the suborder Plesiosauria is probably around 28 to 32 (there are 32 in *Plesiosaurus* and *Macroplata*, and 28 in *Rhomaleosaurus*; primitive Lower Jurassic genera). By the Cretaceous the number of cervical vertebrae ranges from 71 (in *Elasmosaurus*) to 13 (*Brachauchenius*). Trends to increase or decrease the number of cervical vertebrae are evident, and are correlated with small skulls and a short symphysis (increase in numbers) or with large skulls and a long symphysis (decrease in numbers). The primitive number of cervical vertebrae is apparently retained only in one Cretaceous genus, that being *Aristonectes*, with 25 preserved and an estimated 5 missing (Cabrera 1941).

15. Proportions of vertebral centra. Early writers placed much taxonomic emphasis on the variations of central proportions, probably because isolated centra are the most frequent finds of plesiosaurian material. After some statistical work, Welles (1952) demonstrated that central proportions vary intergenerically (taxonomically important variation), but also vary according to the ontogeny (centra shorter in younger individuals) and to position on the vertebral column (neither type of taxonomic consequence). In the present work it is observed that the centrum breadth is always greater than the height (or in dorsals is subequal to height), and so for all regions of the column the ratios of these parameters are of no taxonomic use, whereas the ratio of length to average diameter, especially of the neck region, shows intergeneric variation. In the neck, proportional length is correlated with number of cervical centra such that a relatively long (or short) neck is usually produced both by increasing (or decreasing) the number of vertebrae and by increasing (or decreasing) the proportional length of each. The vertebrae with the greatest proportional length (or shortness in short-necked forms) are always those in the anterior one-third of the neck.

Relative neck length has been recognized as of major taxonomic significance since the publications of Owen (1869), Lydekker (1889) and Seeley (1892), but there has been much confusion of what are here regarded as three interrelated characters. The true relative neck length (i.e. relative to the length of the trunk) is itself a function of the number of cervical vertebrae and their individual relative lengths. For example, *Plesiosaurus dolichodeirus*

(Lower Jurassic) and the genus *Cryptoclidus* (Upper Jurassic) both have 32 cervical vertebrae which are similarly proportioned; however, the former is always regarded as 'dolichodeiran' whereas the latter, having a neck which is relatively shorter than in contemporary genera such as *Muraenosaurus*, is described frequently as 'mesodeiran' (e.g. Delair 1959, Persson 1963). The term 'mesodeiran' is meaningless, and is also misleading since its use implies evolutionary change from the primitive condition.

16. LATERAL KEEL ON CERVICAL CENTRA. The 'lateral keel' (Welles 1952, 1962) or 'lateral longitudinal ridge' (Welles 1943, Persson 1963) is a small but prominent crest of bone which, if it occurs, divides the lateral surface of cervical centra longitudinally into subequal upper and lower concave areas. It is correlated with neck length, and is almost invariably present on anterior cervicals of long-necked forms of the Upper Jurassic and Cretaceous. Its development is presumably associated with the strengthening of neck muscles and ligaments which would have been required for the efficient mechanical management of the elongated neck. It is absent in all short-necked forms.

17. ARTICULAR FACES OF CENTRA. The centra of primitive forms have concave articular faces, but these tend to become flat in long-necked forms and especially in Cretaceous genera. There is also some ontogenetic variation (present work): in 'juveniles' the articular faces tend to be relatively flat and have angular edges and there may be a small central pit, whereas in 'adults' the pit may fill and the edges ossify so as to become more rounded and cause the face to be more concave.

18. SURFACE ORNAMENT OF CENTRA. Superficial surface features of centra such as 'plications', rugosities, extent of the development of a ventral keel and the position of nutritive foramina, have been variously emphasized by early writers. Such features are very variable, and also vary ontogenetically (present work); for example, 'plications' found on the centra of 'juveniles' of *Muraenosaurus* develop into less regular rugosities in the 'adult'. Nutritive foramina follow a regular pattern, being close together (with the development of a keel between them) in anterior cervicals, moving farther apart in posterior cervicals, ascending the lateral surface in dorsals and sacrals and either disappearing or returning to the ventral surface in an irregular fashion (usually multiplied in number) in caudal centra. Surface ornament cannot be relied upon as a primary character for distinguishing species, but may be of secondary use in some cases, as with the forms described by Tarlo (1960).

19. FUSION OF NEURAL ARCHES AND RIBS WITH CENTRUM. In Upper Jurassic forms the fusion of axial skeletal elements is ontogenetic: neural arches and cervical and caudal ribs are free in 'juveniles', but fuse with complete obliteration of the sutures in the 'adult' (present work). Welles (1962) regarded fusion of neural arches and centra as of minor taxonomic importance in Upper Cretaceous forms, and gave 'arches not fused to centra' as a character in his diagnosis of the Lower and Middle Jurassic family Plesiosauridae. It is most unlikely that this character can be applied taxonomically at the family level; but it is nevertheless possible that free neural arches in the 'adult' may prove to be a feature of some primitive forms.

20. HEIGHT OF NEURAL SPINE. Welles (1943) included 'neural spines high or short' in his list of characters available for taxonomic consideration; however, this variation is ontogenetic, the bony part of the neural spines being proportionally shorter in 'juveniles' since they are terminated in cartilage.

21. CERVICAL RIB HEADS. The cervical ribs of all Lower Jurassic plesiosaurs are double-headed (dicranopleurous), and in consequence the cervical centra bear paired facets for the tuberculum and capitulum. There is a trend throughout the whole group to combine the heads into a single structure (ribs cercidopleurous). In forms with a short symphysis this has occurred by the Upper Jurassic, whereas in forms with a long symphysis it is delayed until the Cretaceous. Welles (1962) based the subdivision of his superfamilies upon the number of cervical rib heads; but he did not apply his diagnoses strictly, and included the English Upper Jurassic cercidopleurous genera in his dicranopleurous family Plesiosauridae.

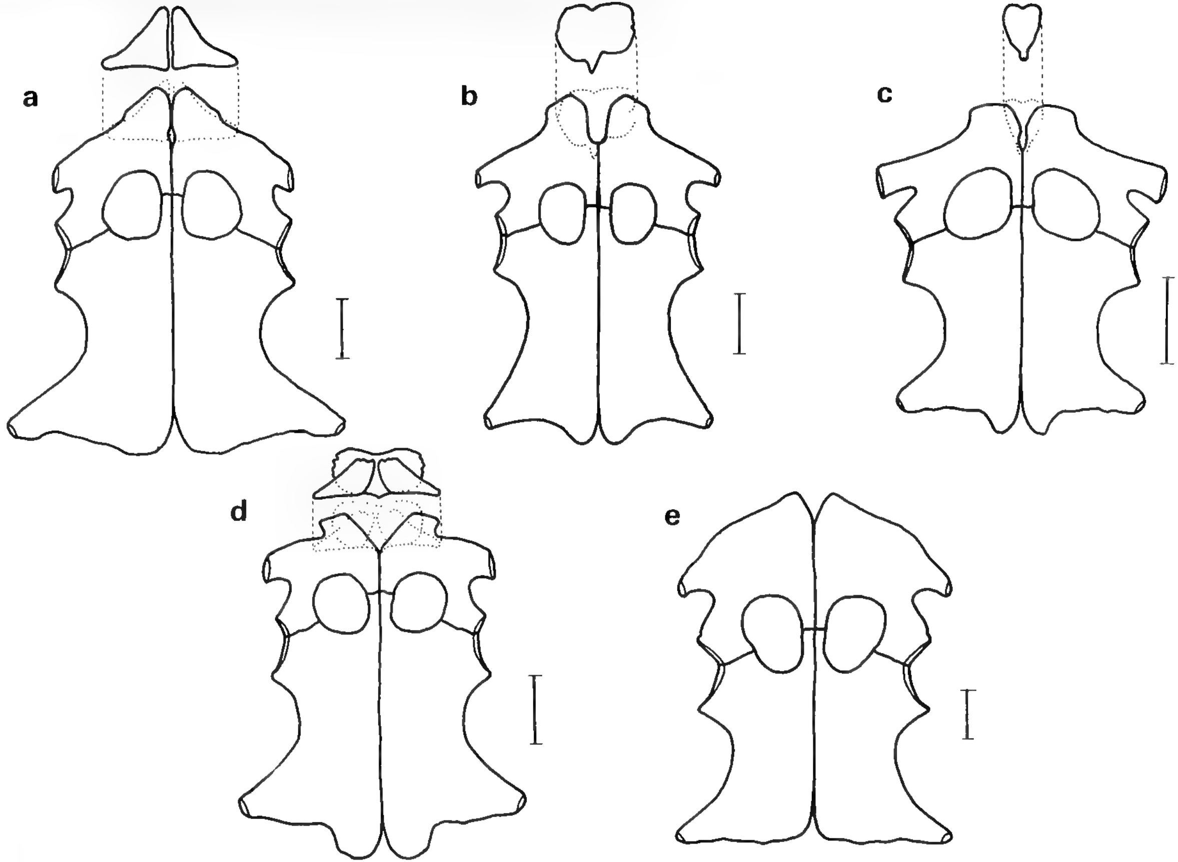

Fig. 43 Comparison of pectoral girdles of English Upper Jurassic plesiosauroids, with dermal elements moved forwards to show ventral rami of scapulae. Dorsal profiles: a, *Cryptoclidus eurymerus* R.2616; b, *Muraenosaurus leedsii* R.3704; c, *M. beloclis* R.1965; d, *Tricleidus seeleyi* R.3539; e, *Colymbosaurus trochanterius* M.M. LL.5513–8. Scale lines represent 10 cm.

22–23. Clavicles and interclavicle. Variations in the development and shape of the clavicles and the interclavicle (elements which are typically very conservative in other reptile groups) have been overemphasized frequently in taxonomic discussion, and have been taken as of primary taxonomic importance at generic and even family level (e.g. by Andrews 1910 and White 1940). It is important that this variation be put into proper perspective.

In other reptile groups the clavicles and interclavicle play important functional roles for which they are structurally adapted. Thus any change in their form reflects a change in their function, and is of importance at a relatively high taxonomic level. However, in all but the earliest plesiosaurs the ventral rami of the scapulae become greatly expanded and meet in the ventral midline superficial to the interclavicle and clavicles. Muscles which once had their origins on the ventral surfaces of the dermal girdle must therefore have transferred to the ventral rami of the scapulae, which thus replace the interclavicle and clavicles both mechanically and as sites for muscle origin.

In plesiosaurs, therefore, these elements are no longer functionally important, and cease to be structurally adapted for the lost functions. Tendencies to modify, reduce and even to lose the clavicles and interclavicle are evident, but as these changes are not of functional significance they must be regarded as of only minor taxonomic importance. Indeed, it is possible to demonstrate variation in the relative development of the dermal pectoral girdle elements within a single species, as for example in *Muraenosaurus leedsii* (see Fig. 21, p. 290).

Clavicles and the interclavicle are retained in a moderately well-developed state in several Upper Cretaceous genera (e.g. *Thalassomedon, Morenosaurus*), and so any supposition that they had been lost in earlier genera in which they are unknown (e.g. *Colymbosaurus*) must be regarded with suspicion unless the number of otherwise entire specimens is large. However, there are forms (e.g. *Muraenosaurus beloclis, Cryptoclidus eurymerus*) in which the clavicles or interclavicle or both are preserved but reduced to insignificance; this trend towards reduction could well have resulted in the loss of these elements in their descendants. The absence of clavicles or interclavicle is an unreliable negative character which should be used with much caution in taxonomic discussion.

24. Ventral process of scapula. In all but the earliest plesiosaurs the ventral processes of the scapulae in 'adults' met in the ventral midline superficial to the clavicles and interclavicle. In 'juveniles' they were separated to a varying degree by cartilage, as was demonstrated by Andrews (1895*a*) in *Cryptoclidus eurymerus*; such variation of length is therefore ontogenetic. The relative width of the ventral process in 'adults' is, however, of some taxonomic use. The process is relatively narrow in many early forms; it tends to remain so in short-necked large-skulled genera, and may become progressively broader in long-necked forms.

25. Pectoral bar. The presence or absence of a median pectoral (scapulocoracoid) bar has been overemphasized and misunderstood frequently by taxonomists. In many Lower Jurassic plesiosaurs this bar does not develop even in the 'adult'; but in Upper Jurassic genera its development is typically ontogenetic, ossification being completed in the 'adult' and frequently followed by fusion of the scapulae and coracoids in 'old adults' (present work). It is probable that many of the Upper Cretaceous forms which have been described (e.g. by Welles 1962, subfamily Alzadasaurinae) as lacking the pectoral bar are in fact based upon 'juvenile' individuals.

26. Posterior cornua of coracoids. The development of cornua is ontogenetic, and so only 'adult' specimens should be considered. There is variation from an almost complete absence of cornua (the width across which is less than the interglenoid width) to a strong projecting development which reaches an extreme condition in *Cryptoclidus* (present work; see Fig. 43).

27. Intercoracoid foramen. The coracoids unite medially along their entire length in all Jurassic forms, and also in Cretaceous large-skulled short-necked forms, but are character-

istically separated posteriorly by a wide intercoracoid foramen in Cretaceous long-necked forms.

28. Anterior border of pubis. Welles (1943 : 199) stated that the 'pubes . . . may become convex anteriorly or concave'. This, however, appears to be an ontogenetic character. 'Juveniles' have rounded pubes which are therefore convex anteriorly; but as ossification reaches the region of the posterior gastralia, concavities in the anterior border appear which mark the places of contact and possible interlock with the plastron (present work).

29. Relative length of ischia. The ischia are relatively short anteroposteriorly in long-necked forms and relatively long in short-necked large-skulled forms (correlation first noticed by Mehl, 1912).

30. Pelvic bar. Welles (1962) divided his family Elasmosauridae into two subfamilies upon the presence or absence of a pectoral bar and a median pelvic bar. However, as with the pectoral bar, anterior growth of the ischia and posterior growth of the pubes towards each other in the midline is an ontogenetic feature. Complete ossification of the pelvic bar (as in *Elasmosaurus platyurus* and *Brancasaurus brancai*) is probably not of major taxonomic significance.

31. Ilial breadth. Welles (1943 : 199) listed 'ilia becoming narrow proximally or

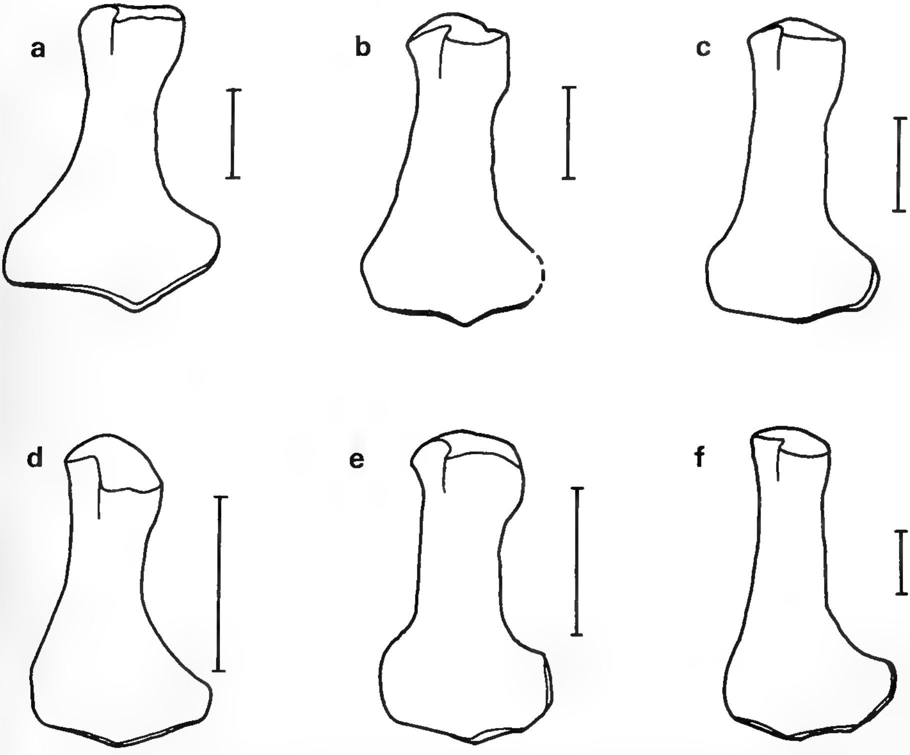

Fig. 44 Comparison of humeri of English Upper Jurassic plesiosauroids, dorsal profiles: a, *Cryptoclidus eurymerus* H.M.G. V.1104; b, *C. richardsoni* R.6696; c, *Muraenosaurus leedsii* R.2426; d, *M. beloclis* R.1965; e, *Tricleidus seeleyi* R.3539; f, *Colymbosaurus trochanterius* M.M. LL.5513–8. Scale lines represent 10 cm.

remaining broad', but without further comment. No evolutionary trends in ilial development have been demonstrated, and irregularities in the form of this element are therefore only of minor taxonomic use.

32. Propodial proportions. In short-necked large-skulled forms (which also have elongate ischia) the femur is larger than the humerus, and both propodials tend to have a slim and elongated appearance which Welles (1943, 1962) termed 'pendulous'. In all other forms the propodials are either equal in size or, more usually, the humerus is slightly larger than the femur; these propodials have a more 'massive' (short and stout) appearance.

33. Capitulum and tuberosity (in humeri) or trochanter (in femora). Welles (1943 : 199) stated that these '. . . may remain connected or show changes leading up to complete separation'. These changes are entirely ontogenetic (present work). In 'juvenile' individuals the capitulum and tuberosity (or trochanter) are covered by a single sheet of cartilage, but as ossification proceeds the isthmus between them becomes reduced in width, and they may eventually become separated completely by a strip of periosteal bone in 'old adults'.

34. Number of epipodials. In early Jurassic forms there are two epipodials in each limb, and these remain the principal epipodials in all later forms. There is. however, a tendency in several genera to produce additional postaxial ossifications in the epipodial row; this is not of taxonomic importance above the generic level.

35. Relative length of epipodials. The epipodials of primitive forms are elongate and dumb-bell shaped, recalling the shape of the epipodials of a terrestrial ancestor. There is a trend throughout the entire order for the epipodials to shorten and widen until they resemble mesopodials in shape, and they may be considerably broader than long.

36. Epipodial foramen. Welles (1943) stated that the epipodial foramen may be retained or lost. In most forms it is evident between the epipodials in both 'juvenile' and 'adult' specimens, but in a few genera (notably in *Cryptoclidus*) it is not revealed until ossification reaches the advanced 'old adult' stage (present work). It is not possible to prove its absence in any species, since in no specimens apparently lacking the foramen are the epipodials actually fused.

37. Proximal shift of fifth metapodial. In primitive forms the five phalangiform metapodials lie distal to the distal mesapodial row. There is a trend throughout the entire order to shift the fifth (most posterior) metapodial proximally into the distal mesapodial row, and this is achieved fully in many Upper Jurassic forms and almost all Cretaceous forms.

38. Extent of hyperphalangy. There is a general trend to increase the number of phalanges. Early Jurassic forms show hyperphalangy up to about ten in the longest digit, and this is increased to a maximum (Welles 1962) of seventeen phalanges in the longest digit in Cretaceous forms.

Analysis of characters

It is probably true to say that constant variants of any of the above 38 variable features of plesiosaurian osteology could, in appropriate circumstances, prove sufficient for the taxonomic distinction of species, and several in combination might distinguish genera. Ranking of taxa above the generic level is more complicated since to be satisfactory the classification must reflect evolution. It is therefore necessary first to establish which variable characters are of phylogenetic significance, to assess their relative importance, and then to formulate a hypothesis of plesiosaurian phylogeny.

The 38 characters listed above may be grouped together into four categories of differing phylogenetic significance, as follows:

Category A. Eight characters (9, 18, 19, 20, 25, 28, 30 and 33) may be dismissed as of no phylogenetic significance since their variations are due largely or entirely to ontogenetic growth. Taxonomic use of these characters should be limited to specific and generic diagnoses; and even here they are likely to prove unsatisfactory.

CATEGORY B. The variation of six characters (10, 11, 13, 26, 31 and 36) is either apparently random (showing no evolutionary trends which may be correlated with those of other characters) or is inadequately known for conclusions about evolutionary trends and correlation to be drawn. A seventh character (4, tooth ornament) belongs largely in this category, except that there appears to be a trend towards reduction and ultimate loss of tooth ornament in the genera *Cryptoclidus* and *Kimmerosaurus*. These seven characters are taxonomically reliable, but as they apparently lack any phylogenetic significance (with the exception mentioned), their use should be limited at the present time to specific and generic diagnoses.

CATEGORY C. Eight characters (1, 21, 22, 23, 34, 35, 37 and 38) show progressive unidirectional evolutionary change which affects the entire order. These changes (general increase in size, reduction of the dermal elements of the pectoral girdle and improvements to the structure of the paddles) are associated largely with adaptation of a once-terrestrial body form to an aquatic mode of life, and occur irrespective of other changes which result in fragmentation of the group. Use of these characters in classification at the family-group level would produce chronologically horizontal divisions and separate all phyletic lineages into primitive and advanced grades.

CATEGORY D. The remaining fifteen characters (2, 3, 5, 6, 7, 8, 12, 14, 15, 16, 17, 24, 27, 29 and 32) exhibit variants of opposing nature which occur simultaneously. The variants frequently show divergent evolutionary trends which increase and accentuate their differences. Furthermore, the variants and trends of any one of these characters are found in association with particular variants and trends of several other characters within this category. Correlation of these associated variants and trends leads to the recognition of phyletic lineages and enables evolutionary hypotheses to be formulated. By combining the essentials of these correlated character variants into family-group diagnoses, and ranking the groups with respect to an evolutionary hypothesis, a classification may be produced which reflects evolution.

It is interesting to note that, of the fifteen characters listed in category D, the first seven occur in the skull. Emphasis in the higher classification of plesiosaurs should therefore be placed equally upon features of the skull and the postcranial skeleton, as is the case in the majority of reptile groups. That such equal emphasis has never before been given to the skull is explained by the relative lack of good skull material compared with the relative abundance of postcranial remains.

The phylogeny of plesiosaurs

In order to recognize phyletic lineages within the Plesiosauria it is necessary to undertake an analysis and correlation of the fifteen category D characters. If the genera *Cryptoclidus*, *Kimmerosaurus* and *Aristonectes* are omitted from consideration, such an analysis indicates clearly the presence of two distinct lineages which agree in essence with those recognized by Watson (1924) and Welles (1943, 1962) and classified by the latter as the superfamilies Plesiosauroidea and Pliosauroidea.

The first lineage ('plesiosauroidean' lineage of Welles 1943) includes forms which have relatively small skulls; a short mandibular symphysis; teeth with slim crowns not worn on their tips; a relatively broad scapular ventral ramus; relatively short ischia; and propodials which are 'massive' and of which the humerus is generally the larger. These forms show chronological trends to decrease the tooth number; to develop large premaxillary and maxillary teeth separated by smaller teeth around the maxillo-premaxillary suture; to increase the number of cervical vertebrae; and to increase the relative length of each cervical centrum. Advanced members of this lineage also develop platycoelous rather than amphicoelous vertebrae; a lateral keel on cervical centra; and a wide intercoracoid vacuity.

The second lineage ('pliosauroidean' lineage of Welles 1943) includes forms which have relatively large skulls; a long mandibular symphysis; teeth with relatively short, broad and strong crowns which frequently show considerable wear on their tips; a relatively narrow scapular ventral ramus; relatively long ischia; and propodials which are 'pendulous' and of which the femur is larger than the humerus. These forms show chronological trends to develop large teeth around the mandibular symphysis; to decrease the number of cervical vertebrae; and to decrease the relative length of each cervical centrum.

The known geological range of both these lineages extends from the base of the Jurassic to the Upper Cretaceous (a few indeterminate remains from Middle and Upper Triassic deposits have been recorded as plesiosaurian) and their ancestors are undoubtedly to be found amongst the nothosaurs of the Trias. Much has been suggested relating *Pistosaurus* to the 'plesiosauroidean' lineage (e.g. Edinger 1935; Welles 1943; Romer 1956), but the relationships of the 'pliosauroidean' lineage have been largely overlooked. Welles (1943) doubted that all plesiosaurs could have descended from pistosaurs, since the 'plesiosauroidean' and 'pliosauroidean' lineages do not show sufficient 'retrospective convergence'. Skull reconstructions of other nothosaurs, for example *Ceresiosaurus* (by Peyer, reproduced in Romer 1966: fig. 188) show that at least some forms had relatively large skulls and a long mandibular symphysis, and so it would seem probable that the two lineages had separate nothosaurian origins.

The English Upper Jurassic genera *Cryptoclidus* and *Kimmerosaurus* (described above), together with the South American Upper Cretaceous genus *Aristonectes* (described from an incomplete skull and partial postcranial skeleton by Cabrera 1941) show distinct characters and trends in their teeth and dentition and in the form of the occipital condyle, and at the same time lack the principal divergent trends which characterize the 'plesiosauroidean' and 'pliosauroidean' lineages. The dentition is regular, lacking regional precocious development. The number of cervical vertebrae (known in *Cryptoclidus* and reasonably estimated in *Aristonectes*) remains about thirty, which seems to have been the primitive number in all lineages; these forms therefore lack trends either to increase or decrease the cervical number. There is also no trend to lengthen or shorten the individual cervical centra, which have proportions similar to the most primitive Lower Jurassic forms. *Aristonectes* is unique among Upper Cretaceous genera in possessing the primitive neck construction.

Four features of the skull serve to unite these genera and to distinguish them from all other forms:

(i) The premaxilla of all other genera bears a total of 5 teeth (some elasmosaurs have secondarily lost the most anterior tooth), but in *Cryptoclidus, Kimmerosaurus* and *Aristonectes* this number is exceeded. There is a definite trend to increase the premaxillary tooth number, which is 6 in *Cryptoclidus*, at least 8 in *Kimmerosaurus* and 15 in *Aristonectes.*

(ii) There is a trend to increase the number of teeth on the lower jaw ramus from 24–26 in *Cryptoclidus* through 36 in *Kimmerosaurus* to 58 in *Aristonectes* (the latter, known from the number of sockets, being the greatest number recorded among the Sauropterygia).

(iii) The teeth (not known in *Aristonectes*) show a trend towards the reduction (in *Cryptoclidus*) and absence (in *Kimmerosaurus*) of the ornament of longitudinal ridges which characterizes the teeth of all other forms.

(iv) The occipital condyle, which in all other genera is formed entirely from the basioccipital, is formed from both the basioccipital and the exoccipitals in *Cryptoclidus* and *Kimmerosaurus*; it is possible that this may also have been the case in *Aristonectes* (see discussion of character 12, p. 329).

The evidence cited above indicates that the genera *Cryptoclidus, Kimmerosaurus* and *Aristonectes* are representatives of a third and distinct phyletic lineage. This lineage has a known geological range from the Upper Jurassic (Callovian) to the Upper Cretaceous

(Maastrichtian). *Cryptoclidus*, with only 6 premaxillary teeth and 24–26 pairs of dentary teeth, is a primitive representative, whereas *Aristonectes* is an advanced form.

Several characters shown by *Cryptoclidus, Kimmerosaurus* and *Aristonectes* (such as those of the neck) are primitive to both the 'plesiosauroidean' and 'pliosauroidean' lineages. There are, however, no characters retained which are primitive only to the 'pliosauroidean' lineage, whereas there are six characters exhibited by these genera which are found in primitive members only of the 'plesiosauroidean' lineage. These are a relatively small skull; a short mandibular symphysis; teeth with relatively slim crowns not showing wear on their tips; a relatively large ventral process of the scapula; a relatively short ischium; and propodials which are 'massive', and of which the humerus is larger than the femur. The postcranial characters are known only for *Cryptoclidus*, but as this is the most primitive representative of the newly recognized lineage it is unlikely that the similarity is due to convergence. It is therefore evident from this analysis that the *Cryptoclidus–Kimmerosaurus–Aristonectes* lineage is descended from primitive 'plesiosauroidean' stock, perhaps in the Lower or Middle Jurassic.

Plesiosaurian classification

Welles (1943) described the two principal phylogenetic lineages, and ranked them as separate superfamilies. Using the single or double-headed form of the cervical rib, he then divided each lineage into two grades which he ranked as families. In 1962 he enlarged the diagnoses of his two plesiosauroidean families (Plesiosauridae and Elasmosauridae) by reference to further characters which show progressive unidirectional evolutionary change. However, he did not adhere strictly to his diagnoses, referring the genera *Cryptoclidus, Muraenosaurus* and *Tricleidus* to the family Plesiosauridae rather than to the cercidopleuran family Elasmosauridae. This inconsistency was noticed by Persson (1963) who, rather than place those genera in the family Elasmosauridae, was led to produce new and less precise diagnoses of the families which then enabled him to include them in the Plesiosauridae.

The reluctance of previous authors (with the exception of Andrews 1910) to include the cercidopleuran English Upper Jurassic genera with the Cretaceous elasmosaurs results from their concept of what constitutes a 'long neck'. Undeniably, these English genera have shorter necks; even *Muraenosaurus*, with 44 cervical vertebrae, has fewer than the shortest-necked Cretaceous elasmosaurs. However, if it is accepted that the primitive number of cervical vertebrae for all the Plesiosauria is of the order of 28 to 32 (as is argued above), then it follows that any form with significantly more than that number shows a trend towards elongation of the neck, and possesses a neck which is relatively long. *Muraenosaurus* and *Colymbosaurus* must therefore be considered to be long-necked forms, whereas *Tricleidus* and *Cryptoclidus* have necks of a (primitive) moderate length.

Neck length, however, is only one of several characters which show progressive evolutionary change in the plesiosaur–elasmosaur lineage, and which may therefore be used to distinguish primitive and advanced forms. Some characters limited to this lineage, such as the development of platycoely and of lateral crests on the cervical centra, are first developed in Upper Jurassic forms (*Muraenosaurus*), whereas the evolution of a wide posterior intercoracoid foramen has occurred only in some Cretaceous forms. One such trend which shows a gradual development is the reduction in the number of teeth borne by the dentary. This decreases from about 24 teeth in each ramus (as in the Lower Jurassic species *Plesiosaurus dolichodeirus*) to 14 in the Cretaceous genus *Thalassomedon*. Of the English Upper Jurassic genera, *Muraenosaurus* has from 19 to 22 teeth on each dental ramus, whereas *Tricleidus* has only 17, this being fewer than in several Cretaceous forms. In respect to this character, therefore, *Tricleidus* is more advanced than *Muraenosaurus*; this is the opposite of their relationship when judged by the relative length of their necks.

Existing diagnoses which divide the plesiosaur–elasmosaur and the 'pliosauroidean' lineages into primitive and advanced grades rely on the heavy weighting of one character, the nature of the cervical rib head. This character has the advantage of easy practical operation; the cervical rib head can be double (primitive grade) or single (advanced grade), with no known borderline case. However, the reduction in number of cervical rib heads from two to one involves all lineages, and as a consequence the taxonomic weighting of this character serves only to cloud the real issue (that of reflecting phylogeny in classification) by drawing emphasis away from the characters which are of special adaptive significance for each individual lineage. One must therefore question the necessity or desirability of such arbitrarily-based divisions.

In the case of the Pliosauroidea, which appears to be a single major lineage, the reduction in the number of cervical rib heads coincides chronologically with the Jurassic–Cretaceous boundary. Thus the Upper Jurassic forms such as *Pliosaurus* and *Stretosaurus*, which show an advanced development of the shortened neck, enlarged head and powerful dentition, are currently grouped together with primitive Lower and Middle Jurassic forms such as *Rhomaleosaurus* and *Macroplata*, and are taxonomically separated from advanced Cretaceous forms such as *Leptocleidus* and *Dolichorhynchops* which they resemble much more closely. Any sizeable taxonomic group will contain primitive and advanced forms; these terms are well understood, and there seems little point in the creation of arbitrary and less meaningful taxonomic distinctions.

In the case of the Plesiosauroidea the issue is now changed by the recognition of a third phyletic lineage which has evolved from primitive members of the plesiosaur–elasmosaur lineage; it is desirable to recognize the elasmosaurs and the new lineage as separate families, and to distinguish these from their common stock. The descendant families are mutually distinct, and the primitive parental family may be defined objectively by ensuring that it contains only those forms which (except by generic or specific innovations) are not debarred from ancestry to both the descendant families.

The newly recognized lineage is represented by the three genera *Cryptoclidus, Kimmerosaurus* and *Aristonectes*; the only available family-group name is Cryptoclididae Williston, 1925 (originally mis-spelt Cryptocleididae). In addition to the progressive trends discussed above, the family is distinguished clearly from all others by two characters, namely, increase in the number of pairs of premaxillary teeth above 5, and involvement of the exoccipital in the formation of the occipital condyle. Two negative features are also of importance in distinguishing the family from the Elasmosauridae, namely the lack of any reduction in the number of pairs of lower teeth below the primitive number of about 24 (there is on the contrary a trend towards the increase of this number, evident even in the primitive genus *Cryptoclidus*), and the lack of any increase in the number of cervical vertebrae above the primitive number of about 28 to 32.

In order to be retained in the family Plesiosauridae, primitive forms must therefore have 5 pairs of premaxillary teeth; an occipital condyle formed from the basioccipital only; not less than the primitive number of pairs of lower teeth and not more than the primitive number of cervical vertebrae. Such forms would not then be debarred from ancestry to either the Elasmosauridae or the Cryptoclididae.

A consequence of this action is to reduce considerably the size and chronological range of the Plesiosauridae, and at the same time to enlarge and extend the Elasmosauridae. In particular, the English Lower Jurassic genus *Microcleidus* Watson, 1909, which has hitherto been included always with the Plesiosauridae because of the double-headed condition of the cervical ribs, must now be recognized as a primitive elasmosaur since it has increased the number of cervical vertebrae to 40 and elongated proportionally each cervical centrum. This genus also demonstrates that reduction in number of cervical rib heads evolved by convergence not only in the two superfamilies but also within the Plesiosauroidea in the families Elasmosauridae and Cryptoclididae.

Only one genus may with certainty be included within the family Plesiosauridae, that being the type genus *Plesiosaurus*. However, this genus has in the past been made a 'catch-all' group, and still remains diverse and in need of revision. It is evident that, of the better-known species, the type species *P. dolichodeirus* and also *P. guilelmiimperatoris* (pro *Guilelmi imperatoris* Dames 1895: 16, emend.) belong in the Plesiosauridae, whereas *'Plesiosaurus' hawkinsii* Owen, 1840 belongs in the Pliosauroidea.

A second Lower Jurassic genus, *Sthenarosaurus* Watson, 1909, is clearly plesiosauroidean but is known from incomplete material. The cervical centra show no definite trend towards proportional elongation, which indirectly implies that the cervical vertebrae may not have been increased in number; but as the skull is not preserved, the presence or absence of cryptoclidid trends cannot be demonstrated. This genus is therefore placed as Plesiosauroidea, *incertae sedis.* All other named plesiosaur genera may be assigned to a family.

There yet remains to be considered the taxonomic position of the genus *Pistosaurus.* Whereas it is generally assumed (e.g. by Romer 1956, Welles 1962, Persson 1963) that the pistosaurs were in some way ancestral to at least the Plesiosauroidea, the nature of this relationship and the relationship to nothosaurs is not understood. In consequence, the genus cannot as yet be classified in either order as a result of phylogenetic arguments, but only for reasons of taxonomic convenience. For the present, an arbitrary line must be drawn which separates the Nothosauria from the Plesiosauria. If the retention or loss of nasals be made the decisive criterion, then the genus *Pistosaurus* must be retained in the Nothosauria; this arrangement permits a classification of the Plesiosauria which is based entirely upon current theories of phylogeny.

The classification of the Plesiosauria which I propose may now be formalized.

A classification of the Plesiosauria

Class **REPTILIA**

Subclass **SAUROPTERYGIA** Owen, 1860

Order **PLESIOSAURIA** de Blainville, 1835

DIAGNOSIS. Sauropterygia in which the nasals are absent; paroccipital processes usually long and slender, meeting squamosal; post-temporal fenestrae large; stapes probably absent; thecodont, with new teeth developing lingual to old and moving buccally to replace them; overall length up to 14 metres; vertebral centra with paired nutritive foramina; coracoids, pubes and ischia developing into large ventral plates; epipodials becoming broader than long; hyperphalangy reaching a maximum of 17. (Diagnosis modified from that given by Welles, 1962.)

RANGE OF ORDER. ? Upper Triassic; Lower Jurassic (Hettangian Stage) to Upper Cretaceous (Maastrichtian Stage).

INCLUDED SUPERFAMILIES. Plesiosauroidea and Pliosauroidea.

Superfamily **PLESIOSAUROIDEA** (Gray, 1825) Welles, 1943

DIAGNOSIS. Plesiosauria with relatively small skulls; mandibular symphysis short, being between the first pair of alveoli only, these not bearing especially enlarged teeth; teeth with slim crowns which do not usually show wear on their tips; at least 28 cervical vertebrae; cervical centra of moderate relative length or elongated; the ventral rami of the scapulae becoming broad; ischia relatively short anteroposteriorly; propodials massive, humerus generally larger than femur.

RANGE OF SUPERFAMILY. Lower Jurassic (Hettangian Stage) to Upper Cretaceous (Maastrichtian Stage).

INCLUDED FAMILIES. Plesiosauridae, Elasmosauridae and Cryptoclididae. The Lower Jurassic genus *Sthenarosaurus* Watson, 1909 is *incertae sedis.*

Family **PLESIOSAURIDAE** Gray, 1825

DIAGNOSIS. Plesiosauroidea with five pairs of premaxillary teeth; about 24 pairs of dentary teeth; teeth ornamented with numerous longitudinal ridges; occipital condyle formed from the basioccipital only; overall length not known to exceed 3 m; not more than 32 cervical vertebrae; cervical centra of moderate relative length; cervical ribs double-headed; ventral rami of the scapulae remaining relatively narrow; epipodials longer than broad; the fifth metapodial retained in the metapodial row; hyperphalangy limited to about ten phalanges in the longest digit.

RANGE OF FAMILY. Lower Jurassic only.

INCLUDED GENERA[3]. The single genus *Plesiosaurus* Conybeare, 1821.

Family **ELASMOSAURIDAE** Cope, 1869

DIAGNOSIS. Plesiosauroidea with a maximum of five pairs of premaxillary teeth; upper tooth row of advanced forms characterized by the development of enlarged premaxillary and anterior maxillary teeth separated by smaller teeth around the maxillo-premaxillary suture; dentary teeth primitively 24 pairs, reducing to a minimum of 14 pairs in advanced forms; teeth ornamented with numerous longitudinal ridges; occipital condyle formed from the basioccipital only, and usually ringed by a constricting groove; overall length from about 3 m in primitive forms to a maximum of 14 m in advanced forms; number of cervical vertebrae primitively *c.* 32 and reaching a maximum of 71 in advanced forms; except for some primitive forms, cervical centra relatively elongated; cervical ribs (primitively double-headed) are single-headed in Upper Jurassic and later forms; ventral rami of the scapulae relatively broad and meeting in the ventral midline in 'adults'; epipodials primitively longer than broad, becoming broader than long in advanced forms; the fifth metapodial shifting proximally into the distal mesapodial row in advanced forms; hyperphalangy of up to 17 phalanges in the longest digit.

RANGE OF FAMILY. Lower Jurassic (Toarcian Stage) to Upper Cretaceous (Maastrichtian Stage).

INCLUDED GENERA[3]. *Microcleidus* Watson, 1909 (Lower Jurassic genus); *Colymbosaurus* Seeley, 1874; *Muraenosaurus* Seeley, 1874 and *Tricleidus* Andrews, 1909 (Upper Jurassic genera); *Alzadasaurus* Welles, 1943 and *Brancasaurus* Wegner, 1914 (Lower Cretaceous genera); *Aphrosaurus* Welles, 1943; *Elasmosaurus* Cope, 1868; *Fresnosaurus* Welles, 1943; *Hydralmosaurus* Welles, 1943; *Hydrotherosaurus* Welles, 1943; *Leurospondylus* Brown, 1913; *Mauisaurus* Hector, 1874; *Morenosaurus* Welles, 1943; *Styxosaurus* Welles, 1943 and *Thalassomedon* Welles, 1943 (Upper Cretaceous genera).

Family **CRYPTOCLIDIDAE** Williston, 1925

DIAGNOSIS. Plesiosauroidea with from 6 to 15 pairs of premaxillary teeth; toothrows regular, teeth decreasing in size distally without any enlargement of special teeth; lower teeth, primitively 24 pairs, increasing in number to 58 pairs in advanced forms; tooth ornament reduced or absent; occipital condyle formed by the basioccipital and exoccipitals and not ringed by a constricting groove; overall length probably does not exceed 8 m; number of cervical vertebrae remains about 28 to 32; cervical centra remain of moderate relative length; cervical ribs single-headed; ventral rami of the scapulae relatively broad and meeting in the ventral midline; epipodials broader than long; the fifth metapodial has shifted proximally into the distal mesapodial row; hyperphalangy of up to 15 phalanges in the longest digit.

RANGE OF FAMILY. Upper Jurassic (Callovian Stage) to Upper Cretaceous (Maastrichtian Stage).

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[3] Junior synonyms and *nomina dubia* have been omitted from these lists of included genera.

INCLUDED GENERA[3]. *Cryptoclidus* Seeley, 1892 and *Kimmerosaurus* nov. (Upper Jurassic genera); *Aristonectes* Cabrera, 1941 (Upper Cretaceous genus).

Superfamily **PLIOSAUROIDEA** (Seeley, 1874) Welles, 1943

DIAGNOSIS. As for the single family Pliosauridae.

Family **PLIOSAURIDAE** Seeley, 1874

DIAGNOSIS. Plesiosauria with relatively large skulls; premaxillae bear 5 pairs of teeth; mandibular symphysis long, extending back between several pairs of alveoli which bear enlarged teeth; from 25 to 40 pairs of dentary teeth; teeth broad and strong and frequently show wear on their tips; teeth ornamented with longitudinal ridges and may also be keeled; occipital condyle formed from the basioccipital only; overall length from 3 m in primitive forms to about 12 m in some advanced forms; number of cervical vertebrae primitively about 30 and reducing to a minimum of 13 in advanced forms; except for some primitive forms, cervical centra relatively short; cervical ribs double-headed in Jurassic forms, becoming single-headed in Cretaceous forms; ventral rami of the scapulae usually remaining narrow; ischia relatively long anteroposteriorly; propodials slender, the femur larger than the humerus; epipodials primitively longer than broad, becoming broader than long in advanced forms; the fifth metapodial shifting proximally from the metapodial row in primitive forms to the distal mesapodial row in advanced forms; hyperphalangy of up to 16 phalanges in the longest digit.

RANGE OF FAMILY. Lower Jurassic (Hettangian Stage) to Upper Cretaceous (Senonian Stage).

INCLUDED GENERA[3]. *Archaeonectrus* Novozhilov, 1964; *Eretmosaurus* Seeley, 1874; *Eurycleidus* Andrews, 1922; *Eurysaurus* Gaudry, 1878; *Macroplata* Swinton, 1930 and *Rhomaleosaurus* Seeley, 1874 (Lower Jurassic genera); *Liopleurodon* Sauvage, 1873; *Megalneusaurus* Knight, 1898; *Peloneustes* Lydekker, 1889; *Pliosaurus* Owen, 1841; *Simolestes* Andrews, 1909; *Stretosaurus* Tarlo, 1959 and *Strongylokrotaphus* Novozhilov, 1964 (Upper Jurassic genera); *Kronosaurus* Longman, 1924; *Leptocleidus* Andrews, 1922 and *Peyerus* Stromer, 1935 (Lower Cretaceous genera); *Brachauchenius* Williston, 1903; *Dolichorhynchops* Williston, 1902 and *Polyptychodon* Owen, 1841 (Upper Cretaceous genera).

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