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THE PALAEOECOLOGY OF THE LOWER LEINTWARDINIAN (UPPER SILURIAN) OF THE WELSH BORDERLANDS AND WALES

by

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University of Glasgow

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Abbreviations:

Fossil names are given in full at the first mention; the generic names are abbreviated for subsequent use. Authors are shown in the faunal list for stratigraphical range charts (eg Fig. 2.4 p 21).

Divisions of the Ludlow Series are abbreviated after the first use. These are:-

Lower Elton Beds	LEB
Middle " "	MEB
Upper " "	UEB
Lower Bringewood Beds	LBB
Upper " "	UBB
Lower Leintwardine Beds	LLB
Upper " "	ULB
Lower Whitcliffe Beds	LWB
Upper " "	UWB
basal Lower Leintwardine Beds (Leintwardine and Aymestrey)	bLLB
higher " " " " " "	hLLB
Basal Upper Leintwardine Beds (Shergold and Shirley '68)	bULB
High " " " " " " "	hULB

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21 Isorthis and Salopina: Population analysis data

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SUMMARY

The aim of the project was to evaluate the parameters influencing faunal distributions, to distinguish between those groups which are strongly ecologically-controlled and those which are stratigraphically useful. The possible diachronism of the biostratigraphical division, the Lower Leintwardine Beds, could then be assessed.

The Ludlow palaeogeography in the Welsh Borderlands and Wales can be deduced, from facies and thickness variations, to include shelf and basinal areas of deposition. The LLB, which are defined in the shelly shelf facies at Ludlow (Holland, Lawson and Walmsley '63) correlate closely with the leintwardinensis zone in the graptolitic basinal sequences. Fieldwork for the project was based on a shelf to basin transect, SE-NW across the outcrop from May Hill to Kerry, in order to examine the pattern of faunal, facies and thickness changes. A bed-by-bed collecting technique was used. The whole fauna was recorded qualitatively and semi-quantitatively from each unit together with the associated palaeoecological and sedimentological data. Additional surveys of single bedding-plane assemblages, lateral traverses along beds, and detailed studies over parts (2-3 m) of the succession were designed to consider the local faunal variation.

Vertical range charts for the stratigraphical data indicate the complexity of the faunal distributions. The results from sections at Ludlow were used for computer cluster analyses; qualitative methods proved useful for correlation of sequences. Fossils in the LLB are typically concentrated into bands with few in the intervening beds, and the assemblages are, vertically and laterally, highly variable.

The fieldwork information was used to compile facies and faunal maps for the Leintwardinian. The ecology of the fossils in relation to their LLB occurrences enables the factors controlling their distributions to be evaluated. Benthonic fossils, except for the infaunal Lingula lata, are confined to the areas of shelf facies through most of the LLB. Shells in slumped strata in the basin have been transported in with the sediment flows from shallower areas. The sparse, graptolitic and pelagic faunas of the basinal successions reflect conditions that were inimical to most benthos; L. lata, however, appears to be indigenous to these areas. The shelf edge sequences have mixed, graptolitic and shelly faunas. Instability in this intermediate region is shown by shelf to basin channelling (eg. Aymestrey) and slumping (Lyepole Bridge). At the

top of the LLB, there is a westward extension of shelly benthos into SW parts of the basin with, or followed by, a facies change to more thickly-bedded, calcareous siltstones. The northern areas (eg. Kerry) still have laminated siltstones with limited faunas at this level.

The environmental significance of the facies distinguished for the LLB was considered. The basal conglomerates in several of the SE inliers, and in IGS borehole material from Brookend (Tites Point) and NE Wenlock Edge, contain bored clasts. These deposits represent hardground formation (ie. horizons of submarine cementation) during periods of non-deposition of sediment. The development of the conglomerates closely parallels the inner shelf on the palaeogeography. The calcareous siltstone facies of the shelf has numerous heterogeneous plane assemblages of fossils which are concluded, from palaeoecological surveys, to be locally derived by periodic current disturbance. Interbedded with these are highly-sorted coquinas, and at Ludlow the sheet-laminated siltstone units, which have been more strongly reworked. Fossils in the latter may have suffered extensive transport in storm-generated or turbidity current sediment flows. However, mixing of faunas has not occurred so that faunal belts were probably wide. Recurrent species associations were compared to Calef and Hancock's ('74) brachiopod communities, for which depth significance was claimed. The widely fluctuating composition of LLB plane assemblages means that different "communities" interdigitate rapidly, or even co-exist; a depth control is not therefore possible. The faunal maps show that each species responds individually to the environment, even though some associations display similar preferences over parts of their ranges. Five sub-faunas are recognised which characterize parts of the succession.

The stratigraphical value of various elements of the fauna was assessed. Graptolite evidence supports the LLB - leintwardinensis correlation, and N. lauensis and encrinurids are useful indices for the ULB. Sessile, epifaunal brachiopods are particularly susceptible to facies control. Their vertical distribution patterns frequently cut across one another. However, wide faunal belts on the shelf mean that the degree of diachronism is usually not great, so the group is of limited use for correlation. The biostratigraphical LLB are concluded not to be significantly diachronous.

The faunal and facies distributions have been used for a palaeobiogeographical reconstruction. Restricted circulation in the basin may have prevented colonisation by benthos apart from L. lata until the top LLB, when the spread of shelly faunas and facies is consistent with a shallowing of the environment.

CHAPTER ONE

INTRODUCTION

The Lower Leintwardine Beds (LLB) are a biostratigraphical division of the Ludlow Series (Holland, Lawson and Walmsley '63), whose base is defined at a standard section in the Ludlow anticline. The boundary here coincides with the base of the chronostratigraphical unit, the Leintwardinian Stage. The pattern of faunal changes in the biostratigraphical classification facilitates correlation across the shelf region. However, in the basinal facies, the faunal assemblages are very different, and zonation relies upon graptolites. Correlation of basinal sequences with the LLB of the shelf is made by the occurrence of Saetograptus leintwardinensis and by reference to the transitional faunas in the intermediate areas.

History of Research:

(A locality map is shown in Fig 1.1 p7)

The Ludlow Formation (Murchison 1833 - p 477) in the type area was first described in detail in 1839 in the "Silurian System". Murchison's classification of the Silurian was primarily lithostratigraphical, although:

> "each subdivision of rocks being characterized by a corresponding suite of organic remains" (Murchison 1839 - p 196).

The tripartite division which he established for the Ludlow Formation (1834 - p 13) was based on the interpolation of the Aymestry and Sedgeley limestone within a thick sequence of clastic sediments, that lay between the Wenlock and Dudley limestone and the Old Red Sandstone Tilestone unit:-

from Murchison (1834 - p 13)	Old Red Sandstone		c. Tilestone
	U. Grauwacke Series	I Ludlow rocks	d. U. Ludlow rock
			e. Aymestry and Sedgeley limestone
			f. L. Ludlow rock
		II Wenlock and Dudley rocks	g. Wenlock and Dudley limestone Wenlock and Dudley shale

Murchison's divisions of the Ludlow Formation were characterised by shelly fossils. He made particular mention of the lowest stratum (10-13 m) of the Upper Ludlow rock member as:-

"very remarkable, being absolutely loaded with a vast number of small Terebratulae of a gryphoid form, named Terebratula Navicula. This shell is seen in abundance in the escarpments at the View Edge, Mocktree Forest, Downton on the Rock, at various places around the Ludlow promontory, and at Aymestry, always occupying the lowest portion of the U. Ludlow Rock, and forming the cap of the calcareous zone at Aymestry... This shell is of great geological value,... being extremely persistent, and marking the same horizon even to a distance of nearly 100 miles. The beds which it occupies are sometimes so calcareous, and pass so naturally into the Aymestry Limestone, that they may in all such cases be grouped with that rock".

(1839 - p 201)

In areas such as Usk, where the Aymestry Limestone was not recognisably developed, he marked its position in relation to the overlying "terebratulite" horizon (Siluria 3rd Ed. 1854 - p 145).

Murchison noted the lack of persistence of the limestone members of both Wenlock and Ludlow Formations outside their type areas, and especially westward into Wales, where there were problems of recognition of the divisions in the contemporaneously-deposited, less fossiliferous, argillaceous strata (1839 - p 195, 215). The typical shelly fossils of the units at Ludlow were relatively scarce in the areas west of Aymestrey, where the faunal changes that took place through the thick sequences of uniform lithology were transitional.

Murchison (1839 - p 215) commented on the common occurrence of graptolites (which he thought to be bryozoa) in the fine, muddy, western facies. The use of graptolites for correlation of Lower Palaeozoic rocks soon became established, following Barrande (1850). Wood (1900) instituted a graptolitic zonal scheme for the "Lower Ludlow rocks" - in which, sensu Lapworth (1880), she included rocks up to the level where graptolites disappeared. She worked in the Ludlow, Builth and Long Mountain areas. Five zones were described, the highest of which was the S. leintwardinensis division. Wood recorded this graptolite up into Aymestry Limestone, but not above it, in the Aymestrey region. In the Long Mountain succession, she found 275 m of strata containing Saetograptus leintwardinensis var. incipiens but no S. leintwardinensis s.s., and suggested that the former type was probably earlier, and the true S. leintwardinensis flags were unfossiliferous in this area (p 443).

In 1906, Elles and Slater classified the Ludlow rocks from the Aymestry Limestone upwards, in the Ludlow and Leintwardine districts, using a zonal scheme based on the brachiopod faunas. They recognised Murchison's "terebratulite" horizon above the Aymestry Limestone as the

Mocktree or Dayia Shale member, which was characterised by crowded shells of Dayia navicula. The unit thickened from 13 m at Ludlow to 45 m at Mocktree. However, because of the affinity of its brachiopod fauna with that of the Aymestry Limestone rather than with that of the overlying strata, and because S. leintwardinensis was found to extend to high in the Mocktree Shales, the division was included with the Aymestry ("Conchidium") Limestone in the Aymestry Group, separate from the overlying Upper Ludlow Group. The Limestone member exhibited similar thickening to the Dayia Shales, from 31 m at Ludlow to 76 m at Mocktree.

Alexander (1936) described the Aymestry Limestone and overlying Dayia Shales in the main outcrop from Craven Arms to Aymestrey, and considered the conditions of deposition of the beds. She pointed out that the base of the limestone unit was diachronous (using graptolite zones), being younger to the east. The limestone was interpreted, from its fauna and facies, as being laid down in shallow water on a current-swept, narrow submarine ridge. The structure was roughly parallel with the Church Stretton Fault, and migrated eastwards with time from the View Edge-Mocktreeregion. It separated an area of heavy sedimentation (a basin) to the west, from one of light deposition (a shelf) to the east. Kirkidium banks were taken to be water-sorted accumulations which, like Lingula specimens perpendicular to the bedding in the shale bands, suggested shallow conditions. Alternations of shale with the limestone indicated periodic subsidence of the growing ridge to bring it back below wave base.

The top of the Limestone facies was clearly marked by a widely-developed, sandy band (15 cm) with numerous Isorthis orbicularis, which passed up into calcareous, nodular, Dayia beds. Generally, the latter graded upwards into thinly flaggy, laminated shales, but in some parts, such as west of Aymestrey, the laminated lithology lay directly on the Limestone. Alexander described slumped, contorted beds within normally-bedded Dayia Shales sequences at Church Hill. Unconformable junctions of the Dayia beds (which had numerous S. leintwardinensis and included water-worn boulders of Aymestry Limestone) with nilssoni-scanicus mudstones and tumescens mudstones were found in this same area, while at Mocktree Quarries, a partly faulted, unconformable junction between the Aymestry Limestone and Dayia beds was described. The D. navicula beds in the Church Hill area were interpreted as the infilling of a steep-sided channel, which cut obliquely through the submarine ridge westwards

at the end of the Limestone era. Then the I. orbicularis band over the rest of the area was taken to represent this period of erosion, although the strike and dip of the Limestone and overlying Dayia beds were mostly in continuity. Both the divisions lay in the leintwardinensis zone, but the base of the Limestone extended, in places, into the tumescens zone.

Areas of the thick sequences of muddy sediments to the west of the Aymestrey-Leintwardine region were mapped using local classifications into divisions that were partly biostratigraphical, but also lithostratigraphical. (eg. Bucknell-Stamp '18; Builth and Cwm Craig Ddu-Straw '29 '37, '53; Kerry and SW Clun-Earp '38, '40; Knighton-Holland '59; Brecon-Kirk '51). Fossils were sparse through great thicknesses of sediment (and relatively scarce throughout compared to the shelly facies of the thinner, eastern successions), and faunal changes were gradational. These studies elucidated the palaeogeographical setting for the deposition of the thick basinal sequences of Ludlow sediments. Series of contorted beds locally within the successions were interpreted by Straw ('37) and Earp ('38, '40) - re. Jones ('37) - as gravity flows down a submarine slope. The opposite directions of movement in the Kerry - Clun Forest area (towards the SE) and at Builth (to NW) indicated an intermediate axial zone between the two regions, trending perpendicularly to the slumps, in a NE-SW direction. This was supported by thickness variations of individual divisions. A depositional environment of an elongated, narrow trough, parallel to the Aymestry Limestone "ridge", was proposed.

Many of the local stratigraphical divisions were named after characteristic index fossils. This led to confusion in correlation of the various regions. A lot of the common Ludlow species are long-ranging, with acmes at different levels from area to area. For example, D. navicula occurs in abundance in the tumescens zone at Builth, above the leintwardinensis zone at Kerry, while the Dayia Shales of Leintwardine are in the latter zone. For correlation, graptolites, being planktonic forms, are considered most reliable. With shelly fossils, it is necessary to compare total faunal assemblages of units, and not the levels of local acmes of a species.

Areas of Ludlow rocks in inliers to the E and SE of Ludlow were mapped and described by a number of early workers (for example, Phillips (1848) in the Malverns, King and Lewis (1912) in Central England), who used local classifications into biostratigraphical (shelly faunas) and

lithostratigraphical units. Since 1952, most inliers (and other areas of Ludlow strata) have been remapped, many in co-ordinated studies instigated by the Ludlow Research Group. The inliers include Usk (Walmsley '59), May Hill and Gorsley (Lawson '54, '55), Woolhope (Squirrell and Tucker '60), and the Malverns and Abberleys (Phipps and Reeve '67). The revision of the classification in the type area of Ludlow (Holland, Lawson and Walmsley '59 and '63) was carried out in order to correlate the relatively thin sequences of the shelf areas across the region. The fauna is dominantly benthonic, and for these areas, acmes of some species were considered to have stratigraphical use.

In the main Ludlow outcrop, the successions of Wenlock Edge (Shergold and Shirley '68), Leintwardine (Whitaker '62) and Aymestrey (Lawson '73(a)) have been mapped. The latter two areas have mixed shelly and graptolitic faunas, reflecting the approach towards the basin. Whitaker ('62) described a series of six submarine channels in the LLB of the Leintwardine region. These trended ENE-WSW and deepened from shelf to basin; they were cut and largely filled during LLB times. Evidence of periodic "flushing-out" of the infilling sediments and slumping into and down the channels shows the instability of this shelf edge area (Whitaker '62 - p 340).

Sedimentological work on the basin region by Cummins ('59) and Bailey ('64) emphasized the importance of sediment transport along the trough in lower Ludlow times, in the form of N- and NE-flowing turbidites. Cummins ('57, '59) described the "Derwen ridge" as an important palaeogeographical element to the west of the depositional basin (the "Montgomery Trough"), separating it from the "Denbigh Trough". Woodcock ('74, '76) investigated the slump sheets of the Ludlow Series in Wales, and while commenting on the similarity in style of tectonic and slump folds, concluded that Ludlow structures were the latter. Periods of slumping were not necessarily synchronous in different areas, so that for stratigraphical correlation reliance was placed on fossils. Slumps continued to be developed up to a high level in the <u>leintwardinensis</u> zone in the Kerry and Clun Forest area. Here, also, they were found to extend progressively further E through time (Earp '38), which indicates the active growth of the western bounding slope of the trough in the Ludlow period.

The base of the chronostratigraphical Stages were defined at stratotypes (Holland, Lawson and Walmsley '63) to facilitate correlation

of shelf and basinal sequences, and for wider stratigraphical reference. The base of the S. leintwardinensis zone was considered to correlate fairly closely with the LLB and Upper Leintwardine Beds (ULB) in the type area, while the Aymestry Limestone is mostly in the tumescens and incipiens (spinose graptolite) zone beneath.

Thickness variations:

Two transects across the outcrop are shown in Figs 1.2 p7 and 1.3 p8 , the one from NW-SE, the other SW-NE. The pattern of thickness changes shows the distinction between "shelf" and "basin" areas of sedimentation, and also the relative rates of subsidence within the basin. The ULB thicknesses indicate the continuing differential sedimentation across the outcrop. Even in the Whitcliffian, when facies and faunal distinctions between shelf and basin areas are much reduced, the depositional thickness differences are maintained (Holland and Lawson '63).

In the thick Ludlow succession at Knighton (min. 1,950 m) the leintwardinensis zone is surprisingly thin, only 30 m (Holland '59). However, the overlying, largely barren, Knucklas Castle beds, which are defined on the disappearance of graptolites, are very thick (460 m). The faunal change could relate to palaeoecological conditions in this part of the basin within Leintwardinian times, when the zonal thickness must be regarded as a minimum figure.

The isopachyte map for the Leintwardinian, (Fig 1.4 p9), modified from Holland and Lawson ('63), shows the curved, easterly convex, form of the palaeogeography. The wide shelf area has thin and attenuated sequences around Gorsley - the "Gorsley axis" of Holland and Lawson ('63). Conglomeratic facies developed in the basal LLB of this region reflect instability around this topographic 'high'. Crowding of the isopachs west of Aymestrey and Leintwardine suggests an axis of down-warping between shelf and basin along this line. The series of submarine channels, cut during the LLB in the shelf edge districts (Whitaker '62; this study - p131), and slumping to the west, for example at Lyepole Bridge (p132), are additional evidence of the slope configuration, and of the instability of the marginal zone. The basinal isopachs extend SW-NE. Downslope slump movement is to the NW at Builth, but towards the SE in the Kerry-Clun Forest area. The latter suggests that the western margin to the trough was parallel. Greater subsidence in the northern part of the basin indicates an axial palaeoslope facing that direction.

Fig. 1.1

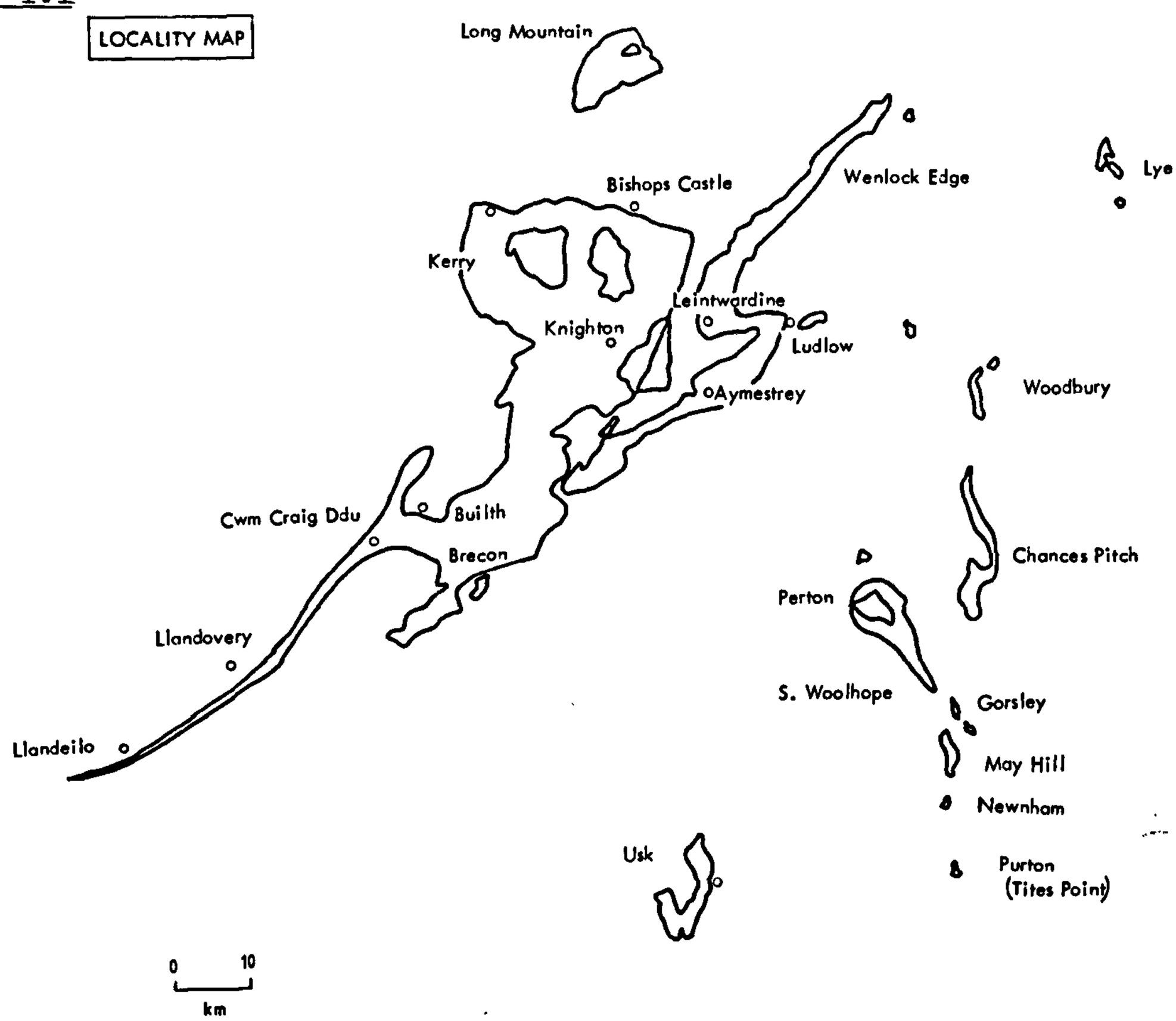

Fig. 1.2

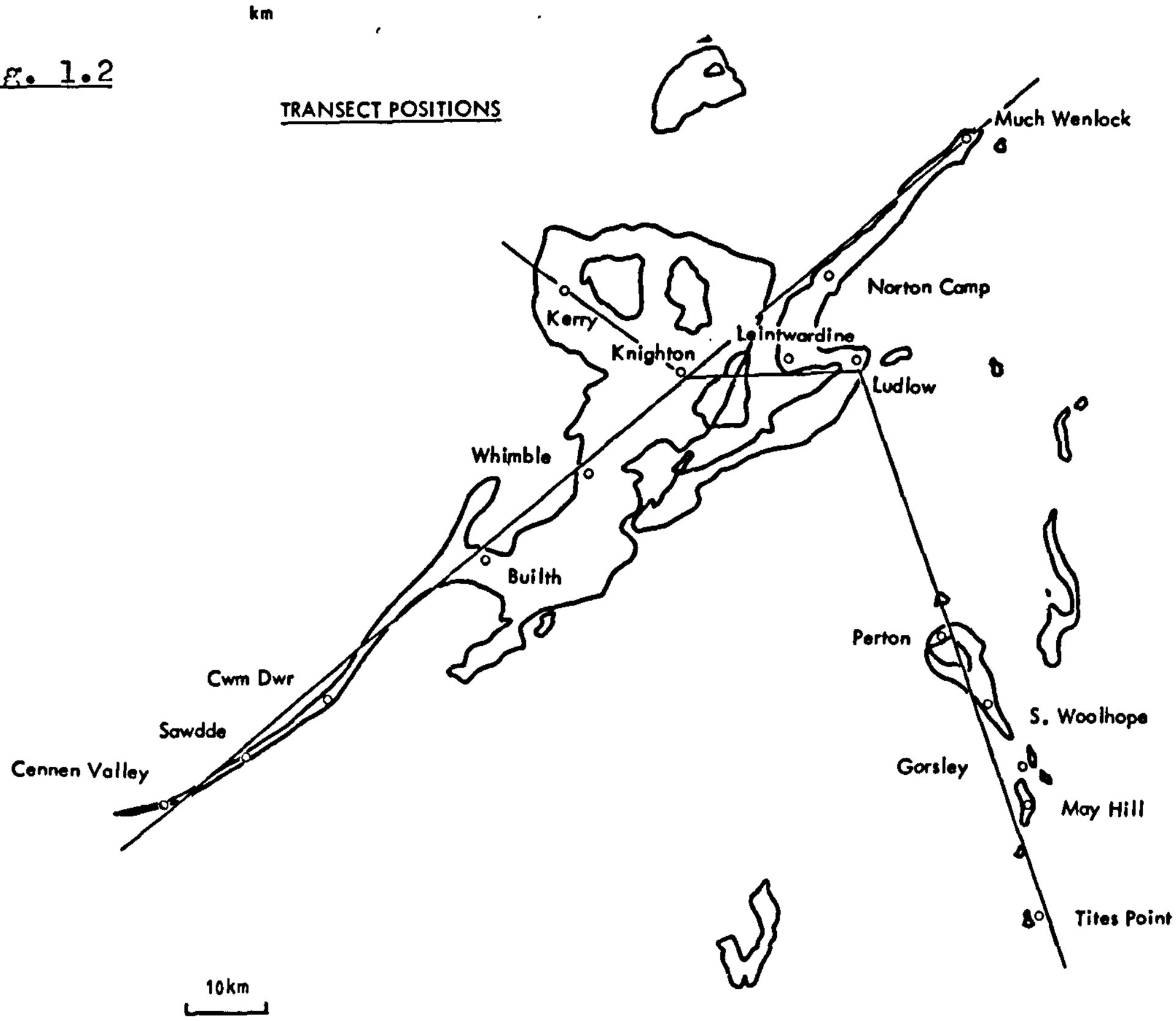

Fig. 1.1 : Locality map for Ludlow outcrop.
Fig. 1.2 : Positions of thickness variation transects.

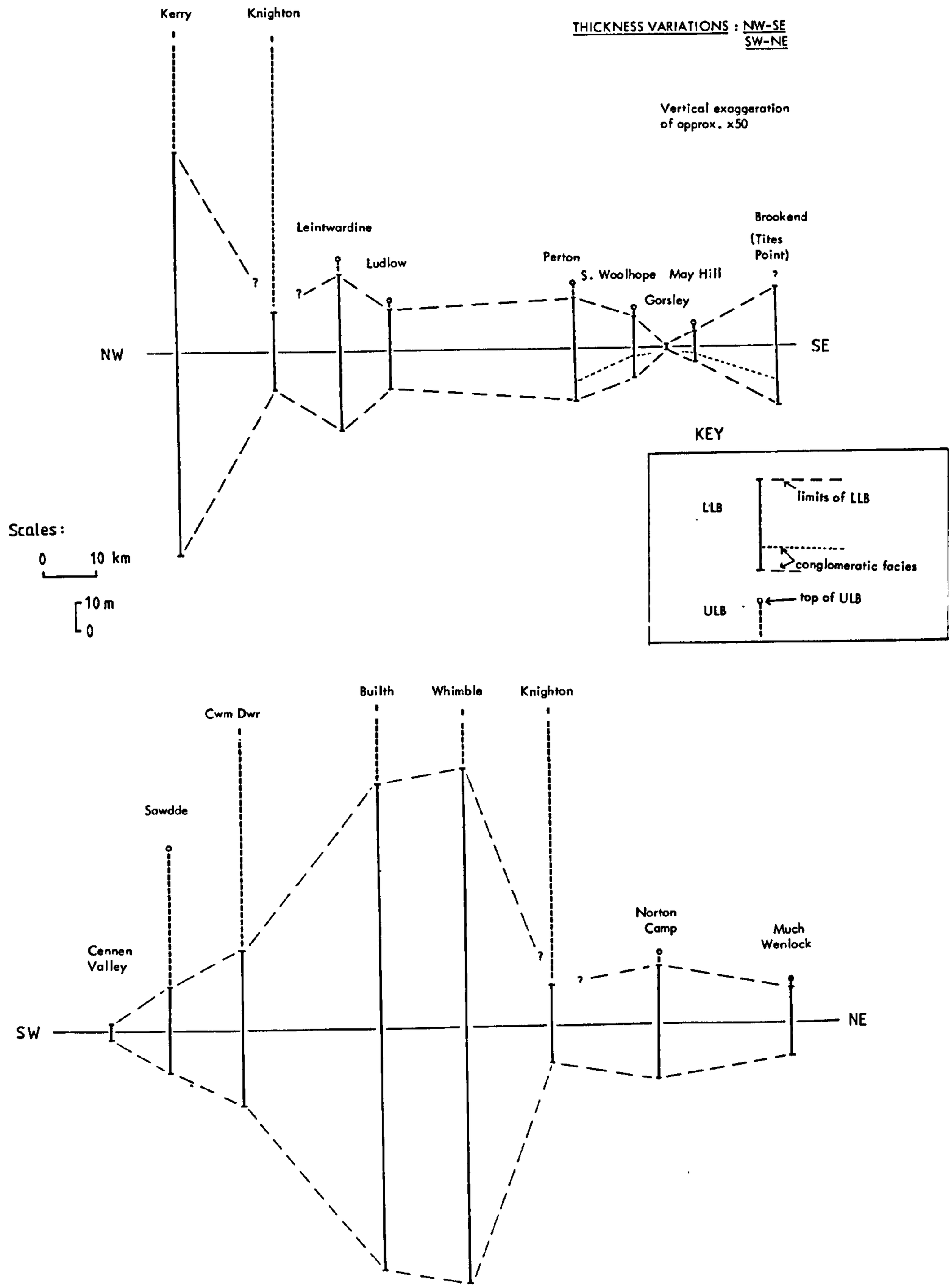

Fig. 1.3 : LLB thickness variations across the outcrop.

Fig. 1.4

ISOPACHYTE MAP
FOR THE LEINTWARDINIAN

Isopach values in metres.
Δ = absent

[Modified from
Holland & Lawson '63]

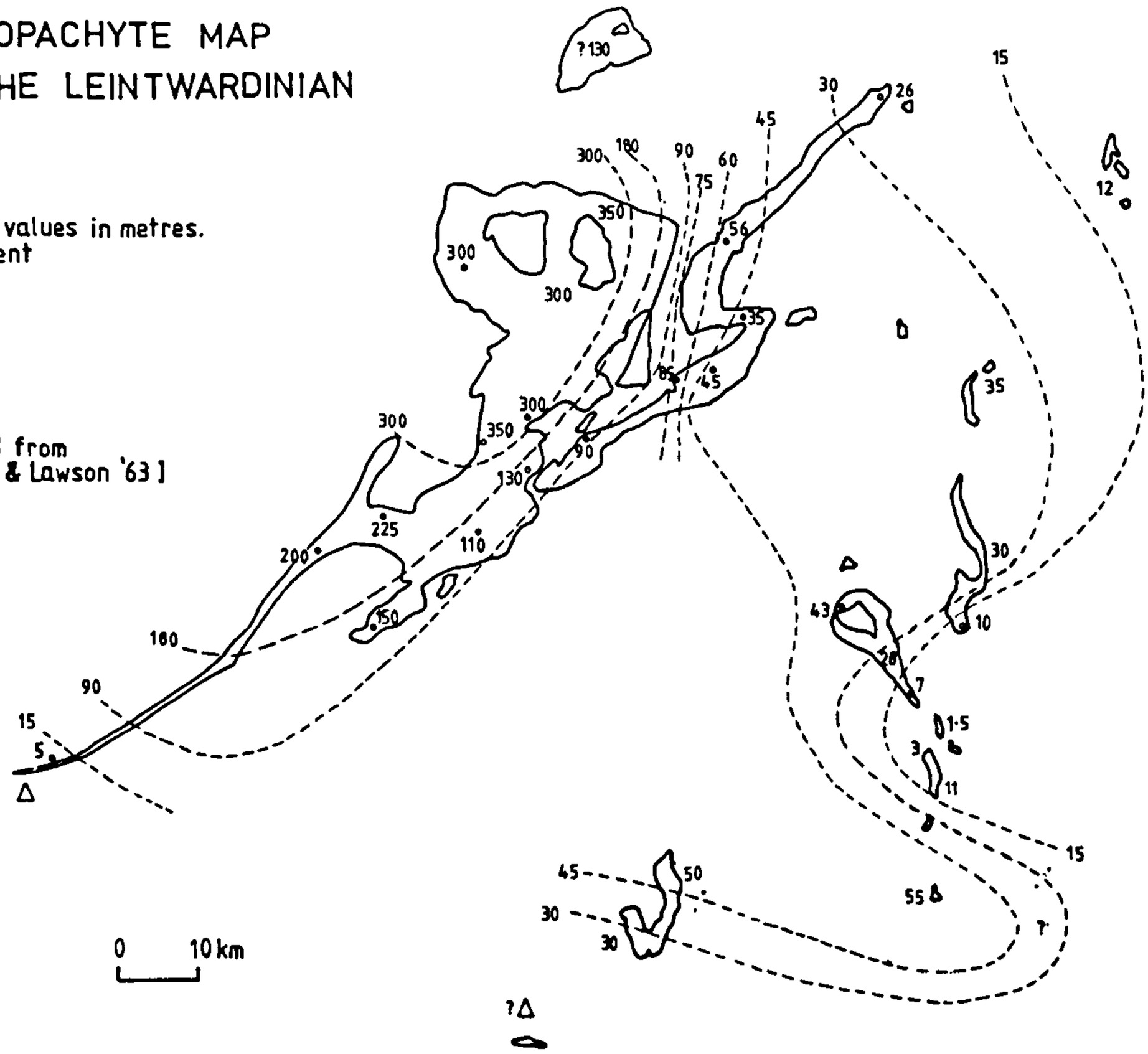

Fig. 1.5

FIELDWORK TRANSECT

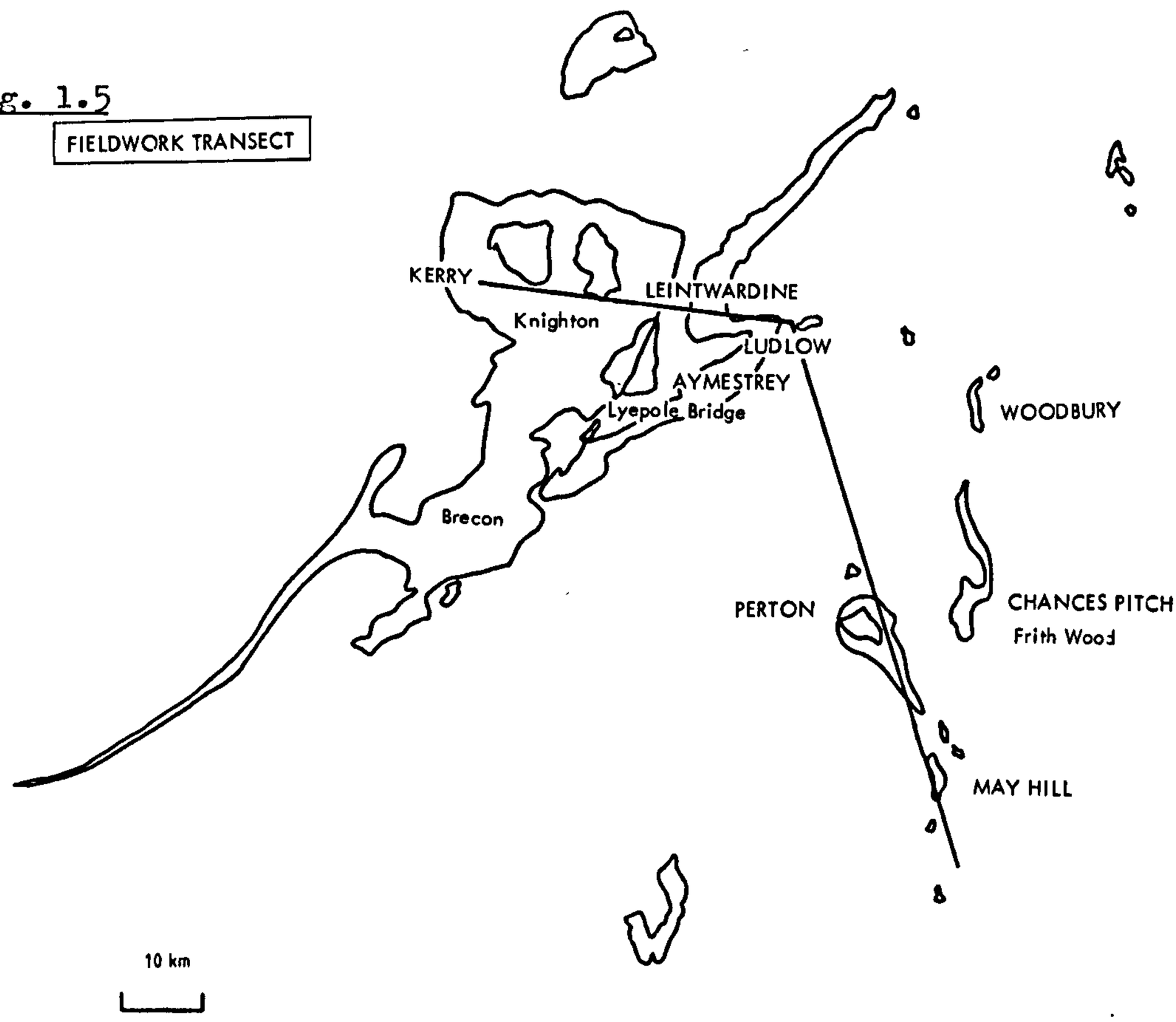

Fig. 1.4 : Isopachyte map for the Leintwardinian.
Fig. 1.5 : Fieldwork transect.

For the Leintwardinian, Holland and Lawson ('63) reported a shelf to basin thickness ratio of 1:8. This is significantly higher than the Eltonian (1:4) and Bringewoodian (1:5) ratios. In the Whitcliffian, a 1:10 ratio is noted, but with a more restricted area of maximum thickness.

Aim and Methods:

The aim of the project was to evaluate the parameters influencing faunal distributions, to distinguish between those groups which are strongly ecologically-controlled and those which are stratigraphically useful. The results enable the possible diachronism of the biostratigraphical unit, the LLB, to be evaluated.

The study is based on a detailed field survey of the succession in localities taken primarily along a shelf to basin transect across the outcrop, from May Hill in the SE to Kerry in the NW (Fig 1.5 p9). Supplementary examination of sequences in the Brecon Anticlinal region, where shelly and graptolitic faunas interdigitate, was made because of the problem of correlation of the benthonic LLB assemblage of the stratotype with the poorly-fossiliferous graptolitic (leintwardinensis zone) basinal sequences. Other localities were selected for further study of parts of the succession - for example, the slumped beds at Lyepole Bridge Quarry (SO.4014.6530), and the angular unconformity between LLB and ULB NE of Wassell Barn, Leintwardine (SO.4164.7561); or for palaeoecological surveys - for instance, Frith Wood (SO.723.404).

The dependence of a palaeoecological study upon a fieldwork survey makes it essential that the collecting method should reflect the nature of the fauna and its distribution. In the LLB, fossils are characteristically concentrated into bands with few in the intervening sediments. Therefore, a bed-by-bed collecting technique was used in order to record the faunal variation. Sampling at set, wider intervals would not have shown the considerable differences found between successive plane assemblages - as, for example, at Wood Green (p 368 ff). The uneven and irregular distribution of fossils is not suitable for "spaced collection" methods. This includes the bulk sampling used by Calef and Hancock ('74) who took a few, geographically widely-spaced collections to be representative of the LLB fauna (see p 383).

Fossils were recorded qualitatively and semi-quantitatively - that is, up to 18 individuals per species - from each unit, together with associated sedimentological and palaeoecological data. The collection

size was fairly subjective, depending to some extent upon fossil density, bed thickness and the composition of the fauna. Representative samples of lithology and fauna were collected. The interbedding of richly-fossiliferous lenses and planes among flags containing few fossils means that collection of a standard volume of rock would not be appropriate. However, samples within localities were reasonable standard. At Aymestrey and Woodbury Quarry, separate records of the first 50 macrofossils found in each bed were taken for comparison with the standard sampling method adopted. The relative scarcity of fossils in the basinal sequences of laminated siltstones (eg. Kerry), compared with shelf sequences, is not fully indicated by the faunal lists; each sample took a much longer time to collect in these sections.

The stratigraphical data from sections in the Ludlow anticline has been used for computer cluster analyses, using both qualitative and quantitive methods. The results are discussed in Chapter 2 (p 38 ff.).

In addition to the systematic sections, quadrat studies of single bedding-plane assemblages and lateral traverses along beds were carried out in order to examine the local faunal variation. Detailed studies of the vertical succession over 2-3 m were made for parts of sequences. Also, palaeoecological tests were applied to individual populations of several brachiopod species.

The stratigraphical data from the fieldwork study are recorded in Chapters 2-4. The information has been used to compile facies and faunal distribution maps - Chapter 5. The ecology of the various fossils is discussed in relation to their LLB occurrences, to evaluate the parameters influencing their distributions. The nature and significance of several of the facies distinguished for the maps is considered more fully in Chapter 6. The faunal characteristics of some shelf sequences are illustrated by the detailed palaeoecological surveys.

The "brachiopod community" concept (eg. Calef and Hancock '74, Ziegler '65, Ziegler et al. '68) is examined. The evidence for repetition of assemblages in the LLB, and the degree of distinction of such associations is discussed, using the whole fauna together with the palaeoecological and sedimentological data to assess the environmental controls. The biostratigraphical use of different fossils is analysed in the context of possible diachronism of the LLB and other Ludlow divisions. From the faunal and facies evidence derived, deductions are made on the LLB palaeobiogeography.

CHAPTER TWO

THE LOWER LEINTWARDINE BEDS STRATIGRAPHY OF THE LUDLOW AREA

The positions of the sections studied are shown on the map of the Ludlow anticline in Fig 2.1 (p 13). The stratotypes for the bases of the Lower Leintwardine Beds and Upper Leintwardine Beds (Holland, Lawson and Walmsley ('63)) were examined. Other sections that provided continuous exposure through parts of the succession were selected for detailed surveys of the vertical faunal and facies changes in the LLB. The base and top of the division were studied in several different localities in order to make a lateral comparison of the changes taking place at these levels in the succession.

Qualitative and quantitative faunal analyses were carried out on the data from the Ludlow sections. The qualitative analyses were used to correlate sequence MF/F - (from the middle LLB), whose position relative to the base of the division was imprecisely known, with the other sequences.

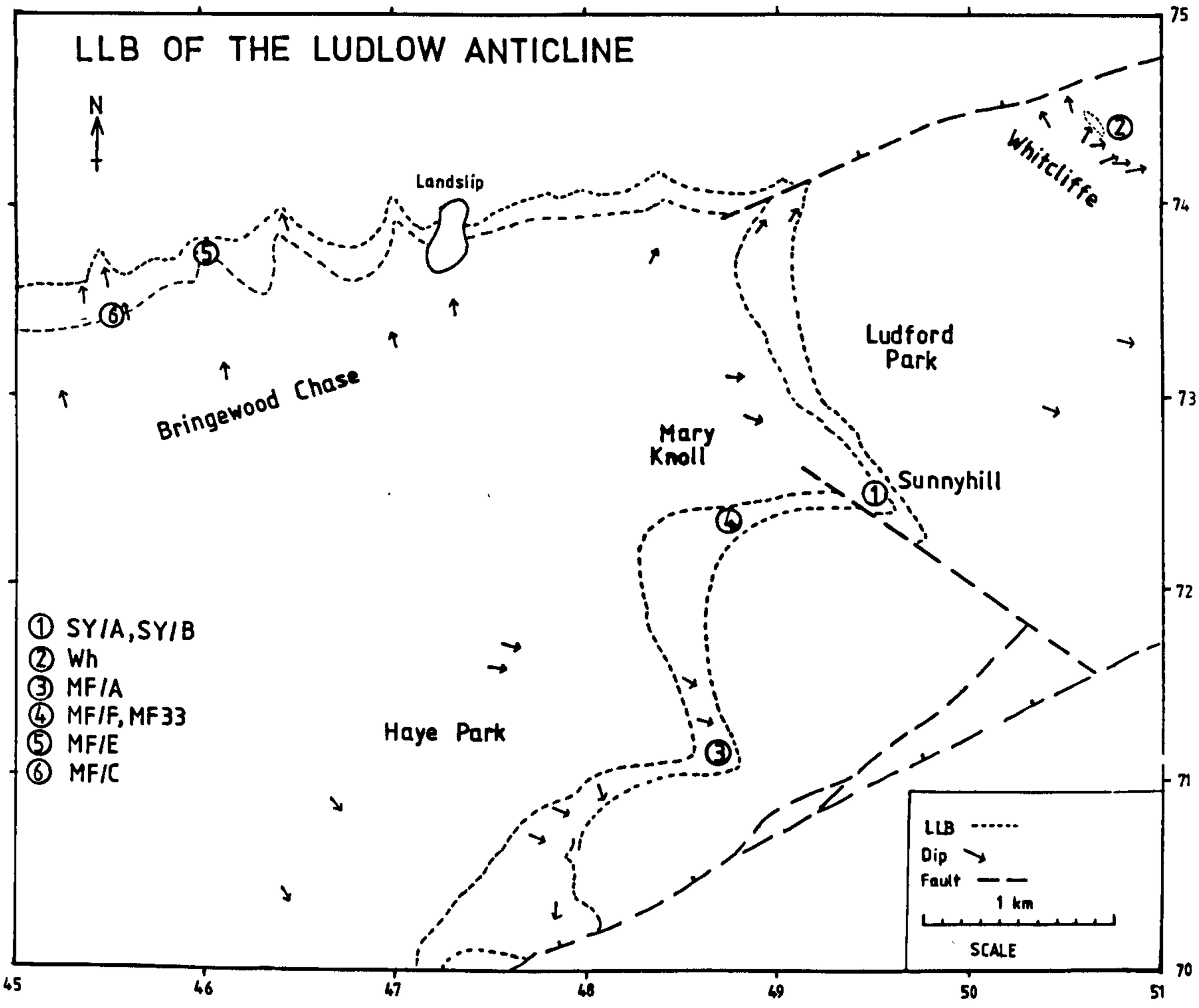

Fig. 2.1 : Map of the Ludlow Anticline showing the LLB sections studied.
(Map taken from Holland, Lawson & Walmsley '63)

1) The Type Section for the Base of LLB and Leintwardinian Stage - Sunnyhill Quarry

(SO 4953.7255 ; Holland, Lawson and Walmsley loc. 30)

Section SY/A - Fig 2.4

Holland, Lawson and Walmsley ('63) placed the base of the LLB, on faunal criteria, within the top part of the Aymestry Limestone rock-stratigraphic unit. The lithological transition from "nodular, irregularly-bedded, massive or thickly flaggy limestones", to "better and more thinly flaggy calcareous siltstones" typical of the Hocktree Shales, takes place about 2.5m above the base of the Leintwardinian Stage at the standard section.

The correlation of the section SY/A - with the standard section of Holland, Lawson and Walmsley is shown in the diagram (Fig 2.2 p15).

The beds below the boundary layer C (- a 0.5cm shale band = SY/A - c) are irregular, nodular limestones and calcareous siltstones, in which fossils, though not common, include forms characteristic of the Upper Bringewood Beds (UBB). In the top 60cm of these beds (B), Holland, Lawson and Walmsley recorded no diagnostic UBB fossils, but decided, because of the lithological continuity with the underlying beds, to place the base of the LLB above the unit. However, in the systematic section SY/A -, typical UBB forms Kirkidium knightii, Strophonella euglypha and Poleumita globosa were found, as well as many solitary corals, in the upper half of B - SY/A - a and b - while the top 15 cm yielded a large Favosites colony (apparently in position of growth). These occurrences support the placing of the boundary above these beds.

Directly above the shale band C, the base of which has been taken to mark the LLB boundary, is an irregular calcareous siltstone band (3 cm thick) containing prominent large branching bryozoans lying parallel to the bedding. Also found in this band was a small piece of a Favosites colony.

The beds higher than C are lithologically similar to those below, and fossils are sparse. However, apart from the Favosites mentioned above, no more forms diagnostic of an UBB age were found above C. The base of the LLB is recognised chiefly by the

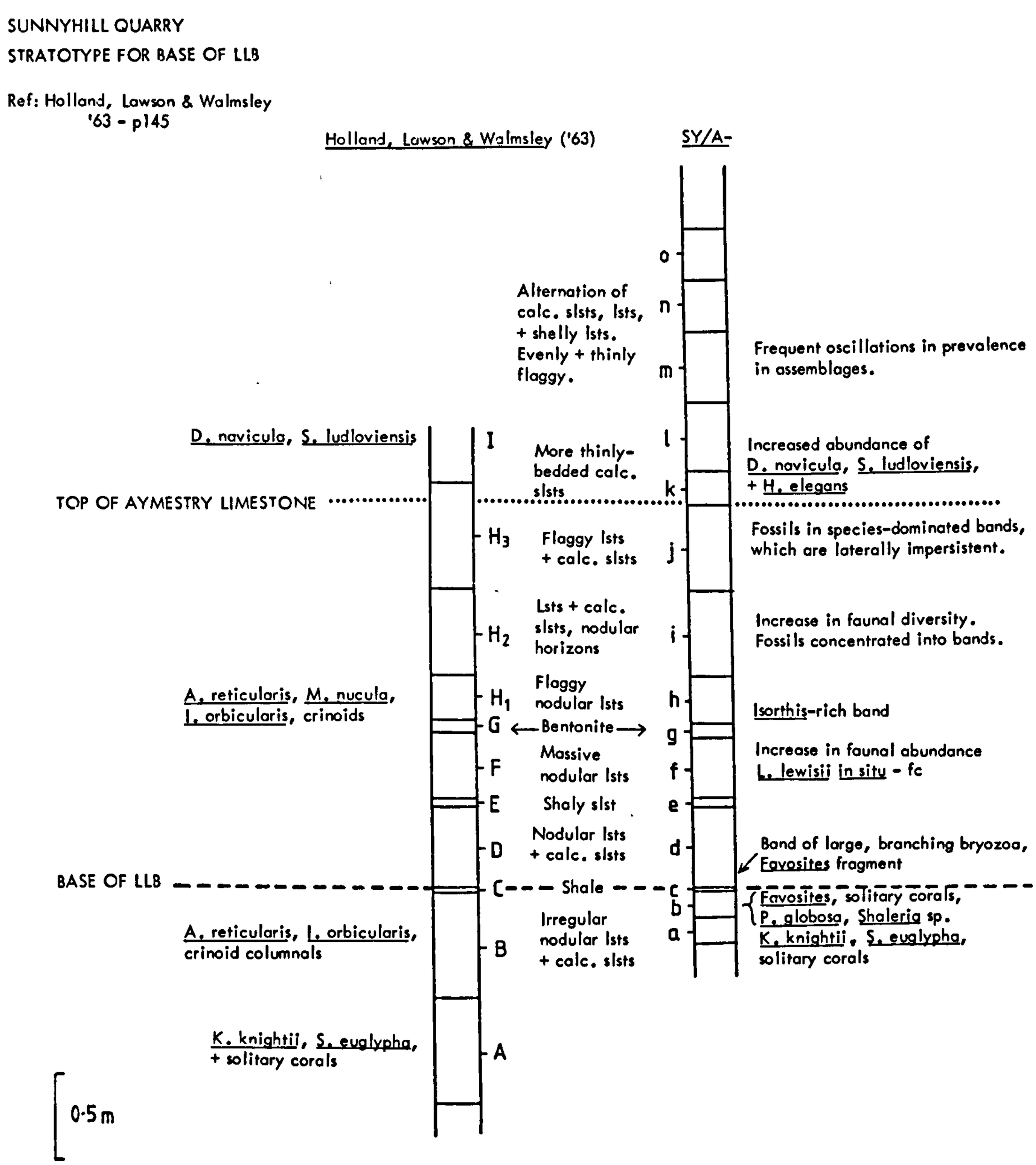

Fig. 2.2 : Correlation of section SY/A- with the stratotype for the base of the LLB and Leintwardinian Stage at Sunnyhill Quarry.

disappearance of typical UBB fossils, many of the common LLB fossils being long-ranging.

Above the boundary layer C, and up to the lithological change which takes place at SY/A - K (Holland, Lawson and Walmsley - I), the limestones become less nodular and more regularly bedded. Both the species diversity and numerical abundance of fossils increase. Two distinct lithological bands - e and g -, were used to divide the sequence; the former is a 4 cm band of olive-greyshale, while the latter is a 7 cm soft clayey shale, which may be bentonitic. The common occurrence of biotite mica in the lowest part of the overlying beds (h) would support this origin for g. (R. Marsh '75 in LRG Bulletin 22, cf. Tucker 1960). The uppermost 1.4 m of the limestone were subdivided into three units, h, i, j (= H_1, H_2, H_3); of these, only the lowest is dominantly nodular (and these nodules are noticeably smaller than those of lower levels), the upper divisions having nodular horizons interbedded with shelly limestones and calcareous siltstones.

A fairly distinct lithological change occurs at the top of j (H_3), with the flaggy to massive, irregular, silty limestones being replaced by thinly, and more regularly, bedded calcareous siltstone flags (k/I). These form the dominant facies type over the next few metres of sequence, interbedded with less calcareous siltstones and with thin limestone and shelly limestone bands.

Faunally, the topmost UBB, though not very fossiliferous, have a varied assemblage dominated by Atrypa reticularis (large individuals) and Isorthis orbicularis - both usually disarticulated - with large Microsphaeridiorhynchus nucula and crinoid columnals. This fauna persists above c (C), but without the accompanying diagnostic UBB forms. The fauna increases numerically in f (F), and Lingula lewisii occurs commonly in situ in these beds. Up to the bentonitic band g (G), the fossils are scattered through the rock, but along with the more regular bedding and less nodular nature of the limestones upwards in the sequence, the fauna begins to be found concentrated into bands.

Directly overlying the bentonite is a band of calcareous siltstones rich in disarticulated valves of Iorbicularis. Species diversity increases in the beds h-j, and though still dominated by brachiopods, the fauna also includes, fairly commonly, several different types of gastropods and bivalves. Within the fossiliferous bands, the faunal composition varies considerably laterally, and the bands themselves are frequently impersistent over only a few metres. Several different brachiopod species are found dominating the fauna of bands, or areas of bands - Shagamella ludloviensis, Dayia navicula, M. nucula, I. orbicularis, and Sphaerirhynchia wilsoni all occur abundantly at levels in these beds. Other horizons in the top part of the Aymestry Limestone facies show the scattered distribution of fossils typical of the lowermost LLB. Apart from the rhynchonellid brachiopods, the fossils are mostly disarticulated specimens.

The facies change that takes place at the top of j (H_3) is accompanied by little change in the qualitative faunal composition, but D. navicula and S. ludloviensis both increase in abundance, and Howellella elegans becomes common. The lowest 1.5 m of flags overlying the calcareous beds have calcareous siltstone bands in which the fossils are concentrated onto planes; some of the faunas are dominated by one or two species, others are diverse. In other bands, shells are distributed throughout the beds, with the proportions of the common species varying laterally and vertically to produce frequent oscillations in numerical dominance. Most of the shells in the siltstones are disarticulated, and shell planes frequently show a predominance of convex-up valves; however, in some shelly limestone bands, articulated, randomly-orientated, shells are common.

2) The Type Section for the Base of ULB: Whitcliffe
(SO.5071.7428; Holland, Lawson and Walmsley '63, loc.3).
Section Wh-

At the type section, the distinction between LLB and ULB is not readily made either palaeontologically or lithologically. The thinly-bedded, green-grey, very calcareous siltstones of the uppermost LLB continue up into the ULB, and it is only in the top metre of the ULB (Total thickness here 5.5 m) that the thicker bedding characteristic of the western facies of this division occurs.

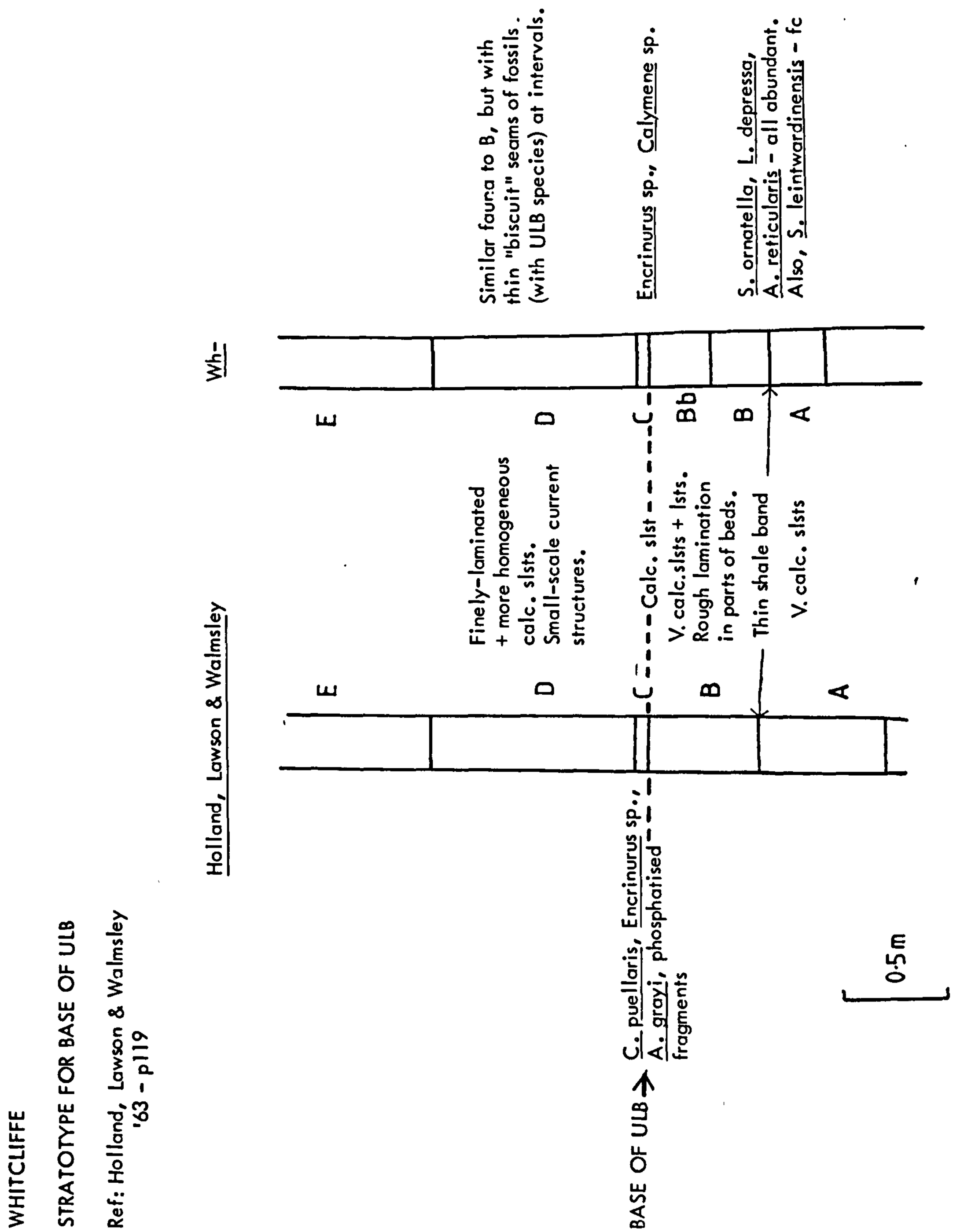

Fig. 2.3 : Correlation of section Wh- with the stratotype for the base of the ULB at the Whitcliffe.

For correlation of the section Wh- with the section described in Holland, Lawson and Walmsley ('63) see the accompanying diagram (Fig 2.3 p18).

The facies of the topmost LLB was a hard, very calcareous siltstone. Intercalation of calcareous and siltier layers produces distinct lamination in some bands, while other parts are more homogeneous in their lithology. The presence of thin calcareous lenses and small ripples in the laminated flags indicate the activity of gentle bottom-currents. Fossils are evenly distributed throughout many beds, but with planes of drifted valves occurring at intervals, and with occasional bands of very shelly limestone. Immediately above the bed taken by Holland, Lawson and Walmsley to mark the base of the ULB (Wh-C/Holland, Lawson and Walmsley-C), the calcareous siltstones (D) have only scattered fossils, and some flags show a very fine lamination with bands of small-scale cross-bedding, and ripple-marked surfaces. Crinkle-marks parallel to the ripples suggest slight downslope movements of partially-consolidated sediment.

The upper flags of the LLB yield a diverse fauna characterised by the very common occurrence of Shaleria ornatella, A. reticularis and Leptaena depressa, together with S.leintwardinensis (RBR), Fuchsella amygdalina, orthocones and proetids. Articulated specimens of both L. lewisii and Lingula lata are found fairly frequently perpendicular to the bedding, possibly in their life orientation within the sediment, in addition to disarticulated drifted valves. Articulated A. reticularis, the preservation of the trails on many L. depressa valves, and the usual wide size range of individuals even in planes of drifted valves of S. ornatella (very few of which are broken), all suggest that these species have not been transported far (see Palaeoecological criteria - Ch. 6).

At the base of bed C (Holland, Lawson and Walmsley - C), a thin fossiliferous seam includes a calymenid free cheek and part of an encrinurid cranidium together with the other fauna. Holland, Lawson and Walmsley also recorded Aegiria gravi from this bed (and

identified Calymene puellaris), and took the 4 cm calcareous siltstone unit as the base of the ULB, defined on these faunal elements. They also noted the presence of some phosphatised fragments.

Beds directly overlying C have only occasional fossils scattered through them; S. ornatella and S. leintwardinensis (RBR) were recorded from low in D (Holland, Lawson and Walmsley-D). Higher beds of D contain a similar fauna to A, B and Bb, (A, B) while occasional thin 'biscuit' seams, which occur from the top few centimetres of Bb (B) at intervals upwards, include the additional ULB forms.

3) Sunnyhill Sections: SY/A-, SY/B-

Figs 2.4, 2.5

These sections cover a large proportion of the succession, from the defined base of the LLB at the stratotype, through to the ULB. The thickness of the LLB here is estimated to be 27 m. Many beds in the quarry - the lower 14 m of section - are hard, very calcareous siltstones and thin limestones. It was difficult to extract samples from the vertical quarry face, and hence the quantitative faunal records are relatively low. The upper part of the sequence is exposed in a new track section above the quarry, where the relative ease of collection is reflected in the numerical records. However, the disparity between the faunal abundances in SY/A - and those in SY/B - is only partly explained in this way; the higher beds are generally much more richly fossiliferous.

The succession and sediments of the stratotype have already been described, up to 4.5 m above the boundary. There is a gap in the sequence of approx 5 m between SY/A - o and the beds qa - za (2.2 m). These beds are very calcareous siltstones and shelly and inorganic limestones, in which the fauna is concentrated into bands. Some beds are finely-laminated, and massive, with monospecific plane-assemblages at intervals. Others are sparsely fossiliferous, more homogeneous siltstones, which are intercalated with shelly limestones, and debris-rich, conglomeratic limestone bands. These calcareous bands frequently have distinct lower boundaries, and

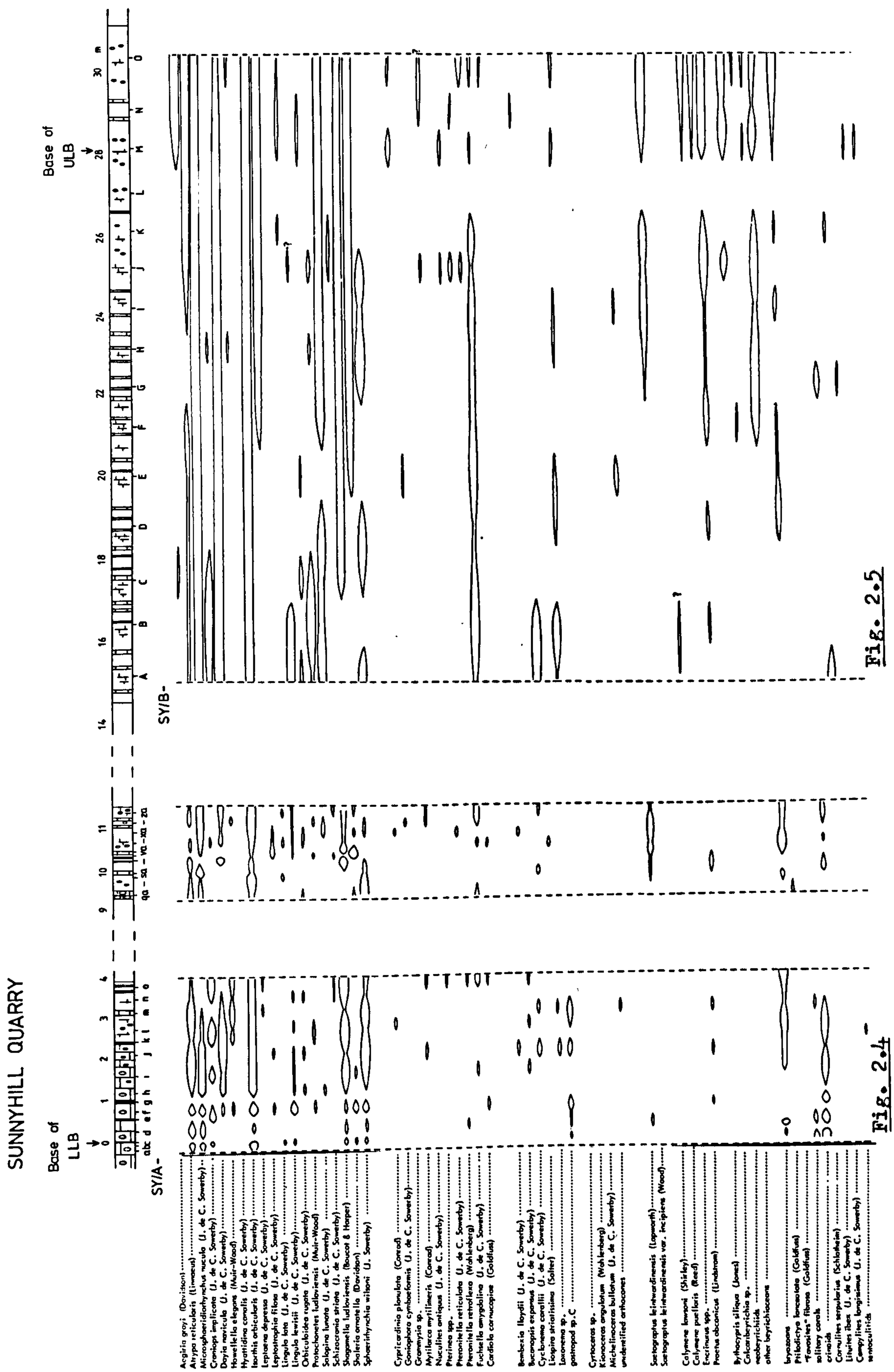

Fig. 2.4 : LLB succession SY/A-, Sunnyhill Quarry.
Fig. 2.5 : LLB succession SY/B-, Sunnyhill Quarry.

contain much fragmental material. The fauna is qualitatively different from the plane-assemblages of the upper flags of the basal sequence a - o. H. elegans does not appear in the upper part of SY/A, where S. ludloviensis becomes increasingly common. The strophomenids S. ornatella and Leptostrophia filosa occur in some bands, and graptolites (which include S. leintwardinensis s.s. and Saetograptus n. sub-sp. (RBR)) are found from sa upwards. The shelly limestones are rich in rhynchonellids, while L. lewisii and bivalves (especially F. amygdalina) occur occasionally, although consistently, in the siltstone flags. Some laminated beds show traces of burrows. These beds are characterised by thin plane-assemblages of disarticulated S. ludloviensis valves, convex-side up.

Section SY/B - follows a gap of about 2 m, covering the succession from 14 m above the base of the LLB up into the ULB. The sediments of the lower 8 m (A - G) are dominantly finely laminated, very calcareous siltstones, often fairly massive, which are interbedded with calcareous and shelly beds. The limestones are often lenses, being laterally impersistent over only a few metres, although some bands are more extensive and consistent in thickness. The flags commonly have undulating surfaces, though are not internally cross-bedded, and characteristically have thin bands and plane-assemblages of drifted shells at intervals. There are few shells in the beds between, and the concentrations are typically monospecific or dominated by only a few species. Intercalated among the laminated siltstones are, apparently unbedded, homogeneous siltstones, in which shells are often more evenly distributed, as well as occurring in dense accumulations at some levels.

Higher up the succession, the proportion of laminated beds in the sequence decreases relative to the "unbedded" flags, and there are occasional nodular horizons. The fauna is still commonly concentrated in bands, with frequently monospecific, closely-packed assemblages. Many of the calcareous laminated beds are more massive, and unfossiliferous. There is no lithological change at the LLB-ULB boundary, although faunally, there is a marked diversification at this level. The siltstones do not become thicker-bedded until several metres above the boundary (-similar to the Whitcliffe ULB in this respect).

The lowest 6 m of section (A - E) have numerous assemblages of abundant, isolated valves of I. orbicularis, D. navicula, and S. ludloviensis, either in monospecific, or in dominated faunas. Several other planes have widely-scattered F. amygdalina valves. The shelly limestones contain broadly similar faunas, although S. wilsoni is especially common, and bivalves are rare. Some of the Dayia-rich limestones include a high proportion of articulated specimens.

Above this level, the fauna becomes more diverse, with the strophomenids L. depressa and S. ornatella increasing rapidly in abundance, and proetids and beyrichiacean ostracodes occurring regularly in the assemblages. S. leintwardinensis (RBR) is found from band G upwards, typically scattered through beds or in small patches. Salopina lunata becomes very abundant, often in different bands from Isorthis-rich assemblages. The distribution of the fossils is similar to the lower part of the succession.

After K (12 m up in the section), A. reticularis becomes very abundant, while S. wilsoni is not found above this level. S. ornatella is found dominating many faunas. The appearance of A. gravi, C. puellaris and Encrinurus stubblefieldi in collection M, along with one specimen of a ?neobeyrichiid ostracode (LC), was taken to indicate the LLB - ULB boundary in this section. Neither A. gravi, nor beyrichiaceans are common over the next two metres (N, O), but the trilobites become more numerous.

Bioturbation:

In the lower section SY/A, burrows were not recorded from the sediments, but signs of bioturbation are common in many beds of the upper sequence SY/B. Frequently, narrow burrows are seen in the laminated siltstones, perpendicular to the bedding. Some beds have a mottled bioturbate texture, resulting from extensive biogenic reworking. Planes covered with a network of fine traces are relatively common. One specimen of a Keilorites squamosus perpendicular to the bedding was found in J; Cornulites serpularius is common in band A, and a few tentaculitids are present in the higher strata. The comprehensive bioturbation of the sediments in this section contrasts with the scarcity of burrowing organisms among the fossils.

The common bivalve F. amygdalina, which may be a shallow-burrowing form (see p 257), could be responsible for some reworking of the sediments. It is most frequently found as disarticulated valves on bedding planes, rather than within the sediment, and may therefore not have been an indigenous form.

4) MF/A -

(SO 488.711; Locs. 61 and 62: Lawson '73) Fig 2.6

The systematic section MF/A covers the upper 10 m of the LLB and the LLB - ULB boundary. Recent excavations of the lower part of the succession have allowed the complete thickness of the LLB, here estimated to be 23 m, to be examined briefly.

The sediments in this area are less calcareous in the lower half of the succession than those further east, which enables a lateral comparison of contemporaneous faunas from different facies to be made.

The basal facies in this section are rubbly nodular limestones and calcareous siltstones, with bands of shaly siltstone. The siltier nature of the Aymestry Limestone is reflected in the faunas: a few solitary corals were found in the topmost UBB, together with small valves of S. euglypha, Amphistrophia funiculata, Shaleria sp, and Dalmanites pygidia. No compound corals were recorded. Branching bryozoans are common, along with typical LLB brachiopods in the siltstones. Bands of comminuted shell debris are fairly common. Large specimens of L. lewisii perpendicular to the bedding, are abundant, many within the irregular limestone nodules. It is difficult to discern the bedding because of the nodular lithology; the size and shape of the nodules are very variable.

The bedding becomes more regular and flaggy within the bottom 2 m of the LLB, although still mainly nodular. Alternations of silty and calcareous bands with thin shelly limestones follow over the next 4 m of the succession, above which the beds are nodular only at horizons. These higher sediments, up to the base of the systematic section, are dominantly finely-laminated calcareous siltstones with very fossiliferous coquinas. Bands and planes of fossils are often monospecific, or composed of few species, and many are discontinuous laterally. Several smooth bedding-plane surfaces appear to be

ripple-marked, although internal cross-bedding was not seen. Calcareous and shelly lenses occur at frequent intervals in the sequence. Interbedded among the laminated siltstones are flags of more homogeneous siltstone.

The basal LLB have a mainly brachiopod fauna, numerically more abundant than the Sunnyhill Quarry equivalents (SY/A -) and including D. navicula, Hyattidina canalis and H. elegans as additional elements to that fauna. Several assemblages are dominated by different single species, but more varied faunas are also common. Fossils are concentrated into bands in some beds, while others have a more evenly-dispersed distribution.

Through the facies transition to more thinly-bedded and less calcareous sediments, the faunal abundance becomes greatly increased without much qualitative change. The assemblages of the shelly limestones are largely composed of disarticulated valves of H. elegans, S. ludloviensis and I. orbicularis, together with many moults of proetids and warburgellids, and shell fragments. In contrast, the siltstone faunas are often composed of only one or two species, and H. canalis and D. navicula are relatively more common. Bands of shell debris are present at many levels in these flags. As the bedding becomes less nodular and more regular, the fossils are typically found in thin bands, with few in the intervening layers. The prevalent species alternate, with D. navicula, I. orbicularis, S. wilsoni, M. nucula and S. ludloviensis all abundant at various levels, and F. amygdalina very common in a number of other, usually separate, bands. The laminated siltstones and shell limestones have similar dense accumulations of shells at intervals which vary from layers only one shell thick to limestones of 5 cm or more. The majority of these bands are impersistent laterally for more than a few metres. In addition to the dominant fossils of the lower bends, S. lunata and L. depressa are important constituents in many assemblages. Characteristically, the shells are disarticulated and orientated convex-side up in the accumulations; but the degree of breakage is often not high. Several planes of F. amygdalina valves have aligned shells. In contrast, assemblages of disarticulated pedicle valves of Davia are more variably orientated either way up;

and in some monospecific calcareous lenses, numerous randomly-orientated articulated specimens of Dayia are among the separate valves.

Throughout the lower part of the succession, up to the well-laminated beds (≐ 6 m of LLB), L. lewisii is consistently found perpendicular to the bedding in the sediments. The individuals were noticeably smaller than those of the top UBB, usually less than 1 cm in length (cf. 2-3 cm). They are very common in beds at several levels, and present in many others.

Above the bottom 4 m of the LLB, H. elegans and H. canalis decline rapidly in abundance. A. reticularis, which is common in the basal nodular beds, is only occasionally found above the facies change to more silty, thinner flags.

Systematic section MF/A (13-24.5 m above the base of the LLB)

The facies of the upper half of the LLB are mostly calcareous siltstones, generally thinly-flaggy, and laminated in parts. Typically, the fossils are concentrated into bands within the laminated beds, while some other, unlaminated siltstones have a more even distribution of fossils. Thin shelly limestones occur at intervals. A number of calcareous bands are more massive, and unfossiliferous; these are also laminated. The proportion of laminated beds decreases upwards in the succession, until they comprise only a minor proportion of the sediments in the upper 5 m of the section. At the faunal boundary between the LLB and ULB, there is no pronounced lithological change, but the higher beds are often more thickly flaggy.

The lowest 5 m of section (MF/A - E to M) has a comparable fauna to that described for the underlying rocks. Bands of shell moulds, crowded with D. navicula, I. orbicularis and S. ludloviensis, occur at frequent intervals. In addition to the lower fauna, A. reticularis, S. ornatella and S. leintwardinensis (RBR, and LC) become increasingly common, and L. depressa and S. lunata are more abundant in these beds. Bivalves are fairly common in many bands, and there are several articulated individuals of F. amygdalina at some levels. The latter individuals are usually dispersed within beds rather than on bedding planes, but bands of drifted, separate valves are also found. L. depressa valves, many with trails, and inverted to convex-side up, are common on micaceous planes of

MF/A-

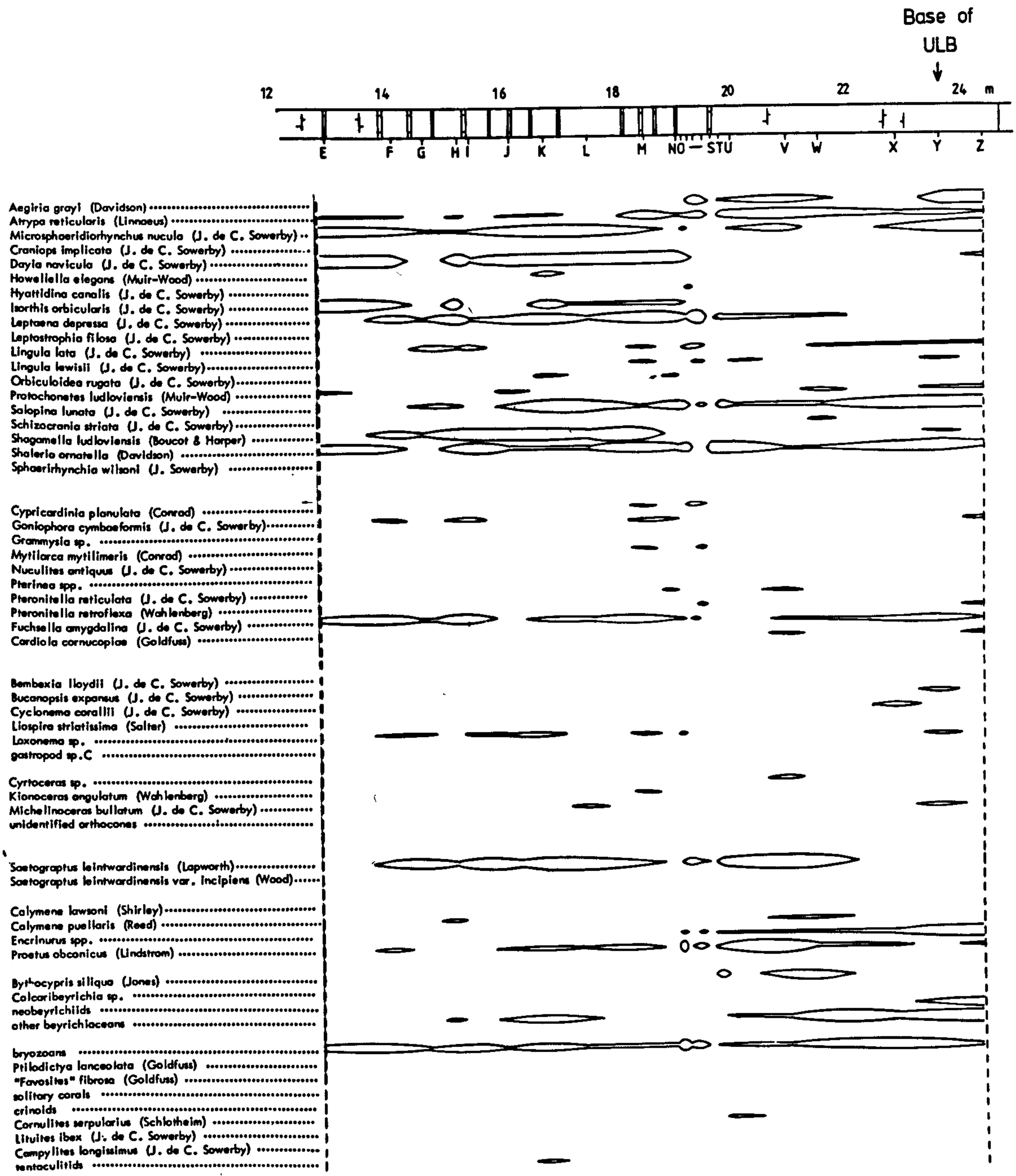

Fig. 2.6 : Systematic section MF/A-.

laminated beds at several horizons. Graptolites are abundant in some unlaminated siltstone beds in which they are randomly dispersed. They also occur sporadically in other beds.

Above M (5.5 m up in the section, 18.5 m up in LLB), there begins a marked faunal change, with S. ludloviensis, I. orbicularis and D. navicula disappearing from the fauna, and A. gravi coming in. S. ornatella, L. depressa and A. reticularis are all abundant in this part of the sequence, and proetids have become much more numerous. At the top part of the section, from U-Z (20.5 m upwards), the fauna becomes more diverse, with E. stubblefieldi, C. puellaris and beyrichiacean ostracodes as additional elements. The base of the ULB was assigned at Y, because of the first appearance of Neobeyrichia lauensis, together with a rich ostracode fauna which also includes Neobeyrichia scissa and Neobeyrichia confluens. Graptolites and L. depressa are not found above W.

The typical Whitcliffe Beds associations of Protochonetes ludloviensis, M. nucula and S. lunata begin to occur with the Leintwardinian forms in the beds immediately over Z.

Except for the lowest 1.5 m of section, individuals of L. lewisii were found perpendicular to the bedding, apparently in situ in a number of beds throughout the succession, particularly in the upper half where they were consistently fairly common. As in the lower part of the LLB in this section, specimens were generally small.

Bioturbation:

The basal LLB in this section are clearly burrowed in some parts, with oblique, and bedding-parallel, traces of narrow diameter (2-3 mm) visible in many siltstones. Throughout the facies transition from the nodular limestones, burrowed bands are apparent at intervals. The lower laminated siltstones frequently have patches in which the bedding has been disrupted, probably by bioturbation. Other beds have single distinct traces which are particularly noticeable against the laminated lithology. These more isolated occurrences, rather than signs of extensive reworking, were noted from the middle portion of the LLB, where laminated beds with shell layers and lenses are characteristic. In the systematic section, well-bioturbated flags are interbedded with ones in which the fine lamination is little disturbed.

As in the Sunnyhill section, there are few preserved remains of organisms that could have been responsible for the reworking of the sediments. Serpulitids and tentaculitids were recorded only occasionally. Therefore, it is reasonable to conclude that soft-bodied deposit-feeders may have been important faunal constituents.

Burrowing bivalves could have been important agents in reworking more comprehensively disturbed, "mottled", beds, although not the narrow traces. F. amygdalina is common in bands right through the succession; some specimens were articulated or open but still hinged, indicating that these had not been transported far. Goniophora cymbaeformis was occasionally found, but always disarticulated. Both forms are thought to have been shallow burrowers (see p257).

5) MF/F -

(SO. 489. 724; Loc. 33 of Lawson '73) Fig 2.7

The section, situated on the western side of the old quarry, covers 4.5 m of beds in the middle part of the LLB. Stratigraphically, the strata are above these with plane-dominated assemblages which were used for palaeoecological surveys (see Ch.6 p363). The fauna of the UBB-LLB boundary, which is exposed in the roadside bank at the east side of the quarry (MF33), is shown on Fig 2.9, p 37.

The sediments are thinly, to moderately-thickly, bedded calcareous siltstones, intercalated with shelly limestone bands and laterally-impersistent, calcareous lenses. The top metre of beds are dominantly more thinly flaggy. The silty beds are frequently hard, massive, and laminated, with alternating,more and less calcareous, bands. The thickness of the individual layers varies from 2-3 mm in some cases to less than 0.5 mm in others. These flags characteristically have concentrations of shells at intervals, with largely unfossiliferous beds between such horizons. The thickness of the accumulations changes rapidly along their length, with even the thick shell limestones (over 6 cm) thinning and dying out in short distances (often less than 1 m). It is unusual for any of the coquinas to persist for many metres laterally. As well as the shelly limestones, small inorganic calcareous lenses and ripples are common in the laminated sequences. Minor sedimentary structures, such as ripple cross-bedding, and small unconformities, are clear in the finely-laminated sediments. Flags

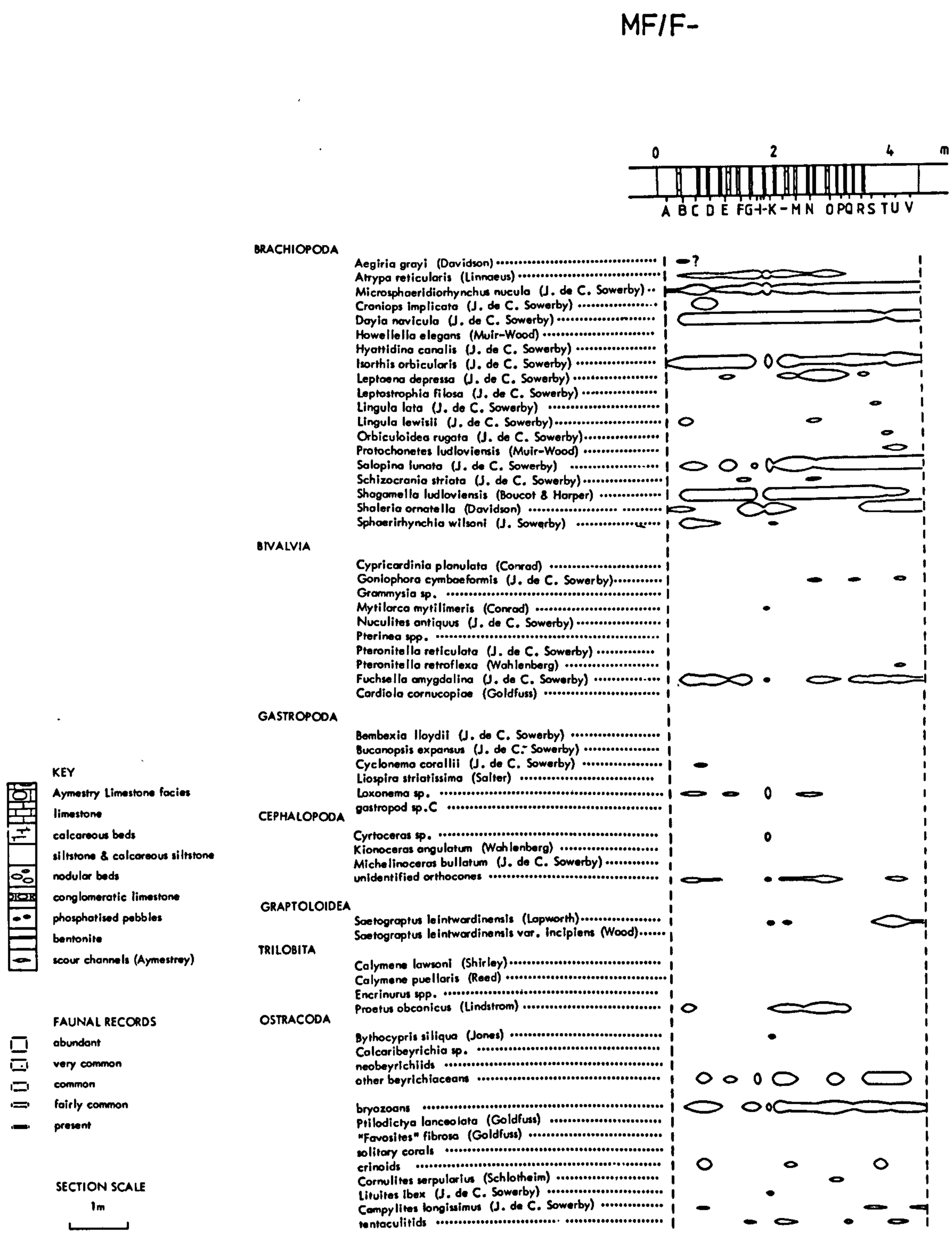

Fig. 2.7 : Section MF/F-, from the middle part of the LLB.

with gently undulating, ripple-marked surfaces were seen at several levels. Interbedded with the laminated flags are more homogeneous siltstones, some of which have fossils distributed throughout. Others are less, or sparsely, fossiliferous, sometimes with patches of wispy, uneven lamination.

The faunas of the laminated and unlaminated beds are similar, with the assemblages characteristically monospecific or dominated by only a few species. The prevalent forms alternate repeatedly. D. navicula, I. orbicularis and S. ludloviensis are the dominant species in the lower half of the section, while S. lunata becomes more consistently abundant in associations, compared with I. orbicularis, in the upper part. F. amygdalina is more common in bands in the lower beds (A-F), although it is found fairly regularly throughout the section. Rhynchonellids are important faunal constituents of many assemblages; S. wilsoni declines rapidly above the lowest metre, but large, strong-ribbed individuals of M. nucula are found abundantly in many beds, and increase significantly in concentration in the higher beds (Q-V), when S. ludloviensis and D. navicula faunas decline in frequency.

A number of plane assemblages of S. ludloviensis have similar associated faunas, of L. depressa valves with trails, S. ornatella, S. lunata, small D. navicula and A. reticularis, proetids and small beyrichiacean ostracodes. Many of the fossils are small specimens. The brachiopods are typically disarticulated, and orientated convex surface upwards. The degree of breakage varies considerably, but is often not high.

One plane (I) has an unusual assemblage of abundant D. navicula, with numerous high-spired Loxonema sp gastropods and several Cyrtoceras sp. and orthocone specimens.

The beds from E to P are, dominantly, laminated fairly massive, calcareous siltstones, with prominent shell lenses, and discrete horizons of fossils. Above this level, the beds become more uneven and flaggy, with more unlaminated siltstones containing well-scattered fossils interbedded among the laminated units. Enteletaceans, and large S. ornatella valves are especially abundant in these beds, with patches of D. navicula and clusters of M. nucula. Bivalves are fairly common too, chiefly F. amygdalina, but also a few G. cymbaeformis. Graptolites (S. leintwardinensis (LC)) occur in the top 90 cm (S-V) of the section, dispersed through the beds.

In this section, L. lewisii was found perpendicular to the bedding only in collection B, where four such specimens were recorded. Rare drifted valves, usually broken, were found in the rest of the sequence.

Discrete burrow traces were noted fairly infrequently except in the topmost 70 cm (T, U, V), where some bands were burrow-mottled. However, the homogeneous texture of some of the lower beds may result from extensive biogenic activity. Individual traces are narrow in diameter (less than 3 mm), and often across, or only slightly oblique to, the bedding planes. More steeply-inclined, isolated burrows were visible in some laminated units.

Serpulitid fragments, and tentaculitids were occasionally found, and rare C. serpularius, from thesestrata. Burrowing bivalves could have been responsible for reworking some sediments; a few articulated F. amygdalina individuals were found perpendicular to the bedding in unlaminated parts of C and U, apparently in their life attitudes. Significantly, neither of the possibly shallow-burrowing species F. amygdalina and G. cymbaeformis (see p.257, 259) are common in the middle part of the section (E-P), where laminated and shelly units are prevalent, but their frequency increases where more homogeneous beds are intercalated with the others. The occurrence of some possibly indigenous specimens is therefore palaeoecologically important. The bedding plane assemblages of mainly drifted valves of F. amygdalina may have resulted from local current reworking of top sediment in which populations of these molluscs were living.

6) MF/E

(SO 4620.7363 = loc.18 of Lawson '73) Fig 2.8

This section comprises the lower part of the LLB, beginning just above the faunal transition at the base of the LLB, but still in the Aymestry Limestone facies, and extending upwards through 8 m of the succession.

The lowest beds exposed are irregular, nodular limestones and calcareous siltstones. These pass up into more thinly flaggy calcareous siltstones alternating with narrow bands of bioclastic limestone, and more inorganic or nodular limestones. Many of the siltstones are nodular, particularly in the lower strata. The bedding of these horizons is uneven, because of the very variable size, concentration, and orientation of the nodules. Lithological changes are largely

gradational, depending upon the relative carbonate content of the sediments. The bedding higher in the sequence is often more distinct; a number of shelly limestones have sharply defined lower boundaries, and fine even lamination is apparent in some siltstone units.

The bottom metre of exposed rocks (Ua-Xa), though less massive and calcareous than the facies at Sunnyhill Quarry, is considered to be the top of the Aymestry Limestone. The fauna shows these to be LLB, and not UBB. The highest diagnostic UBB forms were from a small bank exposure (MF/E - base) approximately 1 m below band Ua. (Unfortunately the intervening beds were not accessible in this section). The numerical abundance of the fauna increases markedly upwards; a feature noted too in the other basal sections. The more massive limestones are not very fossiliferous. Their highly irregular boundaries suggest that they might be aggregations of coalesced nodules. Other limestone bands, though, are more evenly-bedded and bioclastic, commonly with a high proportion of disarticulated and broken shells. In the siltstones, some beds have a fairly random distribution of fossils while, in others, the fauna is concentrated into discrete layers. Most beds are nodular. They vary in composition, with the size, shape and abundance of the limestone nodules being irregular. In beds where A. reticularis is common, many nodules include its large isolated valves. (This species is especially abundant in the basal beds, frequently occurring in virtually monospecific assemblages of disarticulated valves).

The beds become less massive and more regularly flaggy above the bottom metre. Although many siltstones are nodular, the generally smaller size of the nodules, and the fact that they are often confined within certain bands, means that, though uneven, the bedding is clearly discernible. Alternating with the siltstones are thin shelly limestones, carbonate bands composed mainly of fragmental material, and more inorganic deposits. The fauna is variably distributed - clustered on, or scattered over, bedding planes, or dispersed through the sediments. The diversity of the fauna increases, although many assemblages are dominantly composed of only a few species. The prevalent components of faunas vary from bed to bed, and similarly, their relative proportions.

Such faunas are typical of the next part of the succession (D-M), which is less calcareous and less nodular than the lower portion of the LLB. Many of the siltstones appear homogeneous, when the bedding is marked by the thin shell horizons. Other flags show a fine lamination of more and less calcareous bands, although in parts, these sedimentary structures have been destroyed by burrowing.

Above M, nodular beds are again common, and calcareous bands become more prominent. Accompanying this transition is a second acme of A. reticularis, and a decrease in the non-brachiopod components of the fauna. Some of the calcareous horizons are finely-laminated, and unfossiliferous, others are thin, shell layers. Many beds in the sequence from M-R have sparse faunas.

The top part of the section (S-Z) has thicker, richly fossiliferous, shelly limestones intercalated with the calcareous and nodular siltstones, and inorganic limestones. The bioclastic limestones have sharp boundaries with the underlying beds, and contain dense accumulations of shells and fragmental material. Their upper boundaries are less distinct, with the tops very largely composed of fine shell debris. Band S contains patches of fine, green-grey siltstone within the limestone. The strophomenids L. filosa and S. ornatella are common in the limestones, together with rhynchonellids and I. orbicularis, while the intervening siltstones are characterised by disarticulated I. orbicularis and S. ludloviensis, with A. reticularis in the nodular bands. Limestone band X, which had a diverse and abundant fauna, contained graptolites, identified as Saetograptus n. sub-sp (RBR).

Bioturbation:

Burrowed beds were noted throughout the succession, from approx. 50% of the strata. The intensity was high enough in some parts of finely-laminated beds to destroy all signs of the bedding, leaving a mottled appearance. In other bands, the extent of burrowing varied greatly laterally; mostly, only the presence of burrows was recorded for bands and planes.

The majority of the traces are narrow (<3 mm across), variously orientated both oblique to, and parallel with, the bedding. However,

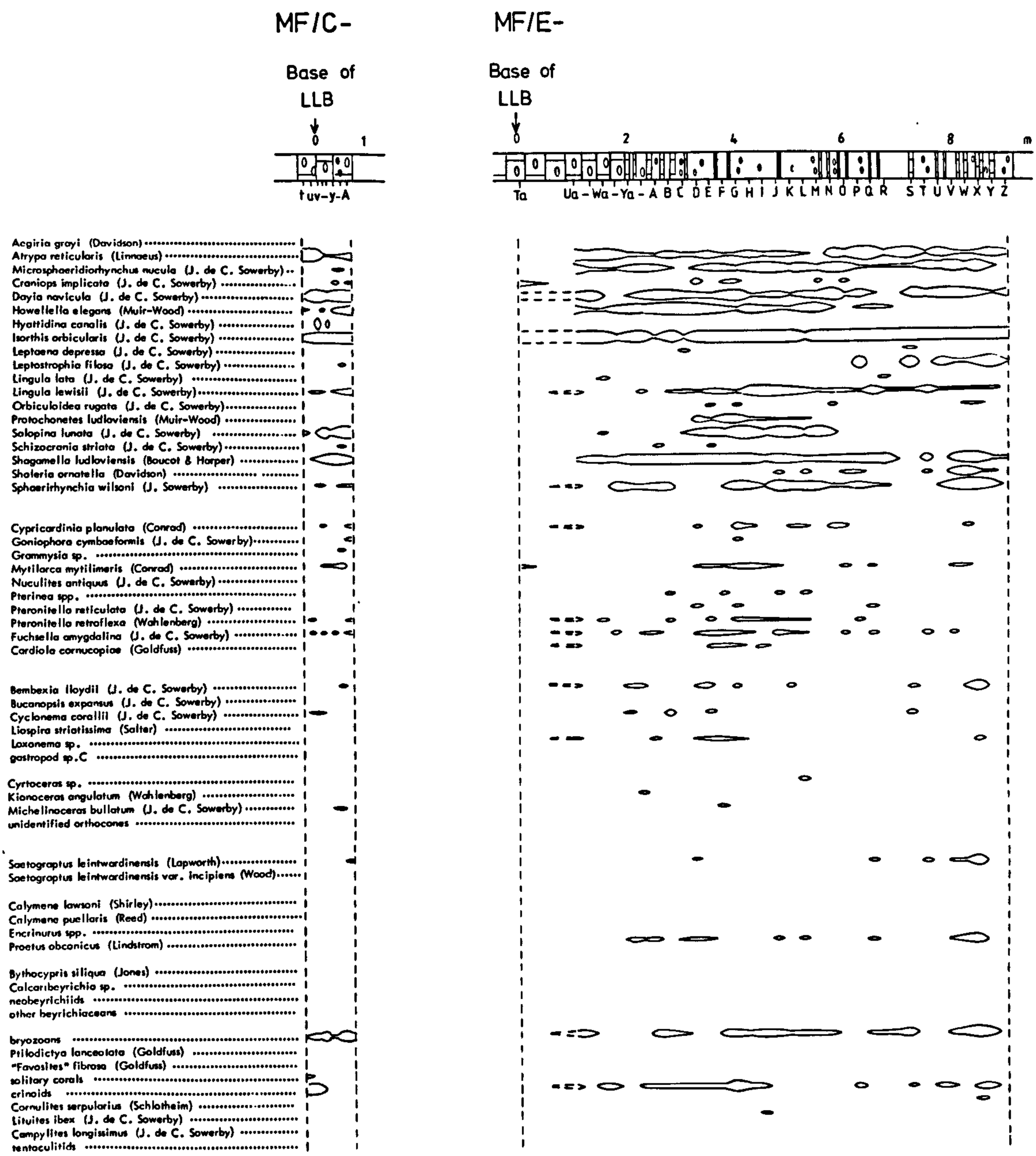

Fig. 2.8 : Sections MF/C- and MF/E- - including the base of the LLB.

in addition, in the bottom 1.5 m of the section, several K. squamosus specimens were found perpendicular to the bedding at various levels. These are wider traces (up to 6 mm), and often associated with them are patches of fine shell debris. The irregular basal strata in the section commonly contain small patches and "stringers" of fragmented shells: these may indicate more extensive bioturbation of the strata.

7) MF/C; MF/D

(SO. 4561 7354: Loc.23 Lawson '73; SO. 4618 7537: loc.19 Lawson '73)

Fig 2.8, 2.9

The base of the LLB is exposed in these two localities, which lie approx 2.5 km west of Sunnyhill Quarry.

The top of the Aymestry Limestone facies is here represented by massive, irregular nodular limestones and calcareous siltstones, more similar to the facies at the type section than the siltier lithology of MF/A. The transition to thinner-bedded calcareous siltstone flags corresponds more closely to the faunal boundary, occurring about a metre above the disappearance of the last UBB fossils.

Section MF/C includes the lithological transition from the UBB-LLB boundary upwards into flaggy calcareous siltstones, through 1 m of beds. The high UBB are rich in corals, both solitary and compound forms, together with large valves of S. euglypha, A. funiculata, and K. knightii, and P. globosa, scattered in the calcareous rubbly beds. These characteristic forms decline rapidly in frequency over one to two metres, while silty beds become gradually more common among the nodular limestones. The bottom collection (t) was taken from the highest bed in which a compound coral (Favosites - enclosed within a nodule) was found: a very nodular calcareous siltstone. The fauna was dominated by large single valves of A. reticularis, and crinoid columnals were abundant. One large solitary coral was noted from 't'. The overlying flags (u) have shaly partings among the nodules. One of these contained a large S. euglypha (BV). This was the last record of any diagnostic UBB forms, and hence the base of the LLB was taken at 'v' in this section.

The beds above are mostly nodular with calcareous and siltier bands, in which the fauna becomes rapidly more numerous. D. navicula,

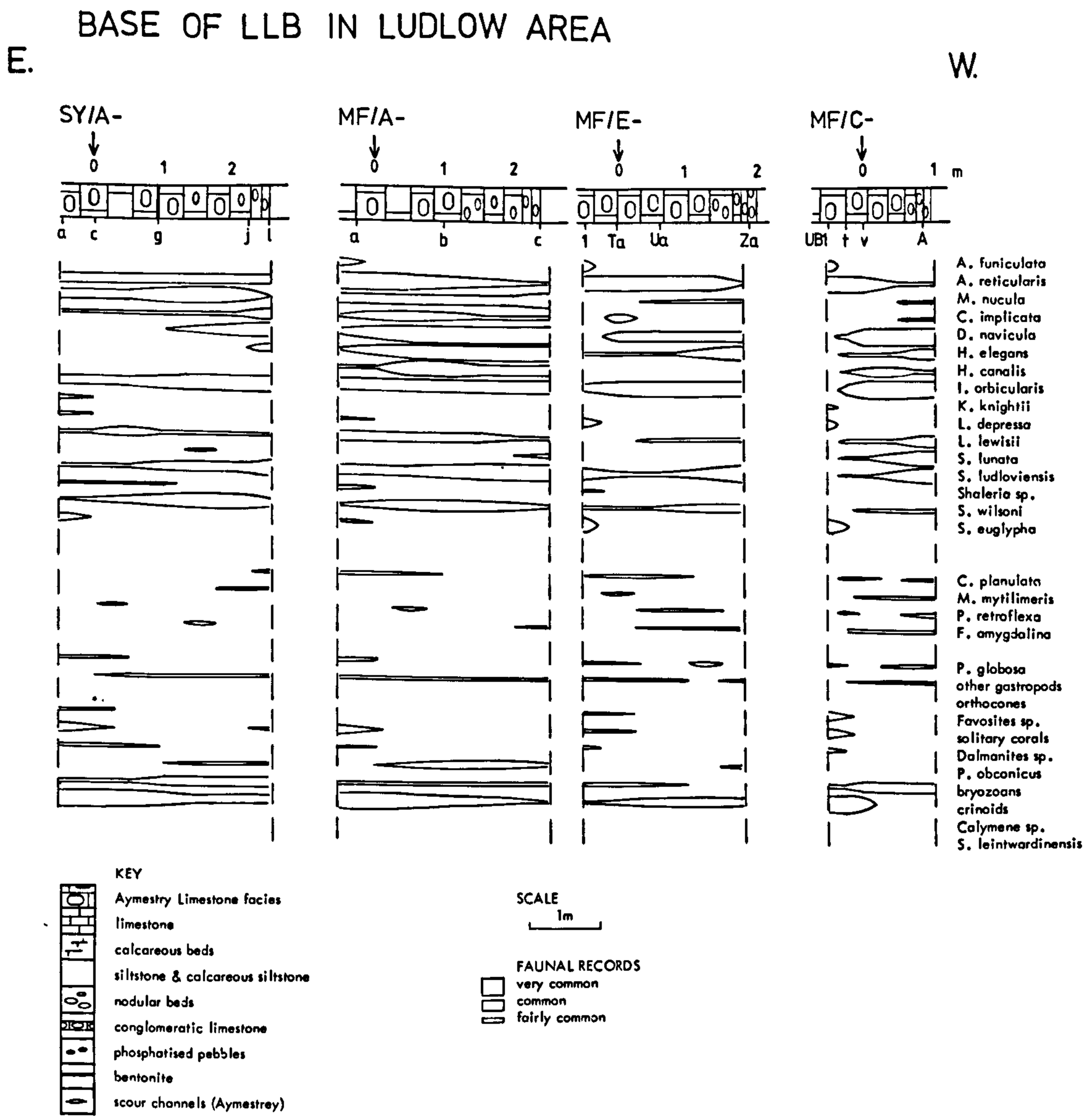

Fig. 2.9 : The base of the LLB in the Ludlow area E-W.
(Faunal list as in Fig. 4.2 for comparison).

I. orbicularis, H. canalis, S. lunata and S. ludloviensis are all very common, but A. reticularis declines in importance. The relative proportions of the different types fluctuate from band to band, and their distributions include both random dispersal within beds and concentrations on bedding planes. The upper beds have persistent, thin shelly limestones packed with S. ludloviensis, and some H. elegans; similar bands, in which H. elegans is more prevalent, were noted in the higher strata above the top band 'A'.

Large specimens of L. lewisii were found perpendicular to the bedding, and occasionally inside nodules, fairly commonly throughout the section. Burrows were seen in some beds, running obliquely through the sediment. Other beds have diffuse burrow-mottling, indicating extensive biogenic reworking.

COMPUTER CLUSTER ANALYSES

The cluster analysis program, by Bonham-Carter ('67), could be applied to both qualitative and quantitative data. Band-by-band records from each of the Ludlow sections were used. Analyses for each sequence, and ones for all the data from Ludlow, were made. The qualitative method records presence or absence of each variable (ie. fossil). For the quantitative clustering, four levels of abundance were taken and absence was also noted. Jaccard's coefficient of association, which ignores negative matches, was used.

The dendrograms produced for the qualitative data had clusters which approximated closely to the stratigraphical succession; vertical changes in the fauna were reflected. The quantitative results illustrated the rapid changes in faunal dominance by successive assemblages belonging to different clusters. However, for further definition, fully quantitative results would be required rather than the semi-quantitative records (up to 18 individuals per species in a collection) obtained in this study. Examples of both the qualitative and quantitative analyses are discussed in the following section.

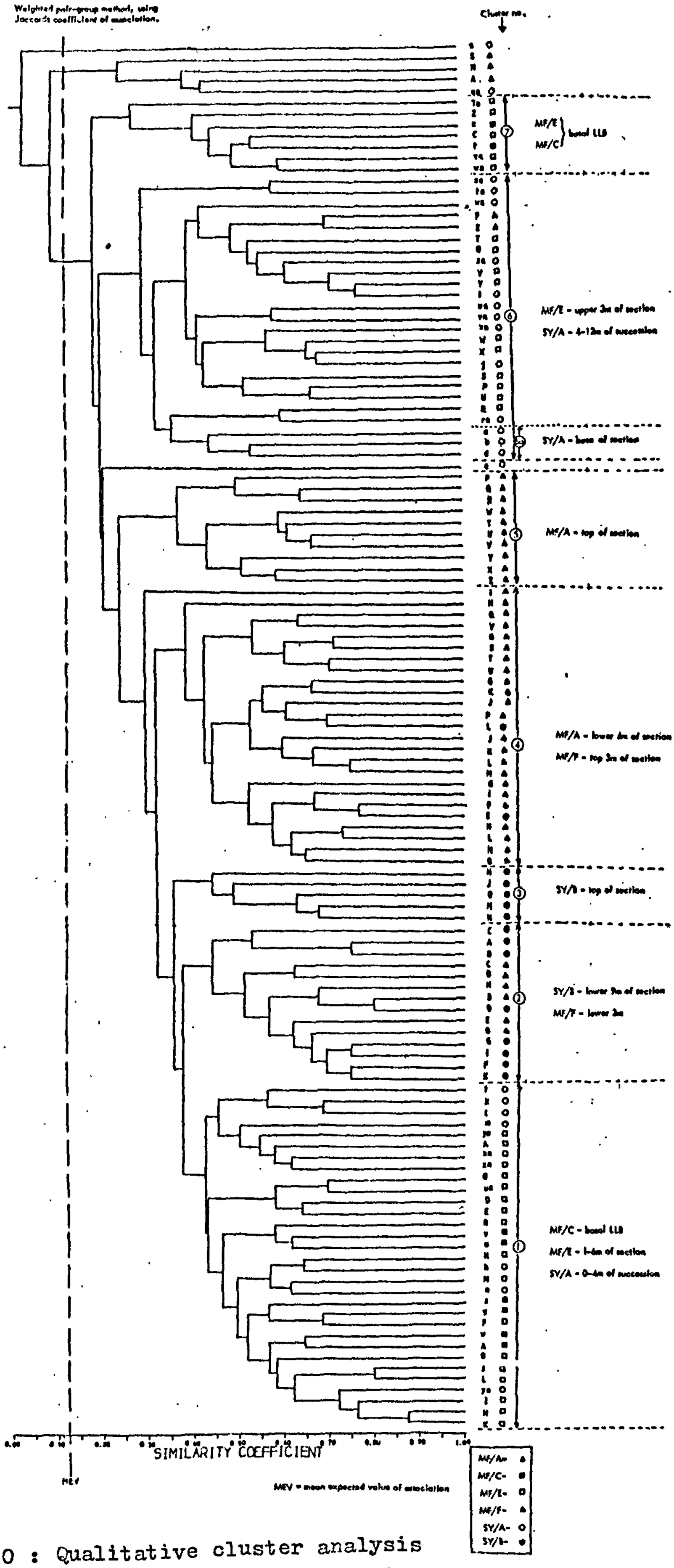

Fig. 2.10 : Qualitative cluster analysis for all the Ludlow area data.

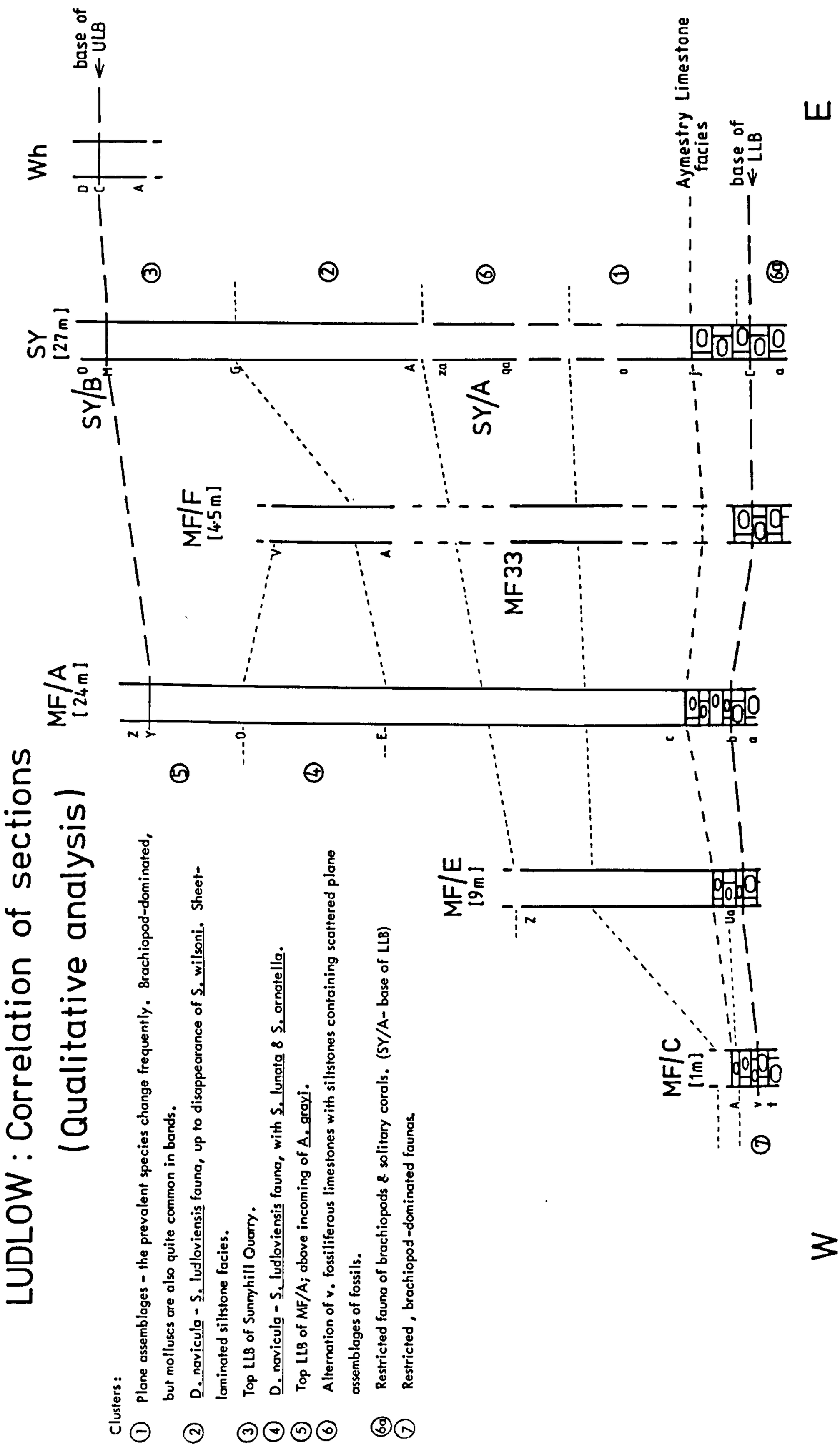

Fig. 2.11 : Correlation of the Ludlow sections using qualitative cluster analysis.

LUDLOW AREA - QUALITATIVE ANALYSIS OF FAUNAL DATA

The faunal data from six sections in the Ludlow anticline (SY/A-, SY/B-, MF/A-, MF/F-, MF/E-, MF/C-) were analysed qualitatively (i.e. present/absent). Seven major clusters were recognised, which form a convenient framework for sub-division of the vertical succession, as well as indicating correlations of the various sequences (see Fig 2.10, 2.11).

The characteristics of the clusters, working from the base of the LLB upwards, are as follows:-

a) 1 and 7:

Group 7 includes basal beds from the two Bringewood Chase sequences, MF/C- and MF/E-. The bands have brachiopod-dominated faunas, with relatively few species. In both sections, the strata are the irregular nodular siltstones and limestones which are transitional between the Aymestry Limestone facies and the more thinly flaggy, overlying, calcareous siltstones of the LLB.

Cluster 1 links the basal beds of the Bringewood Chase sections with those at Sunnyhill Quarry, SY/A-. The assemblages are either brachiopod - dominated, but with a greater number of species present than in 7, or more diverse, with bivalves, gastropods and proetid trilobites forming common additions to the faunas. The smaller clusters indicate these categories of the main division.

The two groupings contain faunas from the bottom 5 m of MF/E- (approx lowest 6 m of LLB), the lowest 1 m of LLB in MF/C-, and the 4 m of succession above the defined base of the LLB at Sunnyhill Quarry. The facies transition to dominantly calcareous siltstones within the basal 2 m of LLB does not correspond to a marked qualitative change in the fauna.

b) 6

Cluster 6 again relates the Sunnyhill Quarry (SY/A-) and MF/E- sections, in the lower part of the LLB. It is convenient to separate a minor cluster 6a from the rest; this comprises the poorly fossiliferous beds at the UBB-LLB boundary of the stratotype (SY/A - a, b, and d). Their fauna is comparable with the members of 7 (ie. relatively few species, and mainly brachiopods), but with the addition of common solitary corals, probably reflecting the more

calcareous nature of the top of the Aymestry Limestone in the eastern part of the area.

The remainder of 6 includes the upper part of MF/E - approx. 6-9 m above the LLB base - together mainly with beds 9.5-12 m above the base of SY/A-. (Gap in sequence of ≏ 5 m between SY/A- a-o and qa-za). The strata in the latter section are very calcareous, nodular siltstones and limestones. The Bringewood Chase section is less calcareous, with generally more abundant faunas, especially in some richly fossiliferous limestone bands.

The group 6 faunas represent a qualitative change from those of 1, marked particularly by the appearance of the strophomenids L. filosa and S. ornatella, and by the loss of H. elegans. Accompanying the faunal changes are differences in the character of the sediments. (This will be discussed further, along with the faunas themselves).

c) 2

No. 2 and the following group, 4, can be used to position the section MF/F- within the succession, by comparison of its faunas with those of sections whose relation to the boundaries of the LLB is known. MF/F is taken from locality 33 of Lawson ('73), and consists of 4.5 m of beds in the middle part of the LLB. They are stratigraphically above the beds used for palaeoecological studies (see Chapter 6), which in turn overlie the UBB-LLB boundary rocks at the western side of the quarry.

Cluster 2 is composed of the lower part of section SY/B- (≏ 9 m, 14-23 m above base LLB), and the lower beds of MF/F-. The faunas commonly contain F. amygdalina with brachiopod-dominated, though fairly diverse, assemblages. The sediments have concentrated shelly bands and coquinas interbedded with fine, parallel-laminated, calcareous siltstones, in which there are thin plane-assemblages of shells at intervals.

d) 4

The upper portion of MF/F- corresponds to the lower beds (6 m, 14-20 m above base of LLB) of section MF/A-, on the Haye Park Farm Rd. The faunas are very similar to 2 in composition and diversity, but are above the top appearance of S. wilsoni, where graptolites, S. ornatella and L. depressa become increasingly common. The sediments

are similar to those of 2.

e) 3 and 5

These two groupings cover the top of the LLB and LLB-ULB boundary in sections MF/A- (19-24 m above LLB base) and SY/B- (23-30 m above base of LLB). The two sections remain discrete in the clustering, in spite of their similar stratigraphic position. There is a marked taxonomic diversification of the fauna at this level, with beyrichiaceans and trilobites becoming very common. The levels at which various ULB faunal elements appear relative to each other is noticeably different in the two sections.

The sediments are calcareous siltstones, laminated in parts, in which the fauna commonly occurs in planes or bands. Other beds show a more homogeneous distribution of fossils throughout their thickness.

Faunal clusters

The qualitative faunal clusters correlate closely with the stratigraphical successions, illustrating the vertical changes that take place through the Leintwardinian. The various faunas, and their distribution within the sediments will now be considered in more detail.

1) Basal LLB: MF/C-, MF/E-, SY/A-. Fig 2.9

Qualitative cluster groups a and b.

The base of the LLB is defined by the disappearance of the characteristic UBB faunal elements, to leave a sparse, brachiopod-dominated assemblage with a restricted number of species (clusters 7 and 6a). This residual fauna consistently includes A. reticularis (large valves) and I. orbicularis in all the sections. The calcareous strata at Sunnyhill Quarry have the rhynchonellids M. nucula and S. wilsoni, together with solitary corals and crinoids, as the more frequent additional components. In the siltier, more westerly, facies, D. navicula, H. canalis, S. lunata and S. ludloviensis are important faunal constituents, but there are less solitary corals. The similarity of some of the basal faunas in the Bringewood Chase sections (MF/E-, MF/C-) is indicated by their inclusion into cluster 7. The faunas and facies of the basal beds of MF/A- and MF33 are more comparable with these sections than with those of Sunnyhill Quarry (SY/A-). However, a siltstone band of very large branching bryozoans, from approximately the same level as a similar horizon (in SY/A-d) at the stratotype section, was found in the basal beds at MF33.

The majority of the beds from the lower parts of the sections have been combined into cluster 1. For MF/E, it includes the rest of the beds up to N, which the qualitative analysis for this section alone (Fig 2.12) shows may be conveniently subdivided into two groups. The first of these encompasses bands D-L, and Ua, and represents richer and more diverse faunas than the second group, from which the beds in cluster 7 - Va, Wa, C - have come. The other members of this latter group are beds Xa - B, whose faunas are fairly diverse but have a smaller number of common brachiopod species than the higher beds, and the top beds M and N (and R), whose faunas had few non-brachiopod components. These groupings relate closely to the vertical changes in faunal distribution within the sediments.

The faunas of the beds up to C, in the bottom 2 m of the section (≏3 m of LLB), become increasingly regularly concentrated onto planes rather than dispersed in the sediment, a change which corresponds to the more even, thinner bedding of the siltier sediments. The plane-assemblages become more pronounced in the overlying beds, and typically each is composed of only a few species. It is at this level that the first major qualitative change in the brachiopod fauna occurs, with the addition of S. lunata and P. ludloviensis to the common species. Above M, the sequence again becomes more calcareous and nodular, a transition accompanied by further qualitative faunal change.

The dominant species in the assemblages from D-L alternate frequently, as can be seen from the detailed section in Fig 2.13 (p 46), and also from the quantitative analysis dendrogram (Fig 2.14 p 45) where these faunas are spread in several clusters according to the numerical abundances of the various components. However, in spite of the proportional variation in the composition of the faunas, they remain, collectively, qualitatively similar.

The Sunnyhill section beds which are in cluster 1 - f, h, k, l, m, n - again cover the change from randomly distributed fossils in the basal strata to bedding plane assemblages of fluctuating relative species abundances in the higher part. Fig 2.15 (p 47) illustrates some of the assemblages found in the upper 1.4 m of SY/A, from the beds which have faunas concentrated mainly onto planes and in thin bands. (The transition from the Aymestry Limestone facies to calcareous siltstone flags takes place above 'j').

Fig. 2.12

MF/E : QUALITATIVE ANALYSIS

Weighted pair-group method, using Jaccards coefficient of association.

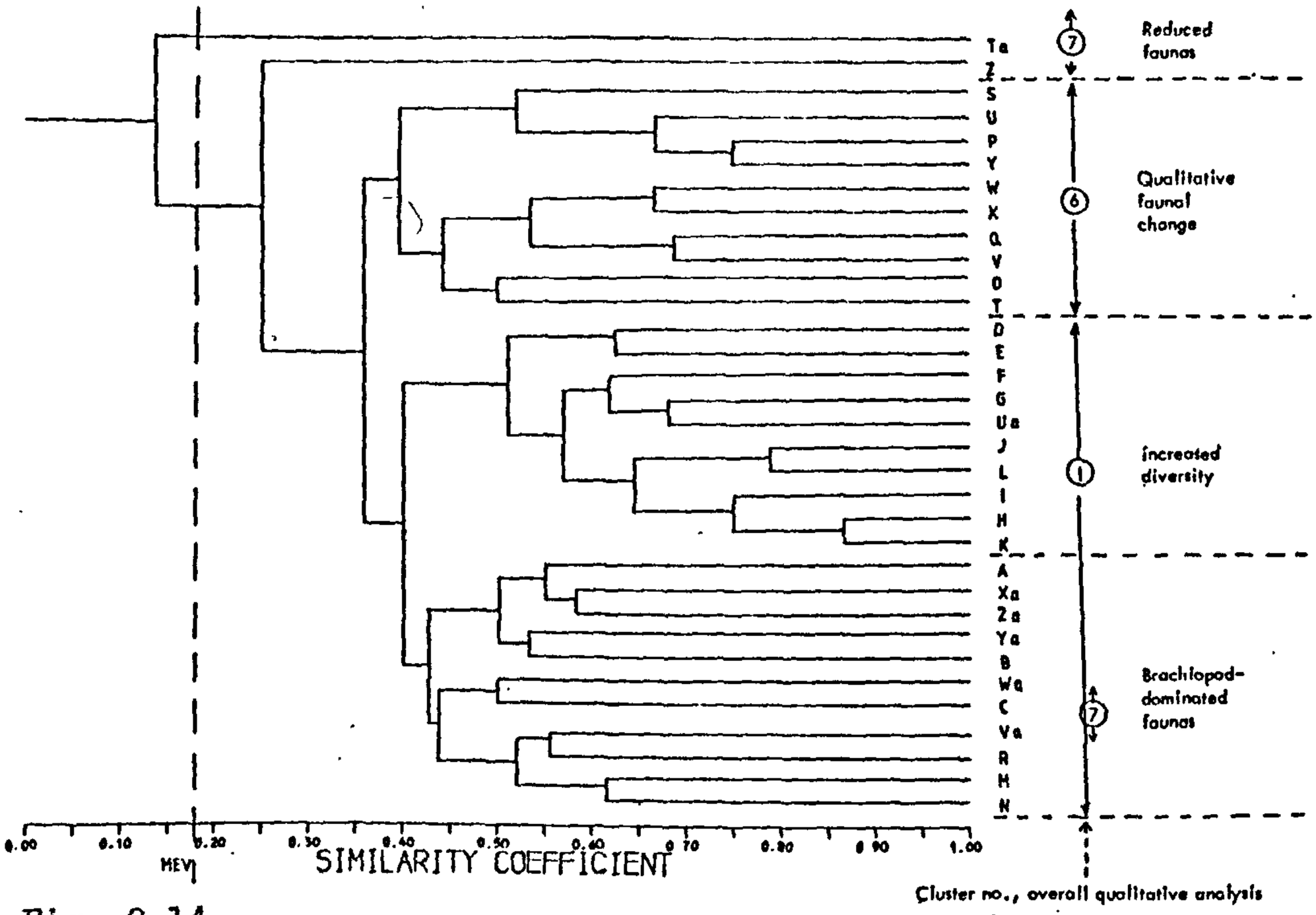

Fig. 2.14

MF/E : QUANTITATIVE ANALYSIS

Weighted pair-group method, using Jaccards coefficient of association.

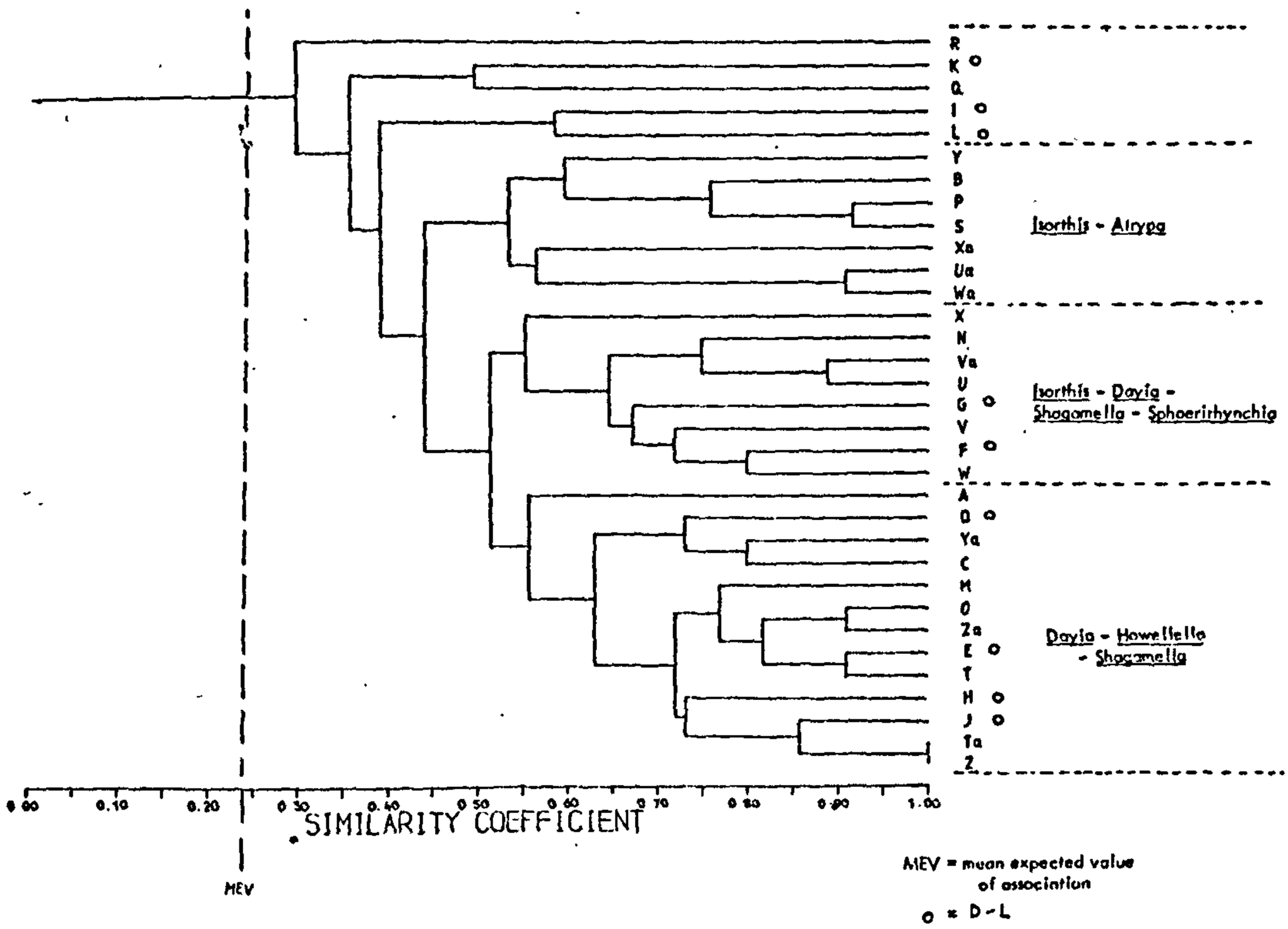

Fig. 2.12 : MF/E- Qualitative analysis, showing clusters from Fig. 2.10.
Fig. 2.14 : MF/E- Quantitative analysis. (Beds D-L marked o).

Fig. 2.13

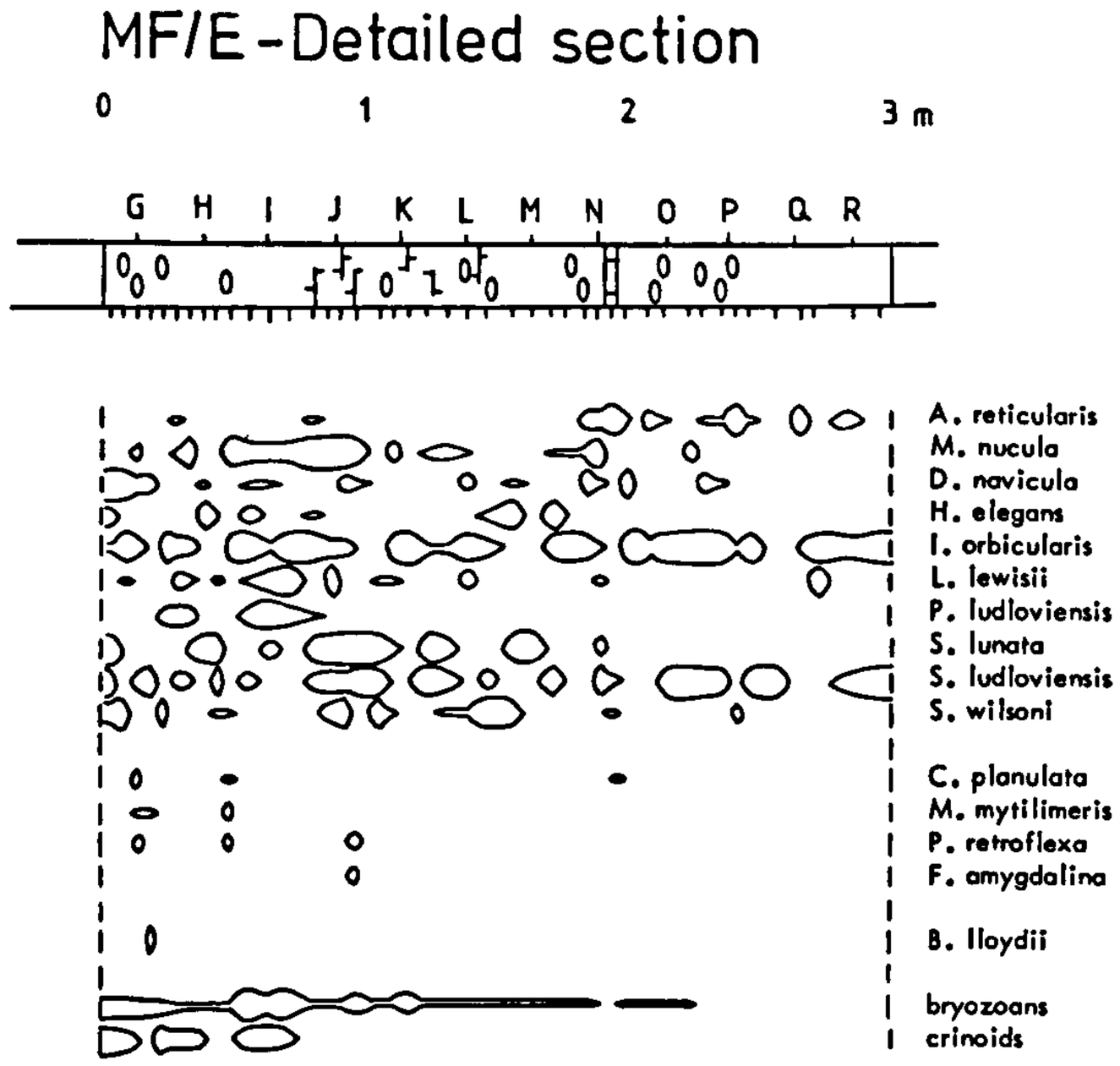

Fig. 2.17

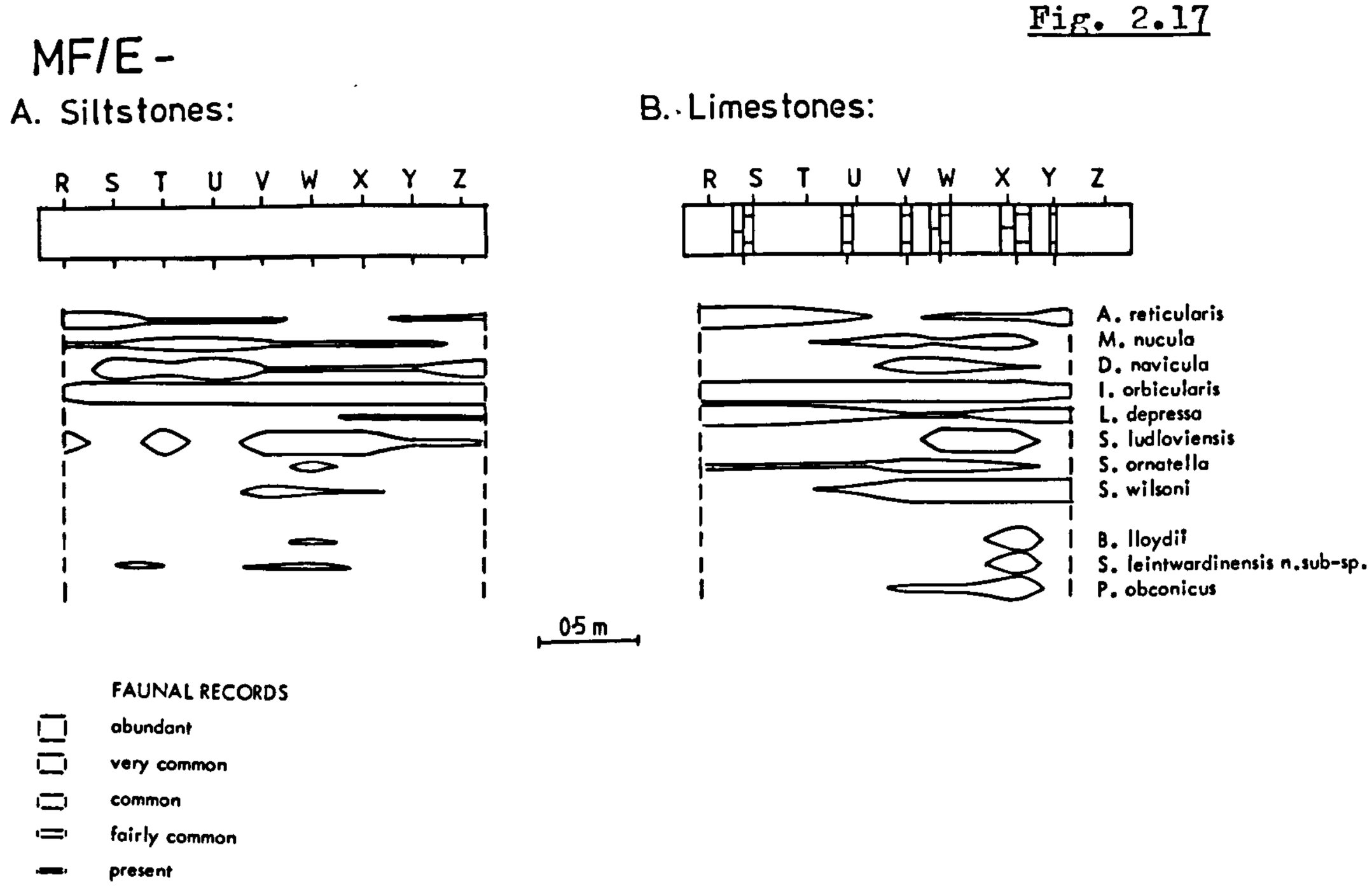

Fig. 2.13 : MF/E- Detailed section G-R.

Fig. 2.17 : MF/E- Comparison of A)Siltstone and B)Limestone faunas R-Z.

Fig. 2.15

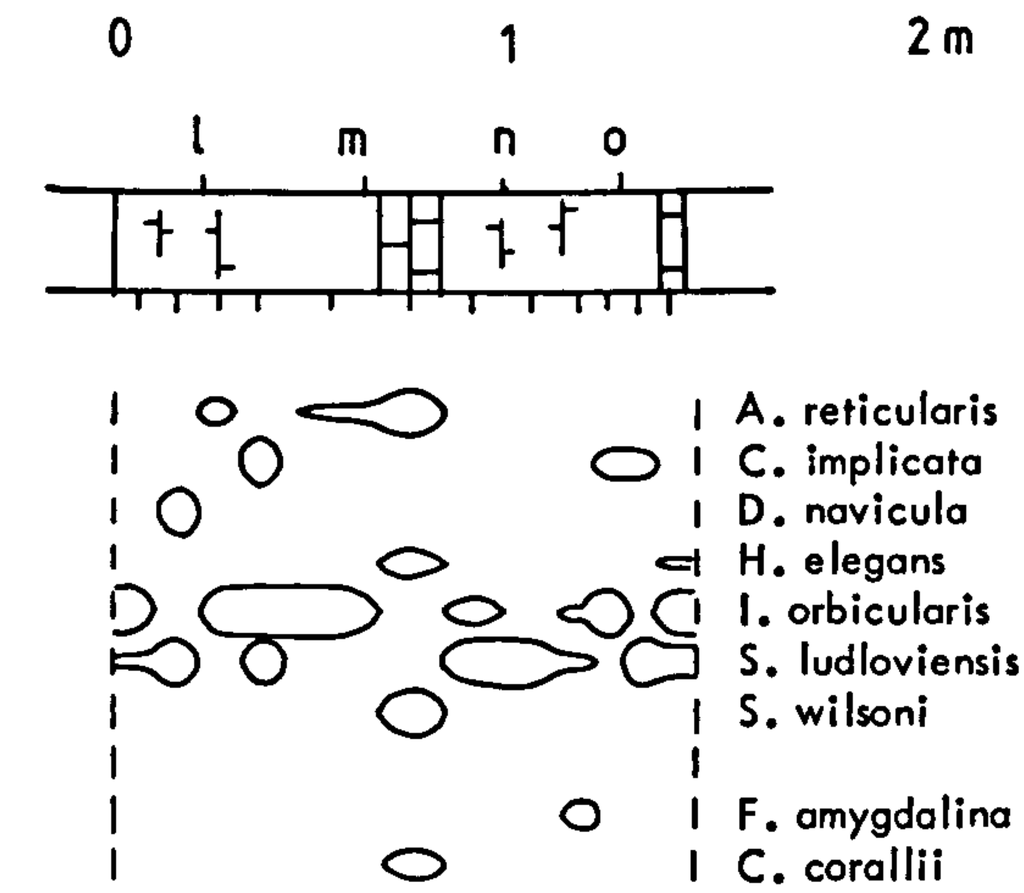

Fig. 2.16

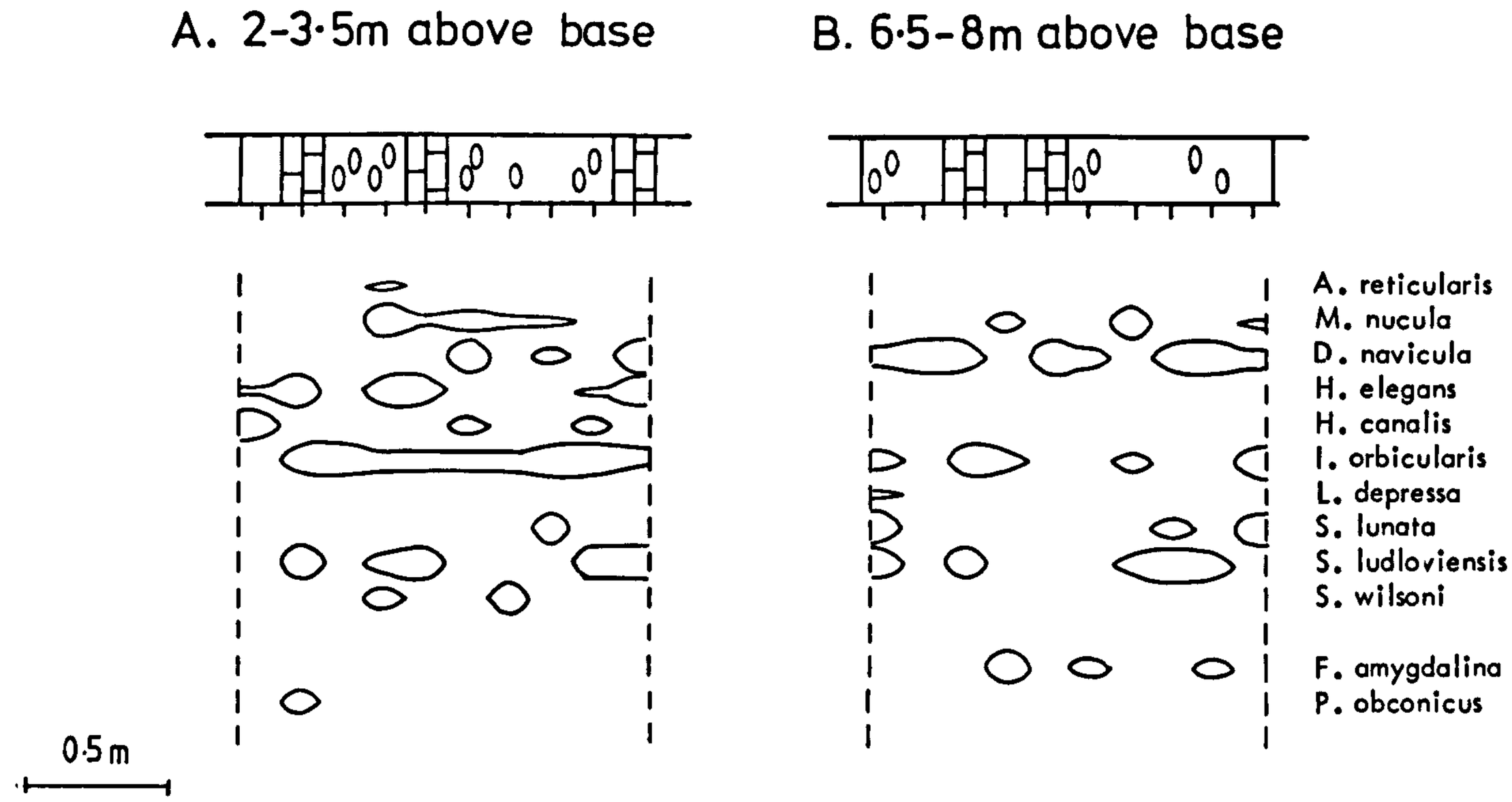

Fig. 2.15 : SY/A- Detailed section.

Fig. 2.16 : MF/A- Detailed section.

The basal LLB fauna in the Haye Park section MF/A- is initially "patchily" distributed. Along with a rapid numerical increase in its abundance, it comes more regularly disposed in concentrated bands within the bottom 2 m of section. Ten assemblages found over 1.5 m of the sequence above this level have been plotted in Fig 2.16-A (p47) illustrating a similar pattern to the other sections of alternating species dominance from one assemblage to another, but very little overall qualitative change.

The faunal charts all show assemblages dominated largely by brachiopods, with only a few bands in which other fossils are prevalent (such as, F. amygdalina in SY/A-ol). However, some of the MF/E- beds have a marked molluscan component within their faunas (eg. G_3, H_2 - Fig 2.14). Higher in the succession, bivalve-dominated bands occur fairly commonly within sequences of plane-assemblages. Fig 2.16 - B (p 47), for the MF/A- section, shows ten assemblages from 1.5 m of flags with fossils concentrated onto planes. At this level, assemblages are commonly dominated by one or two species, and few fossils lie in the intervening beds. F. amygdalina is found commonly in three of the ten faunas.

The beds from MF33 used for palaeoecological surveys (Ch.6) were taken from a broadly similar level in the succession, and again, bivalve-dominated bands are not infrequent (eg. Fig 6.21 no. 9 p365) was taken from one such assemblage).

Cluster 6 links faunas from MF/E- and SY/A-, from levels 6-9 m and 9.5-12 m respectively above the UBB-LLB boundary. For MF/E-, this includes beds O-Z, which the individual qualitative analysis grouped together into one major cluster (Fig 2.12 p45). The faunal change corresponds to the appearance of more laminated, and nodular, calcareous siltstones with interbedded, richly fossiliferous, shelly limestones. These limestones, often debris-rich, have quite different faunas from the siltstones, with a high proportion of the strophomenids L. filosa and S. ornatella, with I. orbicularis and S. wilsoni; the siltstone faunas had abundant D. navicula, S. ludloviensis and I. orbicularis. These compositional differences can be seen in Fig 2.17 (p46) for the beds from R-Z. Graptolites in beds T-X were identified as Saetograptus n. sub-sp. (RBR).

The Sunnyhill Quarry faunas from qa-za come from a sequence of nodular and laminated, calcareous siltstones, with conglomeratic (qa) and shelly limestone bands. The nodular siltstones have a generally sparse fauna, of I. orbicularis, D. navicula, M. nucula and S. ludloviensis. In the shelly limestones qa and sa, rhynchonellids are more common, while the very calcareous laminated beds, ta - va, have planes of S. ludloviensis, and the strophomenids L. filosa and S. ornatella. Beds from sa upwards contained graptolites of S. léintwardinensis s.s. and S. léintwardinensis ? sub-sp. (RBR).

2) Middle LLB: MF/F-, SY/B-, MF/A-

Cluster groups c) and d)

The bottom half of SY/B-, from higher in the succession than SY/A, and the lower beds of MF/F, are grouped into cluster 2. In both the sections, the faunas are from beds which are dominantly well-laminated calcareous siltstones with interbedded shelly limestone lenses and bands. These sediments compose the sheet-laminated siltstone facies discussed in Ch. 6 p375ff. The importance of currents in the deposition of these beds is evident from their structure. There are repeated, erosively-based, fining-up units, which have basal shell accumulations of rapidly variable thickness and generally impersistent lateral extent, that pass up into finely laminated siltstone beds (see Fig. 6.25). Minor sedimentary discordances are common in the laminated beds. The thickness of individual laminated units is usually less than 15 cm, and often only 2 or 3 cm. The laminae are closely banded, silty and muddy layers, which sometimes become thinner at the top of units (Fig. 6.25). However no appreciable change in grain size could be discerned from the lower to upper part of the units. Among the laminated units were flags of unlaminated, or poorly-bedded siltstone.

The faunas are dominated, in both sections, by D. navicula and S. ludloviensis, and I. orbicularis assemblages, both monospecific and more varied in composition. At a slightly higher level, S. lunata and S. ornatella become important constituents of the fauna. The shell limestones are sometimes highly fragmental, and frequently consist of randomly-orientated, dense accumulations of shells. Other beds, though, have well-sorted shell layers in some more extensive

bands. (~~Fig~~). These latter deposits are clearly reworked, as are the thin, plane-assemblages of uniformly convex-up valves which occur at intervals within the laminated beds. In contrast, the disordered and broken shell accumulations probably indicate deposition in more agitated conditions. A number of the Dayia assemblages studied (see p 337ff.) were from the lower part of MF/F-, from monospecific faunas of laminated and unlaminated beds.

Cluster 4, which relates the middle (G-M) and upper (P-V) parts of MF/F- with the lower part (E-O) of MF/A-, includes very similar faunas to those of 2, with comparable fossil distributions and in stratigraphically-equivalent strata. The qualitative analysis for MF/A alone (Fig 2.18 - p51) shows that its faunas divide into two major groups, which coincide with the divisions into 4 and 5 of the overall Ludlow analysis (Fig 2.10 p 39). The first (4) includes those beds in which assemblages of D. navicula and S. ludloviensis are still abundant. The quantitative analysis for MF/A- (Fig 2.19 p 51) shows the consistent abundance of elements in many of the collections, in contrast to the fluctuating species dominance of the assemblages in the lower part of the LLB. Only G and I, which are graptolite bands, and O, where proetids are abundant, have different faunal compositions.

In the upper beds of MF/F-, S-V, and throughout the sequence of MF/A - E to O, graptolites of S. leintwardinensis s.s. (RBR) were found. In the latter section, the proportion of laminated beds decreases markedly above M, a change accompanied by the decline of D. navicula, S. ludloviensis and I. orbicularis, and the first appearance of several fossils.

3) The higher LLB and LLB-ULB boundary: SY/B-, MF/A-
Cluster group e).

The top 5.5 m of SY/B, above J, has a greater proportion of unlaminated calcareous siltstones than the lower beds, although well-laminated units are still common. Erosively-based limestone lenses are less evident, but thin shell horizons of limited lateral extent remain apparent throughout the succession. Beds with fossils evenly dispersed in the sediment become more numerous. Accompanying the lithological transition is the decrease in frequency of D. navicula

Fig. 2.18

MF/A : QUALITATIVE ANALYSIS

Weighted pair-group method, using Jaccards coefficient of association.

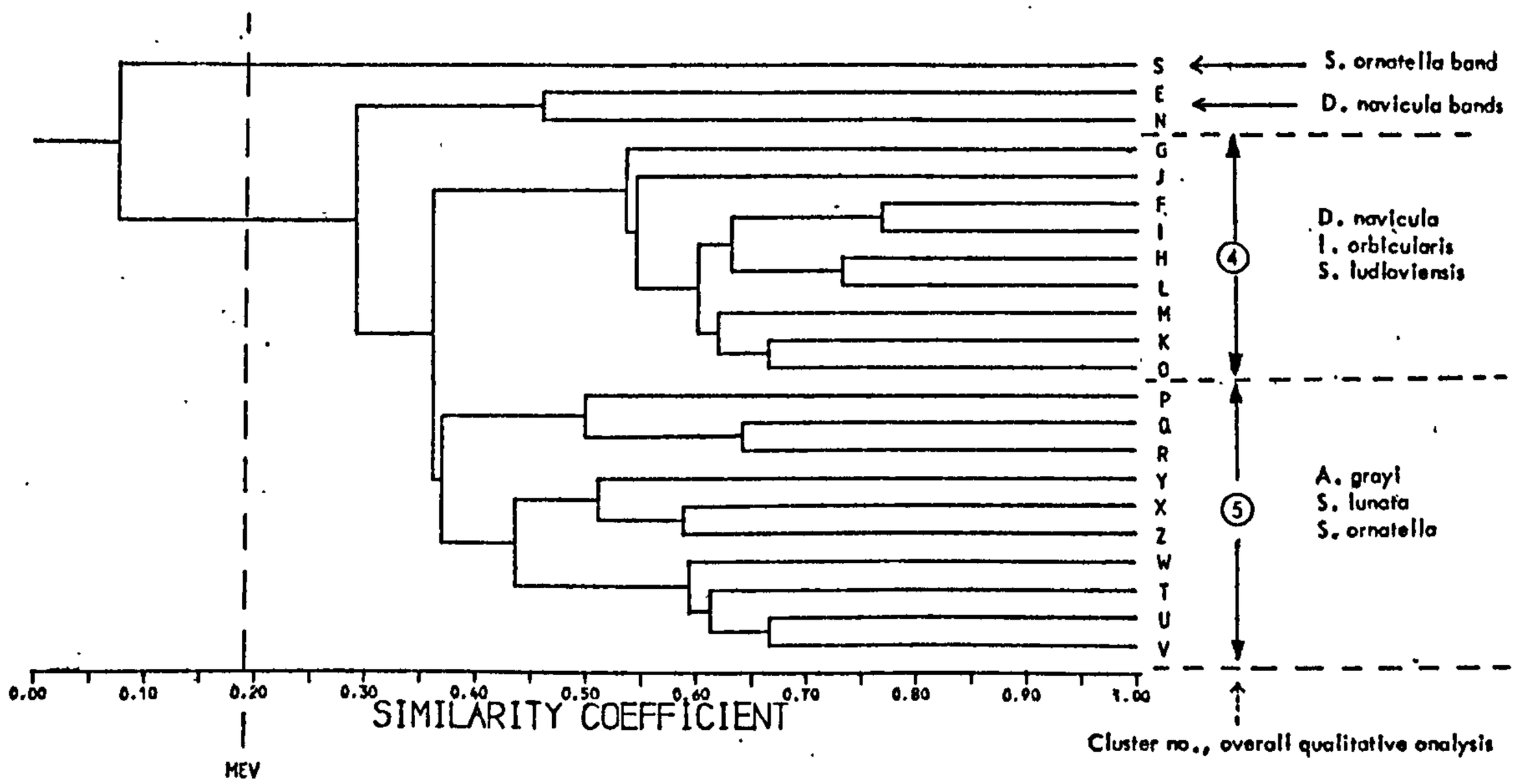

Fig. 2.19

MF/A : QUANTITATIVE ANALYSIS

Weighted pair- group method, using Jaccards coefficient of association

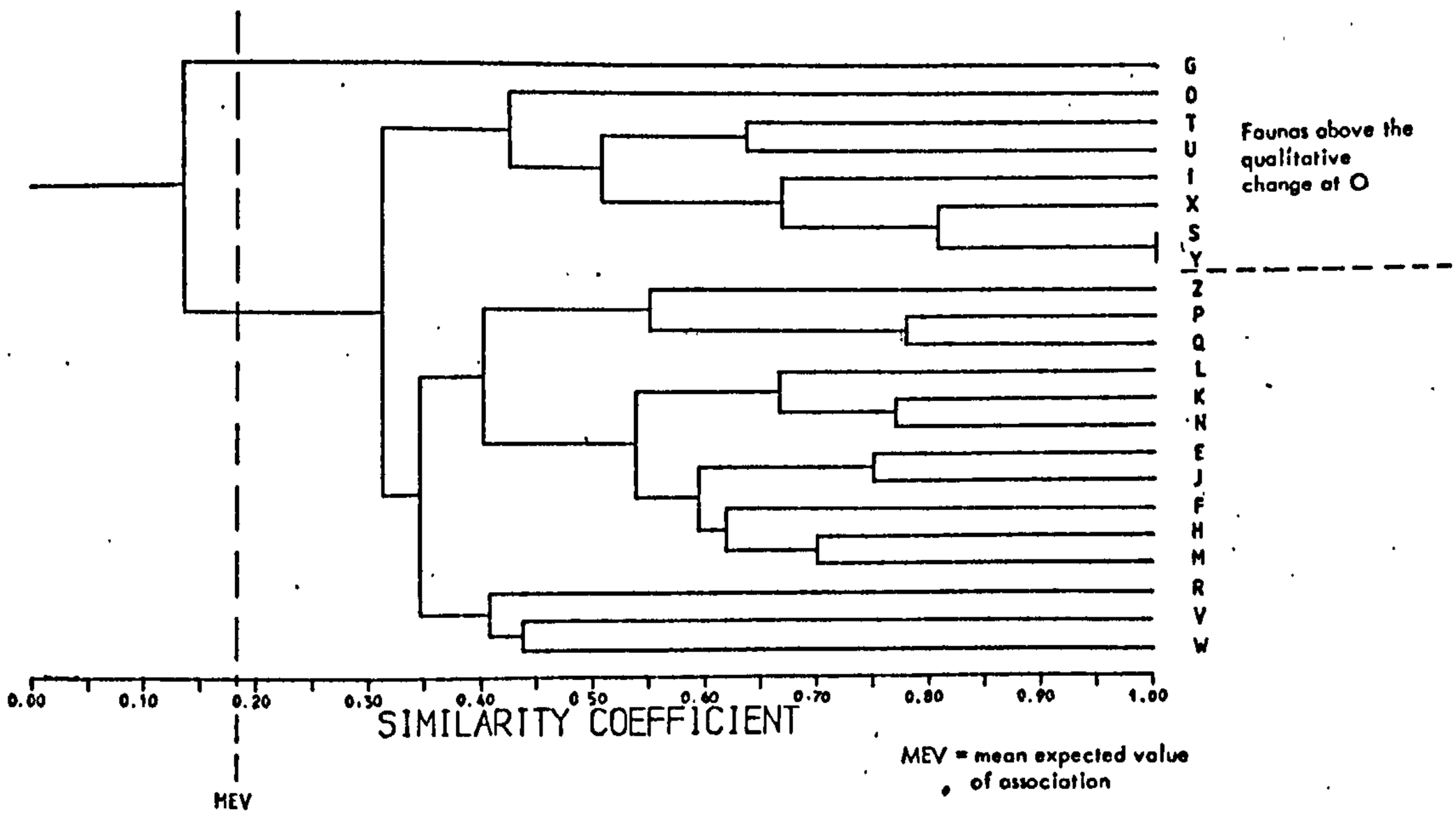

Fig. 2.18 : MF/A- Qualitative analysis, showing clusters from Fig. 2.10.
Fig. 2.19 : MF/A- Quantitative analysis.

and S. ludloviensis assemblages, and the disappearance of S. wilsoni. A corresponding increase in abundance of S. ornatella, often in monospecific assumulations, and of A. reticularis together with L. depressa is seen above this level. Cluster 3 includes these higher beds.

The characteristic distribution of fossils in this part of the sequence is in monospecific or dominated assemblages, where the prevalent species alternate. The faunas of beds in which the shells are randomly distributed are similar to those of the thin bands occurring at intervals. S. ornatella assemblages (see p 356 , assemblages 1-4) were found within the same bed to be both in plane accumulations and obliquely stacked in the sediment, suggesting that periodic local reworking of the top layers produced the bedding plane valve assemblages. Similar characteristics apply to S. lunata, S. ludloviensis, M. nucula and D. navicula faunas: all typically monospecific. Except for the rhynchonellid M. nucula which is generally articulated, the majority of these fossils are single, but little damaged, valves. Occasional D. navicula bands are, however, composed of a high proportion of articulated individuals. Large disarticulated L. depressa (with trails) and A. reticularis are commonly associated in more calcareous, nodular horizons.

The top beds (P-Z) at MF/A-, whose faunas form cluster 5, are comparatively depleted in common brachiopod species. Only S. ornatella, S. lunata, L. depressa and A. reticularis appear commonly in low-diversity assemblages equivalent to those of SY/B-. Other beds have an irregular "patchy" distribution of more diverse faunas, including graptolites - S. leintwardinensis s.s. (RBR), trilobites, beyrichiacean and non-palaeocope ostracodes, and A. gravi.

In contrast to MF/A-, where the incoming ULB faunal indices A. gravi, C. puellaris, E. stubblefieldi and neobeyrichiids first appear at different levels over approx 5 m of succession, at Sunnyhill they all enter within a metre, in collection M - see Fig 2.20 (p53) N. lauensis was identified from MF/A-, together with other neobeyrichiid species (DJS); from SY/B-, only a few small neobeyrichiid specimens were collected, which have not been identified further (LC). At the stratotype on the Whitcliffe (Wh-), which lies further east, again A. gravi and the trilobites come in at one level.

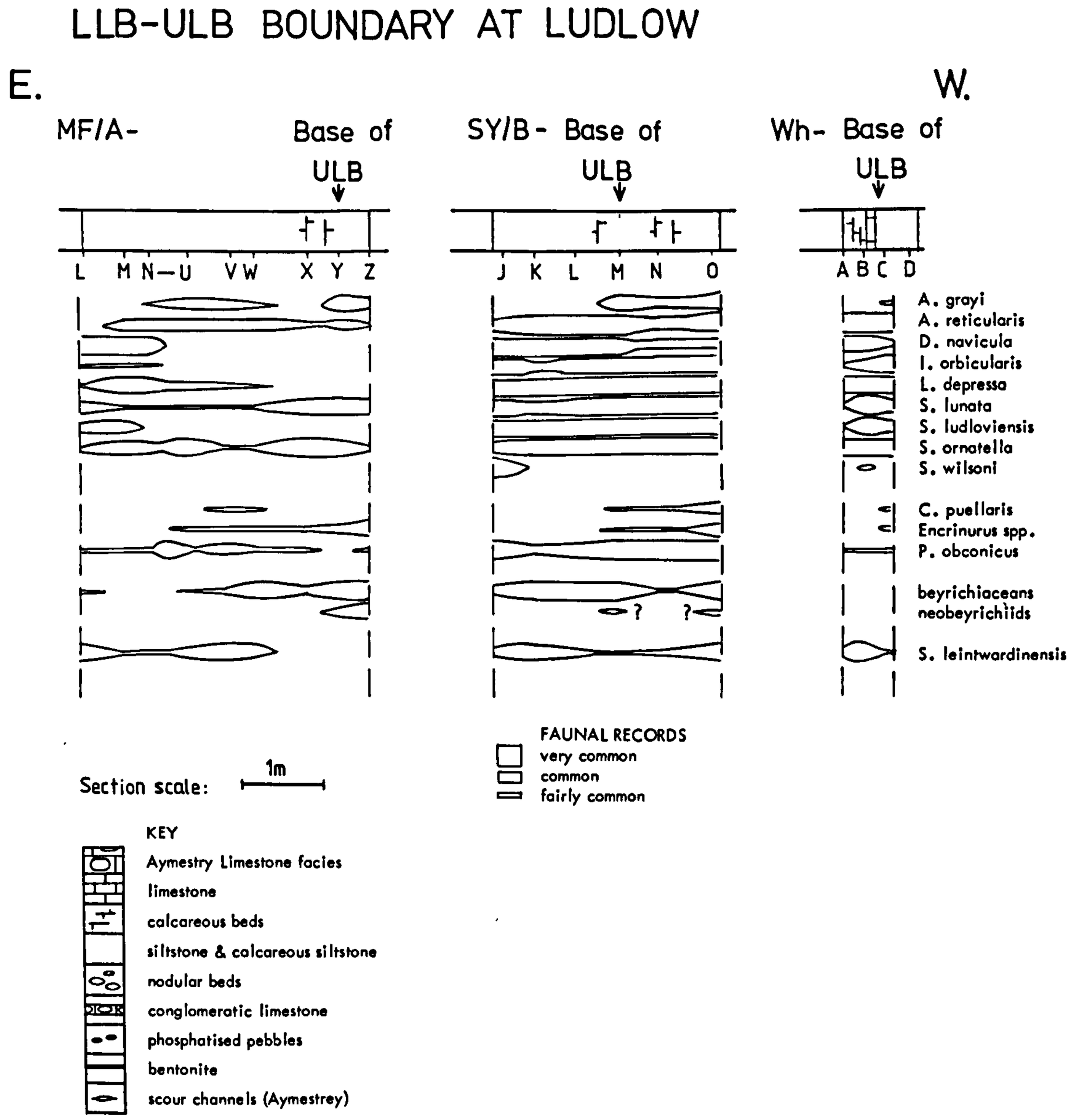

Fig. 2.20 : LLB-ULB boundary at Ludlow E-W.

Neobeyrichiids have not been recorded from this section. Holland, Lawson and Walmsley ('63 - p 118) noted the presence of phosphatised fragments in the bed (C) taken to mark the base of the ULB, which is a thin fossiliferous seam within a series of hard, very calcareous, siltstone

Fig 2.20 shows the differences in the top LLB faunas from E to W across the Ludlow area. The eastern strata are more calcareous, with more abundant and varied brachiopod components to their faunas. S. wilsoni persists to a higher level on the LLB in these sections.

CHAPTER THREE

THE STRATIGRAPHY OF THE SHELF INLIERS

The LLB succession was studied in sections at May Hill, Perton, Chances Pitch and Woodbury (see Fig 1.1 p 7). The vertical range charts (Figs 3.1,2,7,10,13) show the detailed faunal and facies changes of each sequence. Summaries of the major features of the succession in the shelf inliers are given at the end of the chapter.

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1) MAY HILL INLIER: Wood Green and Longhope sections

The Ludlow rocks of the May Hill Inlier were mapped and described by Lawson ('54, '55), who recognised six divisions based mainly on faunal changes. The maximum thickness of the Ludlow Series here is only 75 m compared with 430 m in the type area, and there are several unconformities within the succession. The LLB correlate with the Lower and Upper Blaisdon Beds (Holland, Lawson and Walmsley '63). The base of the lower division may be unconformable; limestone conglomerates rest with sharp contact upon Upper Flaxley Beds (Bringewoodian). The highest part of the latter at Blaisdon contain an UBB fauna with Favosites and solitary corals (Holland, Lawson and Walmsley '63 - p 149), although not in Aymestry Limestone facies. The Lower Longhope Beds, which correlate with the ULB, in some places have a basal phosphatised fragment layer. Another similar horizon is found at their upper junction with the overlying division. The presence of fragment-beds and phosphatised horizons at other levels in the succession suggests that there were numerous diastems in the deposition of these rocks.

A Lower Blaisdon Beds

A1 Wood Green:

Railway Cutting } SO.694.197
Roadside Quarry }

L. Blaisdon Beds: Thickness 3.1 m Fig 3.1

These two sections between them provided complete coverage of the L. Blaisdon Beds. The roadside quarry was more accessible than the railway cutting, which was fairly overgrown. Therefore, most of the measured sequence came from the former. However, the base of the

WOOD GREEN

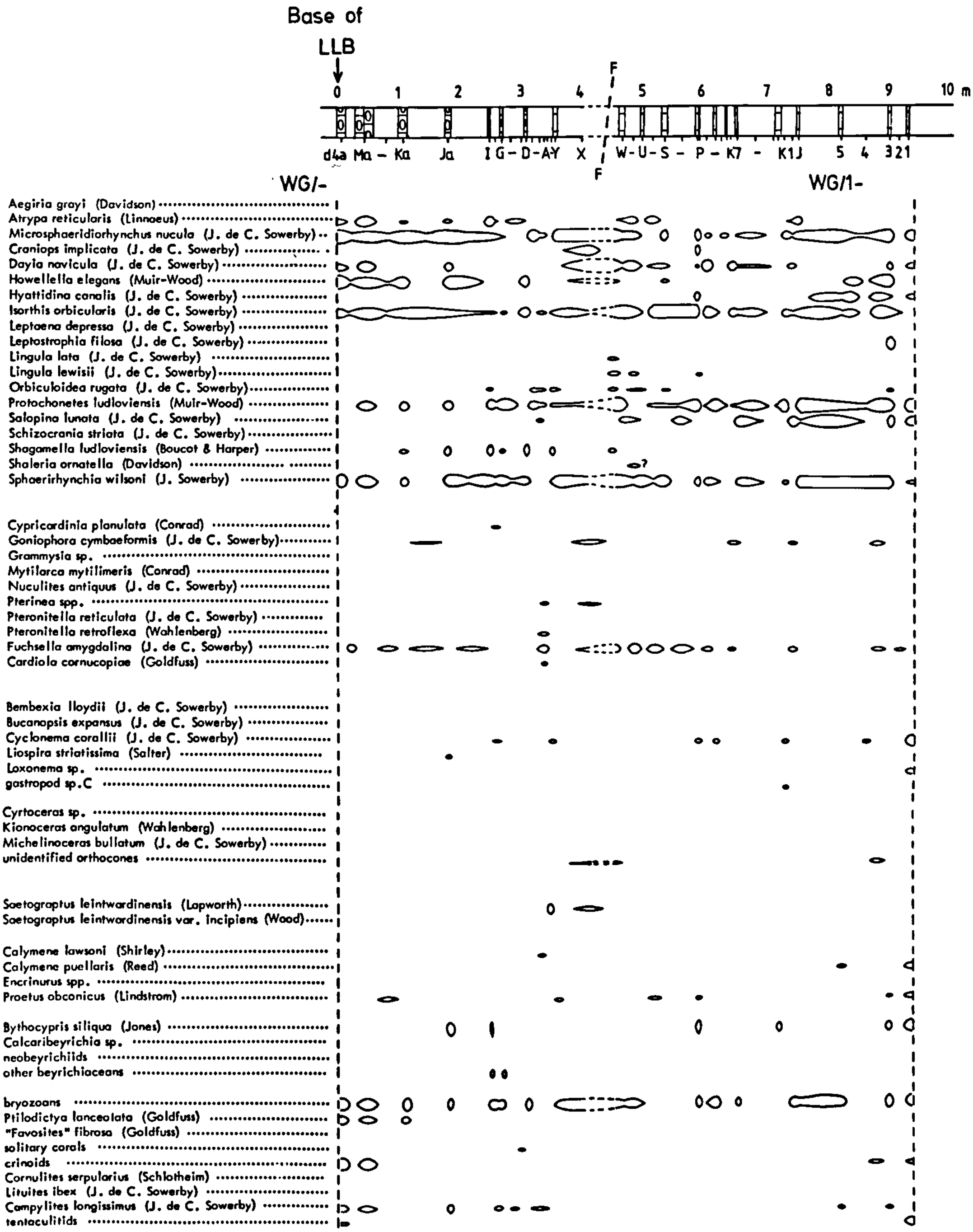


Fig. 3.1 : LLB succession at Wood Green.

L. Blaisdon Beds was not exposed in the quarry, and the basal limestone conglomerate bed - d4a - was therefore collected from the cutting.

The succession is composed of an alternation of conglomeratic limestones and fine muddy siltstones. The bottom 1.85 m consists of four thick (up to 30 cm) bands of coarsely crystalline, fossiliferous limestone containing numerous lithoclasts, separated by fine, olive-grey, muddy and shaly siltstones. In the upper 1.25 m (up to D), the conglomeratic bands are much thinner (up to 6 cm). The top one was taken as the junction between the Lower and Upper Blaisdon Beds.

The limestone matrices are composed largely of broken shell fragments, and recrystallised sparry calcite cement, with very many small elongated, but well-rounded, clasts (mostly longer than 2 cm) of siltstone and silty limestone. Bryozoans are often prominent constituents: both branching and encrusting types were found, and sometimes large pieces of colonies. Ptilodictya lanceolata is characteristic of the lower bands. Many complete shell valves are scattered through the limestone beds. Articulated rhynchonellids are relatively frequent at some levels. Larger lithoclasts (up to 5 cm long) of siltstone, silty and shelly limestone, were especially numerous in the lower deposits. Many clasts are flattened and elongated, but others - the calcareous and shelly ones mainly - are more ovoid or irregular. The edges are generally well-rounded. The majority of lithoclasts lie approximately parallel to the bedding.

Some lithoclasts appear, in section, to have been broken or cracked into smaller pieces. Others, though, have a pitted surface in plan view, and corroded rims. In section, sac-like borings around the edges can be seen. A few of the rounded pebbles had attached bryozoans, which do not appear to have been eroded. This indicates that the bryozoans became attached after the formation and deposition of the pebble. Boring organisms require a hard substrate (Bromley '75), so that the bored pebbles must have been lithified first. The period of boring and bryozoan attachment was apparently after the deposition of the lithified pebbles, before further sedimentation took place. The nature and significance of these limestone conglomerates is discussed in Chapter Six p309-29.

The lower surfaces of the limestone conglomerate bands are fairly sharp, and sometimes erosive, cutting through laminae of the underlying clastic sediments. In contrast, the tops are often transitional, with interleaved siltstones and bands of shelly limestones grading up into siltstones.

The limestone conglomerate bands have faunas dominated by brachiopods and bryozoans. P. lanceolata is confined to the bottom metre of succession, but branching and encrusting bryozoa persist throughout the L. Blaisdon Beds. The ribbed forms M. nucula, S. wilsoni and H. elegans are very common, with some of the rhynchonellids remaining articulated. Separate valves of P. ludloviensis, I. orbicularis, A. reticularis and S. ludloviensis were common, the latter two species being virtually restricted to the limestone faunas. D. navicula pedicle valves, often broken, appear at some levels, again only in the limestones.

The flaggy siltstones which are interbedded with the lower limestone deposits are fine-grained, with muddy and shaly bands. Thin horizons of comminuted shell debris and bands of flattened shells (approx. 0.5 cm thickness) are found occasionally, but the fauna is generally sparse. F. amygdalina is distributed in clusters; some individuals which are still articulated are inclined to the bedding. In the upper 1.25 m of the L. Blaisdon Beds, the siltstones show signs of current activity. They are well-laminated in parts, and there are thin calcareous lenses. Plane assemblages of disarticulated shells (each dominated by one species), and debris-rich planes and lenses (less than 2 cm thick) occur at intervals. Small phosphatised pebbles and nodules are occasionally found in the intervening beds, but bivalves are rare in the upper siltstones.

Narrow (1-2 mm), silt-filled burrows were noted from some of the siltstone beds right through the sequence, with some bedding planes extensively bioturbated. Fossils from the siltstones do not include burrowing forms that could have produced these traces.

The thickness and frequency of the limestone conglomerates decreases through the 3.1m of L. Blaisdon Beds, while the signs of current activity in the interbedded siltstones increase. The

stratigraphical unit was described by Lawson ('55 - p 92) to include the basal limestone conglomerates. It is faunally similar to the overlying U. Blaisdon Beds. Therefore the top conglomeratic band, in which bryozoa are prominent (D), was taken to mark the boundary between the two divisions.

Base of L. Blaisdon Beds:-

The basal conglomeratic band (d4a) has a sharp contact with the underlying U. Flaxley Beds siltstones (whose fauna is Bringewoodian). The absence of Aymestry Limestone facies here may be explained either by an unconformity or by a lateral faunal and facies change. Lawson (p104, '55) preferred the first explanation, with the conglomerates possibly being derived from the erosion of previously consolidated Aymestry Limestone. This is more fully discussed in Ch. Six (p 309ff.). The incorporation of UBB forms in the conglomeratic bands would provide some evidence of the nature of the basal contact. In the bed Ja, the matrix contains some fragments of compound corals (Fig. 6.5). However, no diagnostic UBB fossils were found in these deposits.

A2 Longhope By-pass section:

SO.694.185

This part of the section was overgrown so that the succession here could not be examined in detail. However, two limestone conglomerate beds that came from low in the L. Blaisdon Beds were examined and sectioned. These beds are discussed in the section on the basal conglomerates in Ch . 6.

LH/1, which may have been the basal bed, has numerous small, flattened, but well-rounded, lithoclasts of limestone and siltstone, aligned approximately parallel to the bedding in a debris-rich matrix. Larger pebbles are of limestone and shelly limestone, and though still well-rounded, are more irregular in shape. Large, branching bryozoans are prominent ~~(see Fig. 6.4)~~ and several of the smaller pebbles are formed of pieces of bryozoans.

LH/2, which is the next conglomeratic bed up in the succession, is extremely shelly, with numerous disarticulated valves of A. reticularis, P. ludloviensis, rhynchonellids, D. navicula and I. orbicularis. There are large well-rounded, pebbles of limestone and siltstone, and also many smaller, flattened inclusions. The section showed a large

encrusting bryozoan attached to a big lithoclast (Fig 6.4). The lack of damage to the structure of the bryozoan indicates that it was not transported or reworked after attachment. Therefore, as in the Wood Green conglomerates, it suggests that encrustation took place after the deposition of the pebble and prior to further sedimentation.

B <u>Upper Blaisdon Beds (and basal L. Longhope Beds)</u>

Thickness 8.0 m

Sections:	Wood Green Quarry: WG - , WG/1 -	SO.694.197
	Wood Green Railway Cutting:	SO.694.197
	Longhope Bypass: LH -	SO.694.185

Figs 3.1, 3.2.

The lower 6.5 m of U. Blaisdon Beds are exposed in Wood Green Quarry, following on conformably from the lower division. The section is faulted in the central part of the quarry, but displacement appears to be minor. The upper 4.5 m, and overlying L. Longhope Beds, were examined in a roadside cutting on the Longhope Bypass (A 4136). Correlation of the Wood Green and Longhope sections (Fig 3.3p62) was made partly on faunal similarities, and partly by reference to the Railway Cutting section, which provides a complete section (although mostly overgrown) through the U. Blaisdon Beds. Their thickness here was estimated to be 8-9 m.

The succession comprises an alternation of flaggy siltstones with shalier and more calcareous bands, and thin fossiliferous limestones. Faunal changes are largely gradational.

The lowest beds, in the first 1.5 m above the L. Blaisdon Beds, are unevenly splitting, fine siltstones containing a sparse fauna, interbedded with roughly laminated, more calcareous siltstones with thin (up to 1 cm), inorganic limestone lenses, and with shelly limestone bands. The laminae are generally 1-3 mm thick, but often impersistent, and undulate because of occasional small, cross-bedded ripples. Some limestones (eg WG-Y) are still conglomeratic in parts, indicating the transitional nature of the facies changes through the Blaisdon Beds. Lithoclasts in these deposits are only minor constituents compared to the thicker, lower conglomerates. Some of the shelly limestone bands are laterally extensive, but others die out within only a few metres.

The fauna of the unlaminated siltstones is scarce and patchily distributed. Some graptolites were found - identified (RBR) as

LONGHOPE BY-PASS

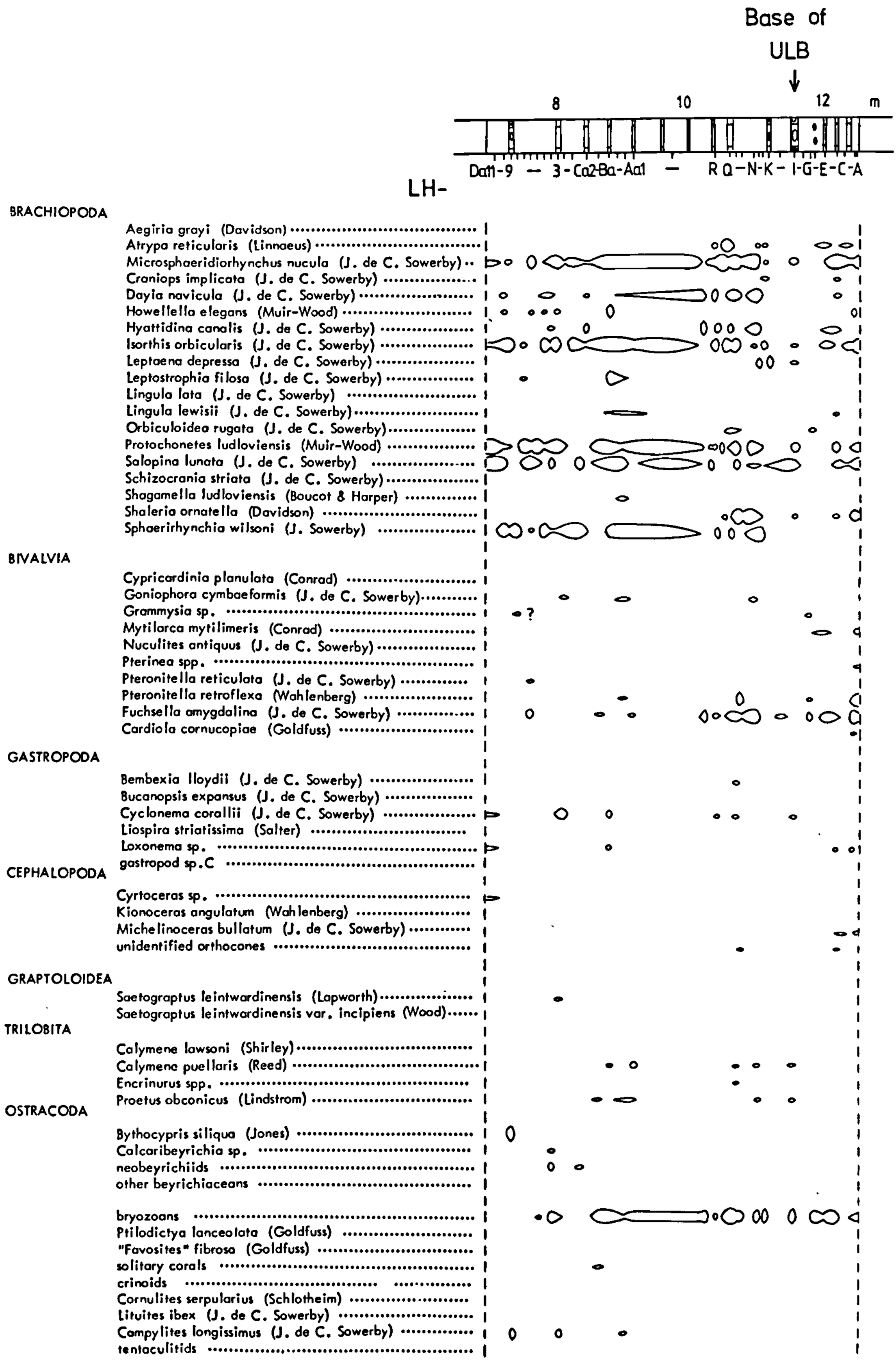


Fig. 3.2 : LLB succession, Longhope by-pass.

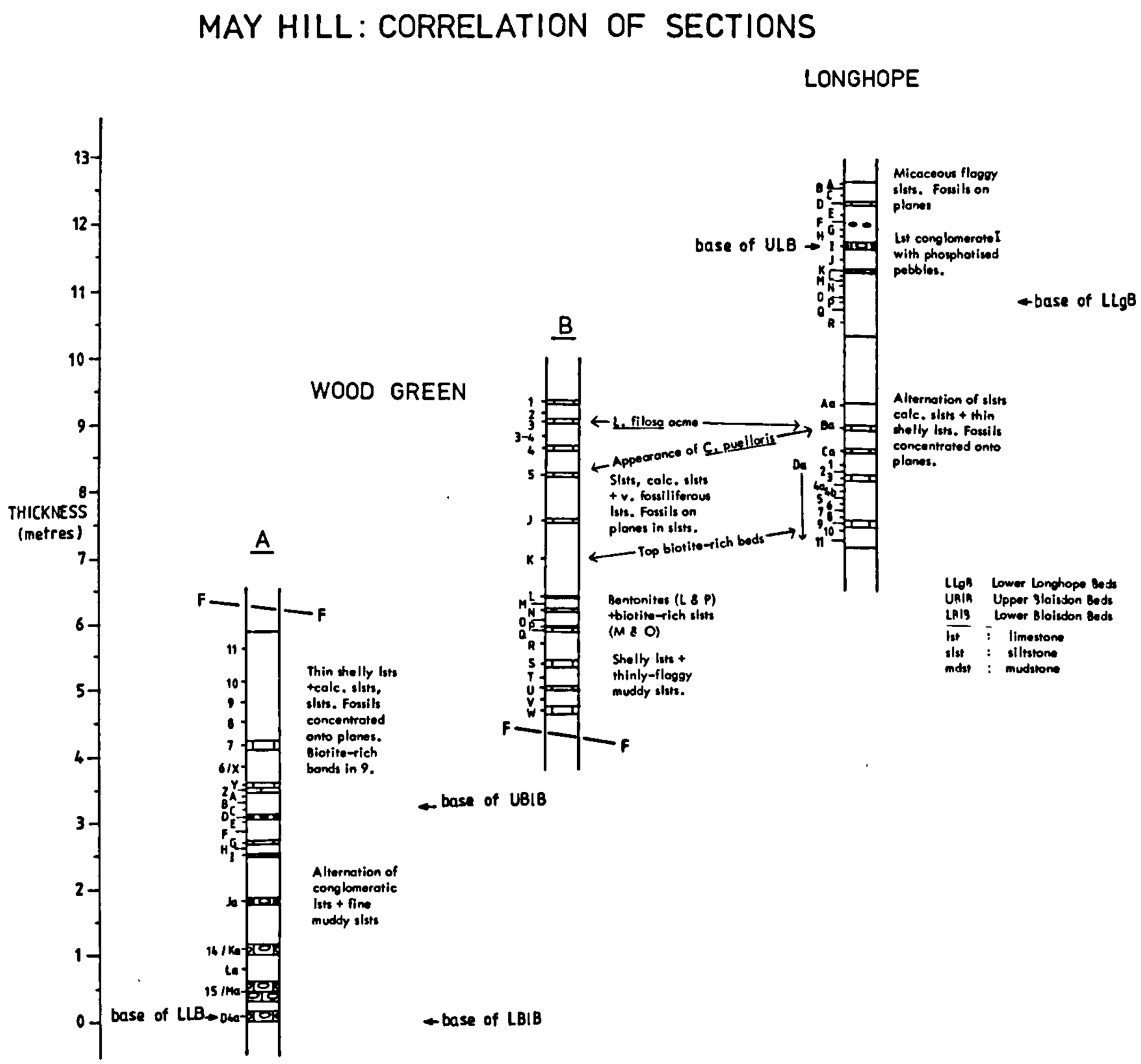


Fig. 3.3 : Correlation of sections, May Hill.

Saetograptus n. sub-sp. in WG-A, and S. leintwardinensis s.l. or cf. primus from slightly higher in the succession, in WG/1-6. The associated fauna includes a few bivalves - F. amygdalina, G. cymbaeformis and Pteronitella retroflexa, and orthocones. Several specimens of L. lewisii, including two apparently in situ, were found in the graptolitic bed of WG/1-6, together with a large broken valve of L. lata but with little other fauna. In the laminated flags, planes of fossils or of shell debris occur at intervals, with few shells in the beds between. Shell horizons become more frequent upward in the succession, when assemblages are commonly each dominated by only one or two species. Many of the faunas are brachiopod-rich, but there are also some bivalve assemblages. The shelly limestone lenses have abundant rhynchonellids in their brachiopod-dominated assemblages.

The bedding of the siltstones becomes more regular upwards in the section. Some flags are well-laminated, with more calcareous, micaceous, and shaly bands. Intercalated with these, and with the poorly-laminated and thicker beds, are thin, fossiliferous limestones. Nodules of green-grey, flinty limestone, which contain shells, are common at some levels. A number of beds in the middle part of the U. Blaisdon Beds have concentrations of small pieces (up to 0.5 mm max. dimension) of biotite mica, mostly finely disseminated but with a few euhedral flakes. The thin units WG-L and WG-P are yellow, friable paper shales, possibly bentonitic. The mica deposits may therefore have been derived from the breakdown of bentonites (Marsh '75, in LRG Bulletin 22).

Some laminated beds have very fine (up to 1 mm), even banding of more and less calcareous layers. The surfaces of laminae are smooth; some are gently undulating. Minor cross-bedding and erosional planes are fairly common. Associated with these beds are calcareous lenses of closely-packed, and often disarticulated or broken, shells, and thin bands of shell meal. The thickness of the shell deposits changes rapidly over small distances (but mostly less than 4 cm max.). Several are only 1-2 m in lateral extent. Apart from the shell accumulations, the laminated units have few fossils, and are fairly massive.

The thicker-bedded siltstones have plane assemblages of fossils at frequent intervals. The relative abundances of the various species fluctuate from assemblage to assemblage, so that the prevalent species

a : Finely-laminated siltstones above shell lens in which disarticulated valves are uniformly orientated convex surface upwards. (Acetate peel, x 4)

b : L. filosa limestone in which shells are haphazardly arranged. The centre of the photograph shows two bryozoans attached to the concave surfaces of shells. (x

Fig. 3.4 : U. Blaisdon Beds, May Hill; lithologies.

recur often. Some assemblages are virtually monospecific, and many have only one or two common forms. Typically, few fossils are found in the beds between shell horizons. The thin limestones are occasionally unfossiliferous, but mostly very shelly or debris-rich. Their faunas range from monospecific to diverse in species, but are mostly brachiopod-dominated. The lateral persistence of these limestone beds is again very variable: some of the thicker bands appear to be consistent over several metres, but others thin out quickly.

The sequence of interbedded siltstones, calcareous siltstones, and shelly limestones, with frequent horizons of fossils continues through the U. Blaisdon Beds. In the top metre of the succession, small phosphatised pebbles are occasionally found in some beds, and finely laminated siltstones with micaceous (muscovite) planes become more common. Band LH-K is a 3 cm debris-rich limestone bed with worn valves of L. depressa and A. reticularis, and small black phosphatised fragments. The bed taken here to indicate the junction with the ULB is slightly higher, at LH-I. This is a conglomeratic limestone (9 cm) with elongated, rounded clasts of limestone, silty limestone and siltstone, whose size ranges from very small (less than 1 cm) up to 12 cm across. The matrix is rich in fossils and shell debris, and includes some small phosphatised nodules and fragments.

Above this level, the sediments are dominantly siltstones. Some are well-laminated and fairly massive, others more thinly flaggy. The pattern of shell assemblages concentrated onto bedding planes continues in the L. Longhope Beds.

The faunal changes through the U. Blaisdon Beds are fairly gradual. The lower plane assemblages (ie. from above the bottom metre) are characterised by large I. orbicularis, M. nucula, and P. ludloviensis. F. amygdalina valves dominate the faunas of fine and muddy siltstones at several levels in these lower beds; one assemblage of convex-up valves (in WG/1-10) shows some alignment of the shells. In the upper 4 m, S. wilsoni and S. lunata become consistently abundant too.

The top beds in Wood Green Quarry (WG/1-5 to WG/1-1: the top metre) include the first appearance of C. puellaris, and an acme of L. filosa. These appearances have been used for the correlation of the Wood Green and Longhope sections (Fig 3.3 p 62): the latter has an equivalent level

around Ca-Aa. Also, the top biotite-rich bed WG-K2 corresponds roughly in position to the top one (LH-Da9) in the Longhope section.

In the top metre of the LLB, there are marked qualitative faunal changes. S. ornatella enters and becomes rapidly abundant, and then at a slightly higher level, S. wilsoni disappears from the fauna. Distribution of the fossils is still commonly in plane assemblages. F. amygdalina, H. canalis, and D. navicula increase quantitatively to dominate some of these higher faunas. A. reticularis and L. depressa are common in the top limestones, at the level where S. wilsoni disappears. C. puellaris, which is present in some shelly limestone beds through the upper 3 m of U. Blaisdon Beds, is fairly common in the boundary conglomerate I, where the fauna also includes proetid pygidia and a glatella of Hemiarges sp. (ATT).

Above I, the fauna shows an increased diversity and abundance of bivalves. The brachiopods S. ornatella, I. orbicularis, and the "Whitcliffe Beds association" of S. lunata, P. ludloviensis and M. nucula, are all abundant in the following metre (LH-I to A) of the section.

The L. Longhope Beds of Lawson (p 93, '55) were defined on the appearance of abundant S. ornatella, with H. canalis and C. puellaris, and therefore included the top strata with S. wilsoni. The junction of the U. Blaisdon Beds and L. Longhope Beds would be positioned slightly lower in the sequence, around LH-P (i.e. 0.8 m below I).

Bioturbation:

Burrows were noted from many of the siltstone beds through the bottom 3 m of U. Blaisdon Beds, in the section A of Fig 3.3 (p 62). Some show extensive disturbance, with numerous narrow (less than 2 mm) silt-filled burrows, while others have only sporadic traces. Some burrows are orientated oblique to the bedding, others lie parallel with it, across bedding planes. The laminated beds show little disturbance of the bedding around the burrows. ~~(Fig 3.4 p)~~. Similarly, plane assemblages of fossils are undisturbed.

Higher in the succession, the upper 1.5 m of section B (i.e. WG/1-5 to 1) again have a number of well-bioturbated units. Here green silt-filled traces are particularly clearly visible in the laminated calcareous siltstone beds. The majority of beds in this sequence are

burrowed to varying extents.

In the Longhope Bypass section, burrows were not recorded from the flags.

Apart from a band rich in tentaculitids at the top of the quarry section (WG/1-1), only occasional remains of Campylites longissimus fragments were noted from Wood Green. Pieces of the latter fossil were fairly common in two limestone bands in LH-Da, but rare otherwise. Thus, there are few remains of organisms that might have produced narrow burrows similar to those commonly found in the U. Blaisdon Beds of the Wood Green section.

May Hill Faunas:

The lower Blaisdon Beds, in the sections examined, are characterised by an alternation of fairly sharply-based, richly fossiliferous limestones, with fine muddy siltstones containing a sparse fauna. The former beds, - the limestone conglomerates - thin upwards in the succession, & higher calcareous beds are shelly coquinas, with only rare pebbles, and with less diverse faunas. The siltstone faunas of the lowest beds are dispersed through the flags. Thin, plane assemblages of scattered shells, and shell debris horizons, appear at intervals in the beds above, but many flags still have patchily distributed fossils. In the U. Blaisdon Beds, the frequency and density of bedding-plane assemblages has increased, and only a minor proportion of beds contain scattered fossils.

The shelly and conglomeratic limestones are inferred to be current-accumulations; they are dominantly composed of epifaunal fossils. Their faunas are substantially different from those of the interbedded siltstones, as can be seen from Fig 3.5 (p 68) for section A of Wood Green Quarry (section shown in Fig 3.3 p 62). The diagram also includes the faunas of higher beds, with the plane assemblages (that have been concentrated onto bedding surfaces by transport or reworking) separated from the widely dispersed faunas found within beds between these horizons.

The limestone bands of the L. Blaisdon Beds have diverse and abundant brachiopod faunas in which ribbed forms are predominant, together with bryozoans. In contrast, the siltstones have scarce faunas, in which F. amygdalina is most frequent. The only brachiopods

Fig. 3.5

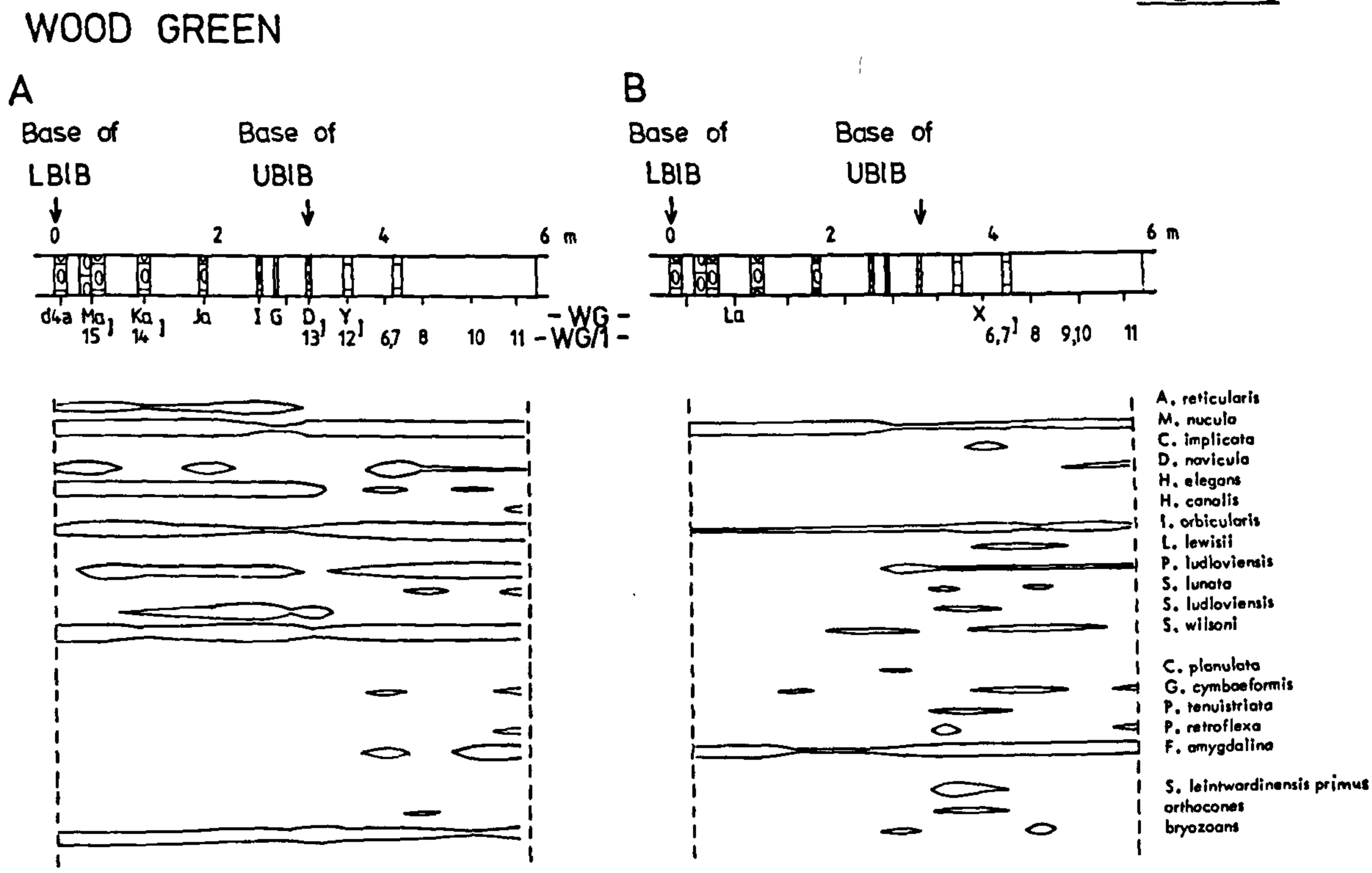


Fig. 3.6

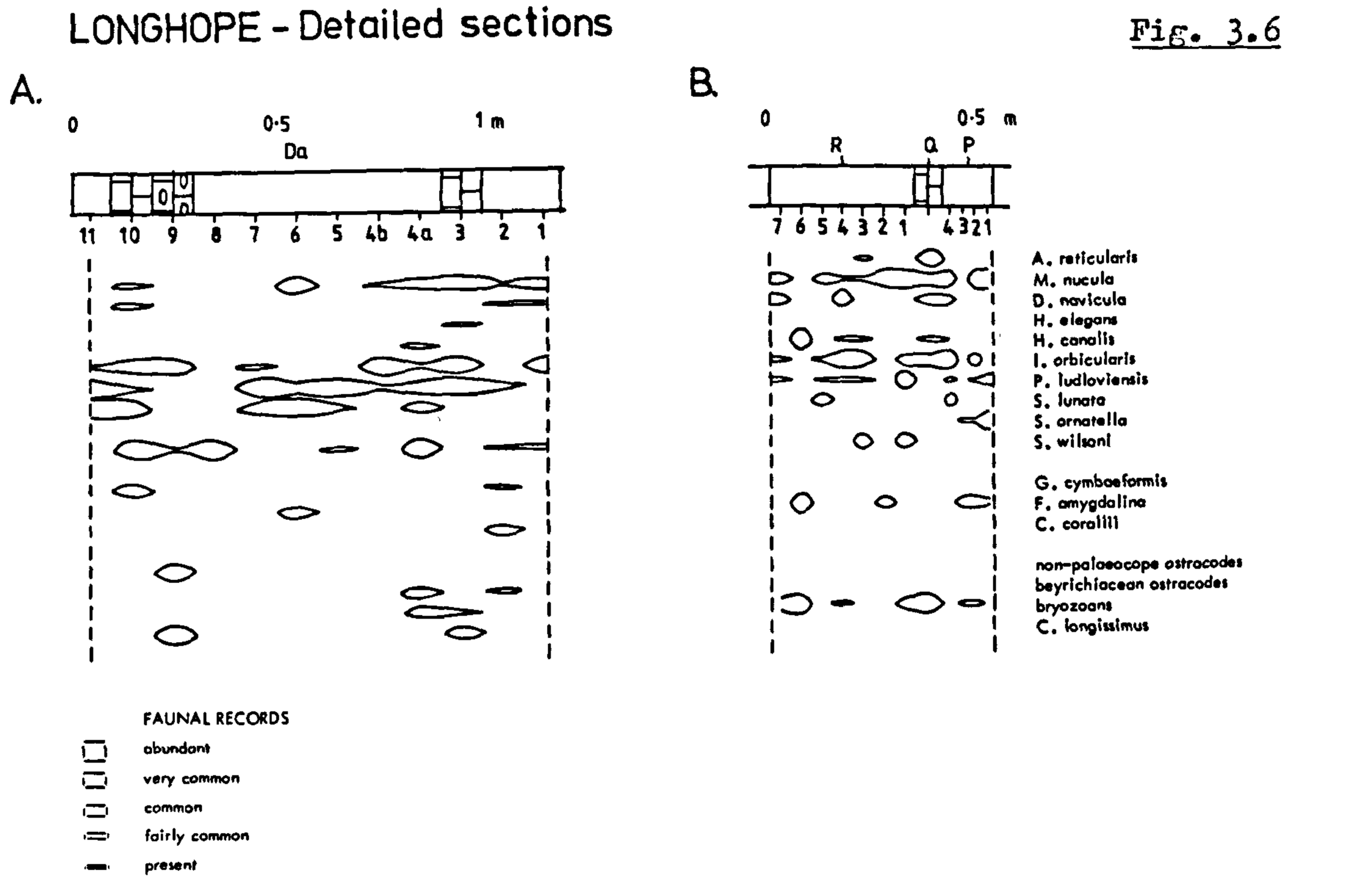


Fig. 3.5 : Comparison of A)Limestone and B)Siltstone faunas of lower 6m of LLB at Wood Green.

Fig. 3.6 : Longhope by-pass - Detailed sections Da and R-P.

consistently found are small numbers of M. nucula and I. orbicularis. The presence of articulated individuals of F. amygdalina in the lower siltstones supports the contention that this species is indigenous to the region (see p 267).

Above the L. Blaisdon Beds, A. reticularis, H. elegans and S. ludloviensis are absent or rare. The faunal distributions of the bottom metre of the U. Blaisdon Beds are transitional between those of the lower division (i.e. very shelly limestones and poorly fossiliferous siltstones), and those typical of the higher strata (i.e. siltstones and thin limestones, with bedding-plane assemblages of shells at frequent intervals). The "transported" category here includes both shell coquinas and bedding-plane accumulations; brachiopods, and especially rhynchonellids, are abundant in the former, while the latter, although mostly brachiopod-rich include occasional assemblages of disarticulated bivalves. The beds in which fossils are more randomly distributed include two horizons of graptolites; the one (WG-A) had no other fauna, and the other (WG/1-6) had rare brachiopod valves, bivalves, and lingulids that were perpendicular to the bedding. Internal moulds of orthocones are fairly common in the poorly-fossiliferous siltstones, together with bivalves, and a few brachiopods.

The higher beds (from 4-6 m on Fig 3.5) have frequent thin, bedding-plane horizons of disarticulated shells. The prevalent species recur repeatedly among often qualitatively similar faunas; many assemblages are composed almost entirely of brachiopods. Planes of F. amygdalina valves are also common, however. The beds with scattered fossils can be seen to have an increased diversity of both bivalves and brachiopods. The brachiopod species are similar to those of the transported assemblages, but their abundances are low. Bivalves are more consistently numerous and more diverse than in the transported faunas.

The broadly comparable composition of shell accumulations and dispersed faunas in the upper part of section A contrasts with the dissimilarity between the two seen in the L. Blaisdon Beds. In both parts of the sequence, bivalves are more abundant in the beds between shell concentrations that are characteristically brachiopod-rich. But there are several changes in the common brachiopod species between the

conglomeratic limestone faunas and those of the higher shelly bands and planes. Correlated with the faunal change is the facies transition to more even, regular bedding, with thin shelly limestone horizons.

This pattern of shell horizons within a sequence of thinly-flaggy siltstones and limestones continues through the remainder of the U. Blaisdon Beds. Overall faunal changes are gradational, but there are frequent oscillations in the prevalent species of faunas. Parts of the sequence from Longhope Bypass (LH-Da, and R-P) have been plotted in detail (Fig 3.6 p 68), to show some of the assemblages found in these beds. The diagrams show the rapid changes in species dominance that result from fluctuating relative abundances.

The bedding-plane assemblages frequently have closely-packed shells. Beds between the horizons have few fossils, but those present are qualitatively similar to the plane faunas. Assemblages rich in bivalves are less common in the middle part (eg. LH-Da) of the U. Blaisdon Beds than in the lower (from 4-6 m on Fig 3.5 p 68) and upper parts (LH-R-P), but are present throughout.

The degree of transport which the fossils have undergone is very difficult to estimate. The majority of shells are disarticulated, and planes and bands of finely-comminuted shell debris are not uncommon. None of the fossils are clearly <u>in situ</u>. The palaeoecological significance of these plane faunas is discussed in Ch.6

2) WOOLHOPE INLIER: Perton

The Ludlow Series (65 - 400 m) of the Woolhope Inlier was mapped by Squirrell ('56) - the southern part, and Tucker ('58) - the northern area. They ('60) sub-divided the Series into eight stratigraphical groups "based primarily upon variations in the faunal assemblage, aided by certain lithological distinctions". (Squirrell and Tucker '60: p 145). There was a considerable reduction in the thickness of individual divisions from the north of the inlier (Perton) to the south. All the divisions except the Upper Sleaves Oak Beds, which are equivalent to the Aymestry Limestone, could be traced throughout the inlier; the latter does not occur in the southern part.

The LLB correlate with the Lower Bodenham Beds of Squirrell and Tucker ('60). The base of this division is marked by conglomeratic limestone bands, while at the top, the overlying Upper Bodenham Beds constitute the distinctive faunal unit of the ULB.

Perton: LLB succession

Perton Quarry: PL/-, PL/B-, PL/1- SO.596.400

Perton Lane Section: PL/A-

The section in Perton Quarry includes the junction with the underlying U. Sleaves Oak Beds, and the following 20 m (approx) of L. Bodenham Beds. The lane section was largely overgrown, but the boundary between the L. and U. Bodenham Beds could be examined here. The upper 7-8 m of the lower division were exposed in part. The total thickness of the L. Bodenham Beds at Perton was estimated by Tucker ('58) to be 40 m.

a) Quarry section:

Fig 3.7

The Upper Sleaves Oak Beds are poorly-bedded, hard, nodular, calcareous siltstones and silty limestones. Nodules of hard, green-grey limestone are very common in the uppermost beds (PL-Xa to C). The nodules are irregular in shape and of widely different sizes (up to 12 cm across), but generally well-rounded. Some lumpy, uneven bands of unfossiliferous limestone appear to be formed of coalesced nodules. Other beds have numerous separate nodules in a calcareous siltstone matrix. Bands composed mainly of broken shell debris are fairly frequent; these look "mottled" in section because of irregular patches

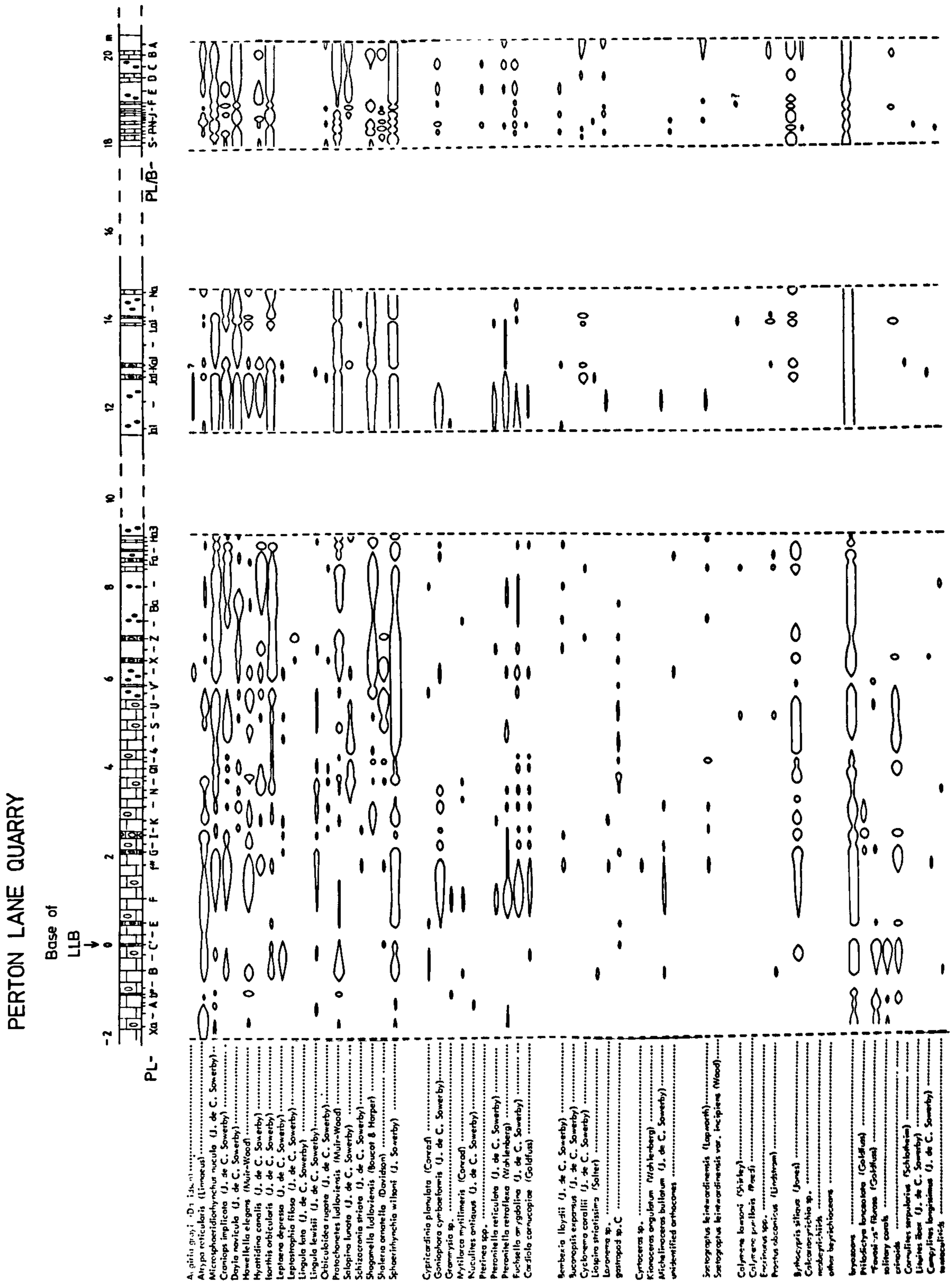


Fig. 3.7 : LLB succession at Perton Quarry.

of siltstone and muddy limestone incorporated within the crystalline matrix. Patches of comminuted shell material are common in the siltstones. Occasional small, flattened mudstone pebbles are found in some of the beds, and mud drapes occur in many siltstones.

The fauna of the top U. Sleaves Oak Beds is sparse, and fossils are widely scattered. Solitary corals and crinoid stems are most abundant; both, on some surfaces, showed signs of a preferred orientation (along a strike NE-SW). Large A. reticularis valves and also complete specimens, and S. euglypha and L. depressa valves, are common in the siltstones, often enclosed within, or on, nodules. "Favosites" fibrosa is more usually in limestones, randomly orientated, although also quite frequently found in siltier beds. The presence of A. funiculata, Shaleria sp., Dalmanites sp., and P. globosa (several large specimens in nodules) is important, because these forms are characteristic of the topmost UBB at Ludlow.

The lithologies of the basal L. Bodenham Beds are similar to those of the higher U. Sleaves Oak Beds, consisting of a series of interbedded, very nodular calcareous siltstones and siltstones, with silty limestones. But pebble-bearing limestones are found in addition to the other facies types in the younger division. Squirrell and Tucker ('60 - p 147) used the lowest of these bands to define the base of the L. Bodenham Beds. In the section studied, PL-C', a hard crystalline, fragmental limestone bed (6 cm thick), which is conglomeratic in parts, was taken to mark the junction. This band lies slightly over a metre above b*, a soft, red-brown shale, which may have been bentonitic (cf. bentonite SY/A-g at the stratotype for LLB).

Many beds over the next 4.5 m (C'-Q) of section are very nodular (see Fig 3.8, p 74), but above this level, the frequency of such horizons diminishes. The nodules are mostly parallel to, or only very gently inclined to, the bedding. They are still highly irregular in size, shape and concentration, but generally smaller (less than 8 cm across) than many from the U. Sleaves Oak Beds. Interspersed among the nodular beds are fine-grained siltstones, some of which have a lamination of muddier and more calcareous layers. Planes of shell debris, or mica, and thin impersistent shell lenses are common in these beds.

West face, Perton Quarry - showing LLB.

Fig. 3.8 : Nodular beds, LLB Perton Quarry.

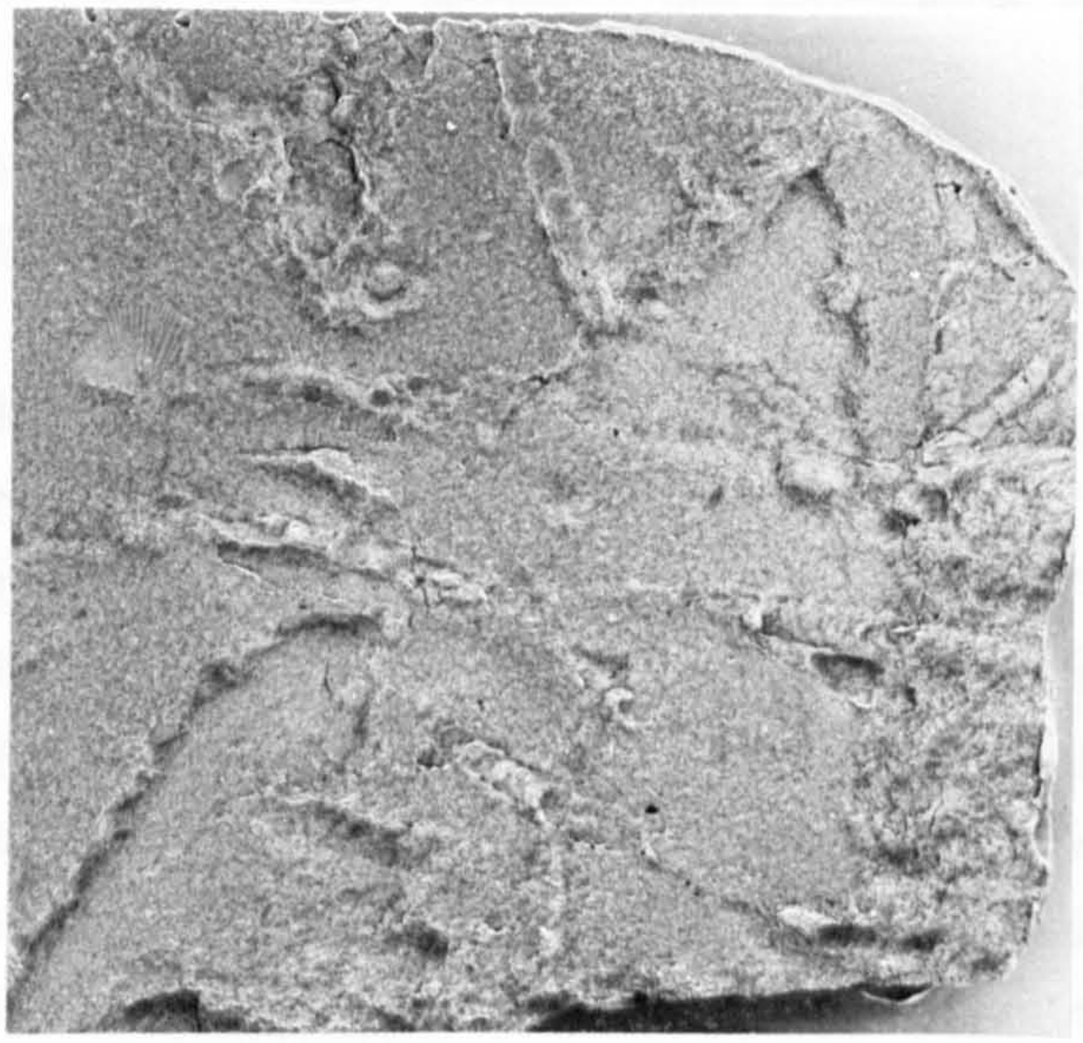


Fig. 3.11 : Burrow traces across siltstone plane of top LLB Chances Pitch. (x 2.5)

The limestones of the lower part of the sequence (C'-Q), as well as shelly and fragmental deposits and inorganic bands, include a number of fossiliferous conglomeratic beds. These frequently have distinct, and sometimes slightly erosive, bases. Numerous, elongated, limestone and calcareous siltstone pebbles are enclosed in crystalline and muddy limestone matrices. The pebbles, which have well-rounded edges, are variously ovoid to irregular (limestones), or more flattened (siltstones) - see Fig 6.7 , p 319. Many are very similar to the matrix in composition, so that, on weathering, their outlines become indistinct. Some of the pebbles contain fossils (eg. A. reticularis, I. orbicularis, S. wilsoni and H. elegans - all common L. Bodenham Beds forms). These conglomeratic bands are richly shelly, with faunas dominated by brachiopods and bryozoa (including P. lanceolata). There is a great amount of broken shell debris in the matrices. Beds of fossiliferous limestone become more frequent upwards in the succession.

The faunal changes from C'-Q are transitional. The siltstones and nodular siltstones have fairly scarce faunas. Bivalves are diverse and very common in thin bands (2-3 cm). Other flags have Craniops implicata, D. navicula and H. canalis valves in separate, scattered plane assemblages. A reticularis valves are still commonly found in nodular horizons, but solitary corals, "F." fibrosa and S. euglypha decline rapidly in numbers above C', and UBB faunal elements are rare above this level. The limestone beds have very different faunas from the siltstones. In the conglomerates, ribbed brachiopods - A. reticularis, S. wilsoni, M. nucula - are most common, with smooth ostracodes, and pieces of branching bryozoans. By the upper metre of sequence, the numerical abundance of the fauna has greatly increased, and thin bands of shells dominated by single species appear quite frequently. S. wilsoni, S. lunata, and H. elegans are all prevalent in some of these beds.

The following 2.5 m of the succession (R-Z) is increasingly calcareous, with more massive beds of limestone conglomerate and nodular silty limestone, separated by thinly flaggy siltstones. The distinction, between the richly fossiliferous conglomeratic bands and the largely monospecific faunas found at intervals in the otherwise poorly fossiliferous siltstones is pronounced. Crystalline limestone

beds of fragmental material with few complete valves, and planes of shell debris, are common. In this part of the sequence, monospecific S. wilsoni coquinas with dense concentrations of shells could be traced for several metres laterally, but then lensed out. Similar beds with other species (eg. S. lunata, P. ludloviensis) are generally less persistent. There is an acme of S. ornatella in this part of the succession.

The remainder of the quarry section (PL/Aa-Ia, Ial-Na, PL/B-S-A) is a more evenly and thinly-bedded series of siltstones, with nodular beds, and thin limestones. Some siltstones are finely laminated, having alternating calcareous and silty layers; others are thicker-bedded and irregularly splitting. Nodules of green-grey limestone are mostly small (less than 5 cm across) and elongated, and are confined to certain horizons. Bands of shelly, debris-rich and unfossiliferous limestones are intercalated among the siltstones. Conglomeratic limestones occur occasionally, but are thin (usually less than 5 cm) compared to lower beds.

Fossils in the siltstone beds are characteristically concentrated into thin bands, in assemblages dominated by one or two species. The prevalent species recur very frequently. A number of different articulate brachiopods are found to monopolise faunas, and bivalve-rich beds are very common. Bands of fine siltstone, in which large branching bryozoa are abundant, occur at several levels. There are many horizons of finely-comminuted shell debris, and broken shells.

A lot of the shelly limestone beds (often only 2-3 cm thick) are very comparable to the siltstone assemblages in having monospecific faunas. These are close-packed, lenticular, shell accumulations, like those found in R-Z. Their lateral extent varies greatly, but again the S. wilsoni bands seem to be most persistent. The carbonate cement in many of the thin shelly limestones appears to be biogenic in origin. If coquinas were traced laterally, the thicker parts of the band were shelly limestones, while at the thinner, peripheral regions, the shells were in a siltstone matrix. As well as the monospecific limestones, there are many beds (often thicker (up to 12 cm) than the former type) which contain varied shelly faunas; a few of these beds are conglomeratic, with pebbles of silty limestone. In the more diverse

limestone faunas, many brachiopod species are common together, but gastropods, trilobites, ostracodes and bryozoa are also important constituents of the assemblages.

The top beds in the quarry (PL/B-S to A) have an increased frequency of shelly limestones compared with lower in the succession. Both monospecific species-rich faunas are common. S. lunata and S. ornatella become common in these beds.

Above PL-Z, the faunas are consistently much more abundant than in the lower beds. Individual assemblages differ considerably, both qualitatively and quantitatively, but there is little overall change through the next 13 m of the succession. Of the brachiopods, M. nucula, C. implicata, D. navicula, H. canalis/I. orbicularis, P. ludloviensis, S. ludloviensis and S. wilsoni occur in great numbers. Bivalves remain common in some siltstone beds throughout, while gastropods increase in numbers in the upper half.

Monograptid fragments were present in PL-f*, and then rarely in a few beds up through the quarry section. The only specimens identified to species level (RBR) were from the shelly limestone bed PL/B-A; they were Saetograptus n.sub-sp.

Bioturbation: (Traces of bioturbation were difficult to identify because of the high degree of post-depositional compaction that has affected the rocks).

The U. Sleaves Oak Beds at the bottom of the section (PL-Xa-C) include some flags with numerous fine muddy drapes and silt-filled traces of burrows. Most are on bedding-planes or only slightly oblique to them. Similar bioturbation effects were seen in some flags in the lower part of the L. Bodenham Beds (in PL-f* and F). In the laminated siltstones in PL-J, L and N, sporadic silt-filled burrow traces could be seen in the sediments, and several plane surfaces had networks of narrow traces across them. The "mottled", bioturbate texture of some beds indicates extensive biogenic reworking of the sediment. Bivalve-rich bands rarely show signs of bedding structure, and often have diffuse muddy patches within the sediment. However, the distortion of the shells is pronounced, so that the mottling could be a compactional feature. Few beds above the lower 4 m of L. Bodenham Beds have distinct

traces of burrows, but many have a bioturbate texture.

b) Lane Section: PL/A-

The top 7-8 m of L. Bodenham Beds were intermittently exposed in the roadside bank north of the quarry. The lowest few metres are dominantly uneven siltstone flags, with occasional thin lenticular limestones (2-3 cm) which help to define the bedding. The following 3-4 m have frequent shelly and fragmental limestone beds (which lie with sharp distinction on beds below) among well-bedded, laminated siltstones and more thickly-bedded flags.

The lower siltstones have a fairly scarce fauna, concentrated onto planes and in the thin limestones. Bivalve assemblages are dominated by F. amygdalina, while M. nucula, P. ludloviensis, and I. orbicularis are the most common brachiopods in the planes of well-scattered valves. The higher limestone beds are richly fossiliferous, with faunas qualitatively similar to those of the top part of the quarry section, but the interbedded siltstones have few plane assemblages, of limited diversity. A C. puellaris glabella was recorded from one limestone bed, and several calymenid pygidia and free cheeks were found among the shelly bands.

Squirrell and Tucker ('60 - p 148) positioned the base of the U. Bodenham Beds on the disappearance of S. wilsoni, D. navicula and H. canalis, and the acme of S. ornatella. In this study, the decline of the first species was found to be very rapid, and corresponded to a sudden increase in abundance of the strophomenid S. ornatella. A conglomeratic shelly limestone bed (with ovoid clasts of silty limestone) PL/A-A (12 cm) was taken to indicate the junction. This was the first fossiliferous limestone which contained no S. wilsoni, and it lay directly above siltstones with planes of abundant S. ornatella valves. Higher laminated siltstone beds have large valves of L. depressa (with trails) fairly common at some levels; these planes have much fine shell debris and mica flakes.

Beds above the conglomeratic horizon are interbedded siltstones and calcareous siltstones, with thin fragmental and fossiliferous limestone beds and lenses. Many siltstones are finely to more thickly laminated, others are poorly-bedded. The lamination is of interdigitated

calcareous, silty and micaceous layers. Planes and bands of fossils occur at frequent intervals. S. ornatella (disarticulated valves) is abundant in many assemblages, often monospecifically. M. nucula, S. lunata and P. ludloviensis dominate many faunas; pteronitellids are common in separate planes. Ostracodes - both smooth forms and beyrichiaceans (of several different species) - are concentrated in thin horizons of shells and fine debris. The faunas of the siltstones are diverse; brachiopods and bivalves are numerically dominant, but ostracodes, gastropods, tentaculitids, cornulitids, orthocones and bryozoa are additional components of many assemblages.

Burrows are common in many of the siltstone flags in the top L. Bodenham Beds and basal strata of the upper division. They are most clearly seen in the laminated beds. The traces are narrow (2-3 mm) and generally oblique to the bedding; the disturbance of the lamination results in a mottled appearance to parts of some beds.

Perton: Faunal distributions:

Fig 3.9-A (p 80) shows the faunas of beds from f* to Q. It illustrates the difference between the conglomeratic and shelly limestone faunas of G, I, K and P, and those of the interbedded siltstones and nodular bands. The former have ribbed brachiopods, bryozoa, smooth ostracodes and crinoid columnals most commonly. The latter include beds of bivalves (especially G. cymbaeformis), and separate assemblages of brachiopods where the smooth shelled species D. navicula and H. canalis are frequently prevalent. Bryozoa are consistently common, and numerous bands of shell debris occur throughout the sequence.

Fig 3.9-B shows a similar detailed section from beds PL-Ial to Na (approx. 11.5-14.5 m above the base of the L. Bodenham Beds). The typical distribution of faunas here is in plane assemblages dominated recurrently by different species, but with beds of richly-fossiliferous limestone interspersed among the other beds. Jal, Kal and Lal are examples of the species-rich faunas, dominated by brachiopods, with bryozoa, smooth ostracodes, gastropods (Cyclonema corallii), and proetids (in Lal). Some more restricted assemblages can be seen in the upper half of Ia2 (:*-1* on diag.), where five successive faunas

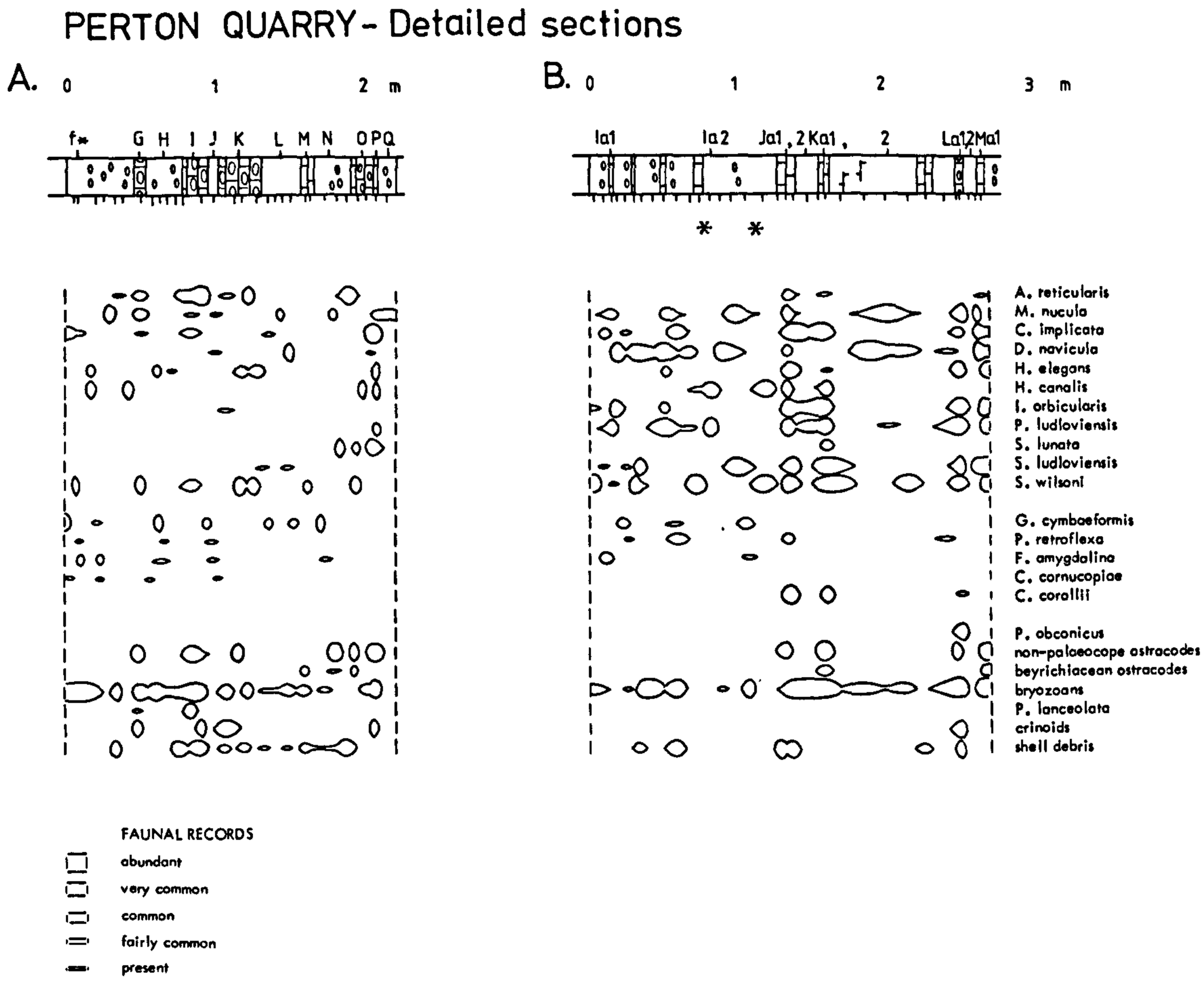


Fig. 3.9 : Perton Quarry; Detailed sections A) f*-Q and B) Ia1-Ma1.

are dominated by 1) H. canalis and P. ludloviensis, 2) D. navicula, 3) M. nucula and S. ludloviensis, 4) bivalves, and then 5) S. wilsoni and H. canalis.

Some of the shelly limestones of S. wilsoni were traced laterally, when representative populations from different areas of the same band were examined (see p 353). The shells from each sample had normal size-frequency distributions, with only very narrow size spreads, and the mean size was found to change laterally. The results indicate a high degree of size sorting in these deposits. In contrast, a population from one of the limestones with a varied fauna (PL/B-B) had a much broader size range, although again normally-distributed. (A S. ornatella population from this same band showed a comparable wide size spread relative to other plane-assemblages measured). The high degree of broken shell material in the carbonate matrices, and the sharp basal contacts of these beds suggest that the deposits represent transported accumulations.

3) MALVERN HILLS: Chances Pitch SO.748.403; ABBERLEY HILLS: Woodbury Quarry SO.743.637
Frith Wood SO.723.404

The Silurian rocks of the Malvern, Abberley and Ledbury Hills were mapped and described by Phipps and Reeve ('67). They recognised the Aymestry Limestone Formation, composed of the Rilbury Siltstone Member (lower), and the Aymestry Limestone Member (upper). The two units displayed complementary thickness changes, with no evidence of a break in deposition between them. The base of the limestone was therefore diachronous; it appeared to be oldest in western areas, and youngest in the south. The top boundary of the limestone in the northern part was also diachronous, the upper strata containing a fauna identical to that of the succeeding Mocktree Shale. (Phipps and Reeve '67 - p 348-9).

The LLB fauna corresponds to that of the Mocktree Shale. This Member everywhere overlies the Aymestry Limestone Member. Bands of limestone conglomerate are common in the basal part of the succession over much of the region. These increase in thickness and frequency towards the south. At its upper limit, the Mocktree Shale Member is followed by the Woodbury Shale Member, which is lithologically similar, but comprises the S. ornatella beds. The rock-stratigraphical unit was defined by Phipps and Reeve ('67) to describe the faunal acme of this strophomenid. It is approximately equivalent to the biostratigraphical division of the ULB.

A) Malverns:

The succession was examined at Chances Pitch, on the Malvern-Ledbury road A449 (SO.748.403). The road cutting provides a section through from the top of the Aymestry Limestone Member to the Whitcliffe Flags, with fairly continuous exposures for much of the sequence. In Frith Wood (SO.723.404), some large, weathered, bedding-plane surfaces were used for palaeoecological surveys. These are discussed in Ch. 6 p368.

B) Abberleys:

In Woodbury Quarry (SO.743.637), the very steeply dipping rocks include the whole thickness of the LLB. Much of the succession was accessible.

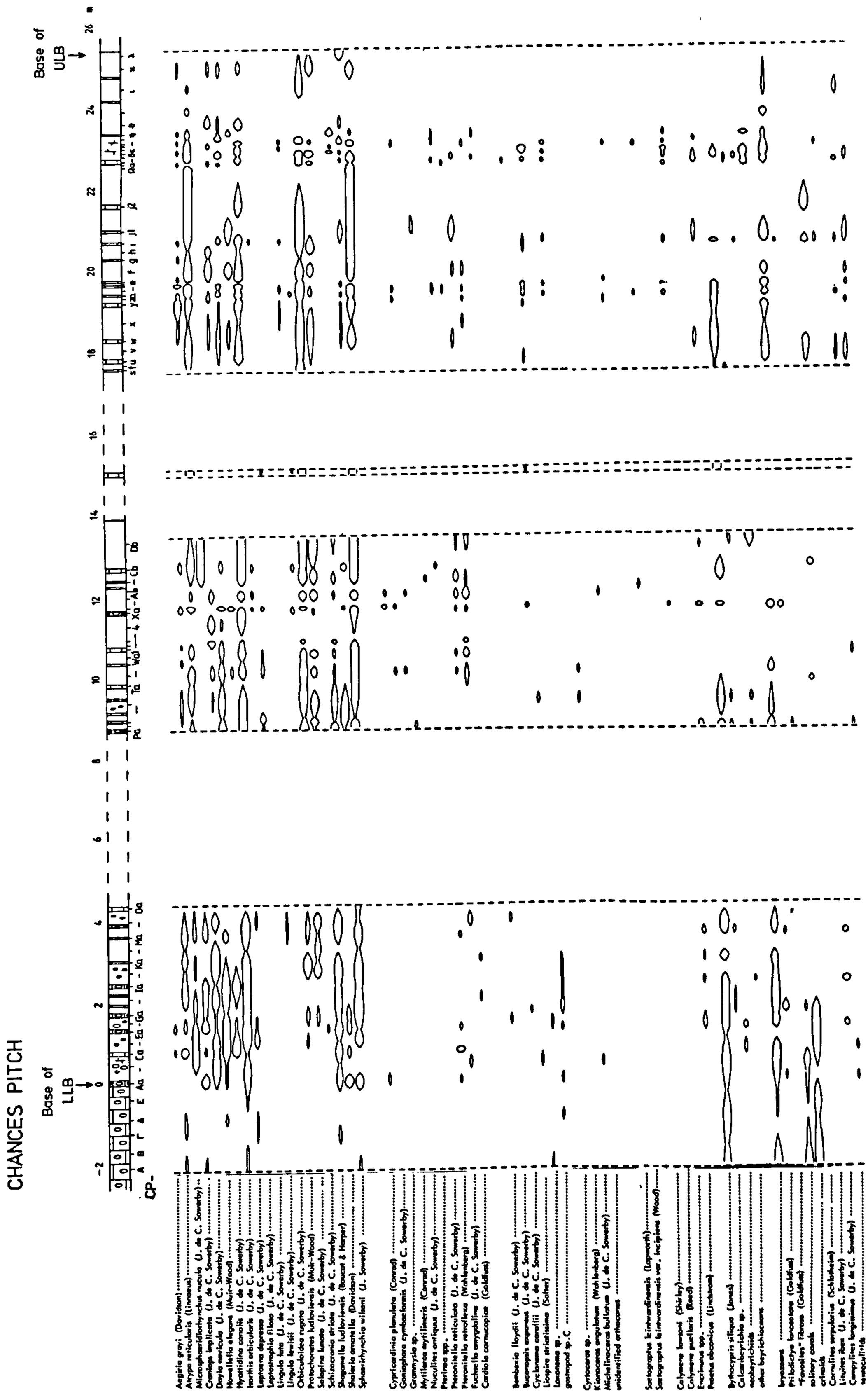


Fig. 3.10 : LLB succession at Chances Pitch.

A. Chances Pitch - LLB succession:

Fig 3.10

The LLB in this section are about 25 m thick. The succession is composed mainly of thinly flaggy siltstones, calcareous siltstones and limestones, but the sediments are more calcareous towards the base.

The bottom of the sequence is in the Aymestry Limestone facies of massive, irregular, nodular limestones and calcareous siltstones. Nodules are composed of bluish, muddy unfossiliferous limestone, or are more crystalline and contain shells and shell fragments. Some lumpy, uneven, but continuous, beds of limestone appear to be formed of coalesced nodules. These deposits are very hard, and massive, with only rare fossil fragments. Nodules range in size up to 15 cm across. They are well-rounded, but very irregular in shape. In the 2 m of succession from A to E, nodules are often fairly spherical, but in higher strata they are more flattened, elongated parallel to the bedding. A thin fine shale unit (2 cm) between beds A and B may have been bentonitic.

These lowest beds are only sparsely fossiliferous, and shells are widely dispersed. Patches and thin horizons of finely comminuted shell debris occur at intervals. A. reticularis (large valves) are relatively numerous in the calcareous siltstones, on or near nodules. Within nodules, S. euglypha, L. depressa, and A. funiculata valves, smooth ostracodes, and large specimens of P. globosa are fairly common. Solitary corals are concentrated in the siltstones, occasionally inside nodules. The fauna includes some valves of S. ornatella, and Dalmanites pygidia and free cheeks. A number of the fossils are forms characteristic of the top UBB at Ludlow.

The lowest conglomeratic limestone horizon (CP-Aa) was taken to indicate the base of the Mocktree Shale Member. This is a bed (15 cm) of silty limestone containing abundant, ovoid, silty limestone pebbles. Valves and fragments of I. orbicularis were common in the matrix.

The following 2.5 m of succession (Aa-Ia) consist of massive conglomeratic limestones, interbedded with fine muddy siltstones, nodular and calcareous siltstones, and limestones. The bedding, though at first still poorly defined, is thinner than in the strata beneath, and becomes more regular upwards in the sequence. Some of the siltstone

beds contain small, flattened mudstone pebbles and phosphatic nodules. Thin, impersistent shelly and debris-filled lenses, which are infrequent in the lower beds, increase in number and extent. This is reflected in the quantitative increase in faunal abundance that takes place over the bottom few metres. The conglomeratic beds are fossiliferous silty limestones with numerous well-rounded, flattened or ovoid pebbles of calcareous siltstone, silty and shelly limestones. The clasts are generally parallel to the bedding. Their size varies considerably up to 10 cm across, although mostly less than 5 cm.

With the more thinly flaggy bedding of the siltstones, the fauna becomes concentrated onto bedding planes and into thin shell bands. Many assemblages have only one or two prevalent species. The dominant forms change frequently in the higher beds. The less regular strata below have fewer, widely-dispersed fossils, of a limited number of species; a qualitative increase in diversity accompanies the upward change in distribution of the fossils. Above Aa, UBB forms are rare: a few S. euglypha valves, and large P. globosa specimens were found in the lower Mocktree Shales, while Shaleria sp. was fairly common in limestones of the bottom 1.5 m. The beds from Aa to Ia have facies and faunas transitional between the UBB Aymestry Limestone and LLB Mocktree Shales.

The residual fauna after the disappearance of UBB fossils is dominated by the brachiopods A. reticularis, M. nucula, D. navicula and I. orbicularis, together with bryozoa. In the higher beds, H. elegans, H. canalis, S. ludloviensis and S. wilsoni have also become very common. The diversity of the fauna increases too, with bivalve and gastropod species, ostracodes and proetids forming minor components of many assemblages.

The following 9 m of succession (Ja-Wa) consist of a thinly flaggy series of siltstones, calcareous siltstones, and thin limestones. Nodular horizons are less common above the lower few metres. The limestones include unfossiliferous, shelly and debris-rich, and conglomeratic beds. Many of the deposits are lenticular, dying out laterally in only a few metres. Some monospecific shell accumulations have carbonate cement in the central areas of dense shell concentration, but at the thinner parts of the coquina the matrix grades into calcareous siltstone. Other fossiliferous limestones have more varied

faunas; these beds are also commonly conglomeratic. In this part of the sequence, conglomeratic bands are generally thinner (less than 10 cm) and more shelly than in the lower strata, and pebbles are less numerous. The siltstones are still characterised by plane assemblages of fossils. Few shells are distributed in the intervening beds.

P. ludloviensis and S. lunata increase rapidly in abundance to become prevalent in many assemblages in this part of the sequence. H. canalis and D. navicula are both less consistently common than in the lower beds. There is little qualitative change in the fauna from Ja to Wa, except that S. ornatella and L. filosa appear in the upper part (Pa-Wa) of the sequence. Many of the fossil concentrations comprise thin shell limestones. Monospecific rhynchonellid bands of S. wilsoni and M. nucula include varying proportions of articulated shells along with much debris; other species are largely disarticulated, and many valves are broken.

Above Wa, the frequency of limestones decreases, and conglomeratic bands are not common. As well as thinly flaggy, calcareous siltstones and fine muddy siltstones, there are some more massive, laminated beds. The latter have alternating calcareous and silty bands, intercalated with thicker, unfossiliferous limestone beds. There are periodic shell lenses and debris horizons. The thickness of individual laminae ranges up to 2 mm, although most are less. Minor discontinuities in the bedding are frequently seen.

The laminated beds have very few fossils in between the shell horizons. Their plane assemblages include much broken shell debris along with disarticulated valves, and beds of shell meal are fairly frequent. The thicker-bedded siltstones have many bivalve-rich assemblages as well as brachiopod-dominated faunas. Bivalves have become more diverse and abundant above Ta, with valves of P. retroflexa and F. amygdalina common in bands, and lesser numbers of other species. Graptolites in CP-Ab, identified as S. leintwardinensis s.s. (RBR), came from a bed in which the only other fossils recorded were rare valves of F. amygdalina.

The lithology remains similar through to the top of the LLB and into the ULB, but micaceous shaly siltstone units and very calcareous laminated beds become more prominent in the upper strata. Very

fossiliferous limestones have faunas dominated by rhynchonellids, P. ludloviensis and I. orbicularis. All these fossils are similarly abundant in siltstone assemblages. S. lunata, D. navicula, H. canalis, large branching bryozoa, and bivalves are the other prevalent forms of plane faunas. Towards the top of the succession, the brachiopod association of S. lunata, M. nucula, and P. ludloviensis, characteristic of the Whitcliffe Beds, becomes very abundant in bands. There is an increase in diversity of the fauna over the top 5 m, with gastropod species, orthocones, trilobites, ostracodes, and tentaculitids all becoming frequent constituents of faunas. A few graptolites were found in bed Ed.

The ULB index fossils appear over several metres of succession. C. puellaris was first identified (LC) in CP-α, although ecdysed skeletal elements of calymenids were found in lower beds. It was common at levels in the following metre of calcareous laminated beds, together with proetids (Proetus obconicus). S. ornatella, after being consistently present in small numbers through several metres of succession, becomes abundant in the topmost flags (λ) in virtually monospecific assemblages. Neobeyrichiid ostracodes of Neobeyrichia nutans (DJS) were identified from beds i, and Bd, but no N. lauensis were found. (The former species, in Gotland, occurs at a slightly lower level than the latter). A. gravi was not recorded from this section. Monospecific bands of S. wilsoni persist up into the flags (λ) where S. ornatella has become abundant, but the rhynchonellid becomes rare over the next metre above λ.

The base of the Woodbury Shale unit of Phipps and Reeve ('67), indicated by the presence of abundant S. ornatella, may be placed at λ. The S. ornatella acme correlates with the ULB of Holland, Lawson and Walmsley ('63). The base of the latter here is difficult to define because the faunal changes of the stratotype occur over several metres of succession, and there is no facies distinction between the LLB and ULB.

Bioturbation:

The basal interbedded conglomeratic limestones and calcareous siltstones include bands in which uneven silt-filled burrow traces are common. These were most clearly seen in fine, debris-rich siltstones.

A specimen of K. squamosus was also recorded from one such bed in Ba. The top surfaces of some limestone beds (eg. Ea) were irregular, with diffuse patches of siltstone from the overlying beds being incorporated into the calcareous matrix. This mixing probably results from biogenic activity. A disturbed internal fabric can be discerned in the siltstone (see Fig 6.10).

Higher in the sequence, siltstone beds with burrow traces were noted at several levels. Bioturbated sediments are common above Wa. Some parts of laminated beds show extensive disruption of the bedding, but other bioturbated beds have only sporadic burrow traces. The graptolites in CP-Ab were found in a well-burrowed siltstone bed.

The very calcareous laminated flags at the top of the LLB have many bedding planes covered with a network of narrow (approx.1 mm) silt-filled traces (Fig 3.11 p74). Some traces are gently inclined to the bedding; however, these disturb the lamination very little. The fairly common occurrence of tentaculitids in the upper part of the succession may be significant with relevance to these burrows. In addition, pieces of C. longissimus and occasional C. serpularius specimens were recorded from several horizons, so that remains of possible burrowing organisms were relatively common. The lower part of the succession had few fossils of burrowing organisms.

Chances Pitch - Faunal distributions:

Fig: 3.12

The top strata of the Aymestry Limestone Member (UBB) have few fossils, irregularly distributed within the beds. Above the basal conglomeratic limestone Aa (taken to indicate the base of the Mocktree Shale Member), the faunal abundance and diversity rapidly increase. As the bedding becomes more regular and thinner, the fossils are typically concentrated onto planes and in bands. The faunal and facies transition at the base of the LLB takes place over the lower 2.5 m of the succession (- beds Aa-Ia). Within this thickness, the last characteristic UBB fossils disappear from the fauna.

Many shell horizons are laterally impersistent. Faunas, which generally include a high proportion of shell debris, are dominated recurrently by different species. A number of thin limestones are composed of closely-packed shells with very little interstitial cement;

CHANCES PITCH - Detailed section

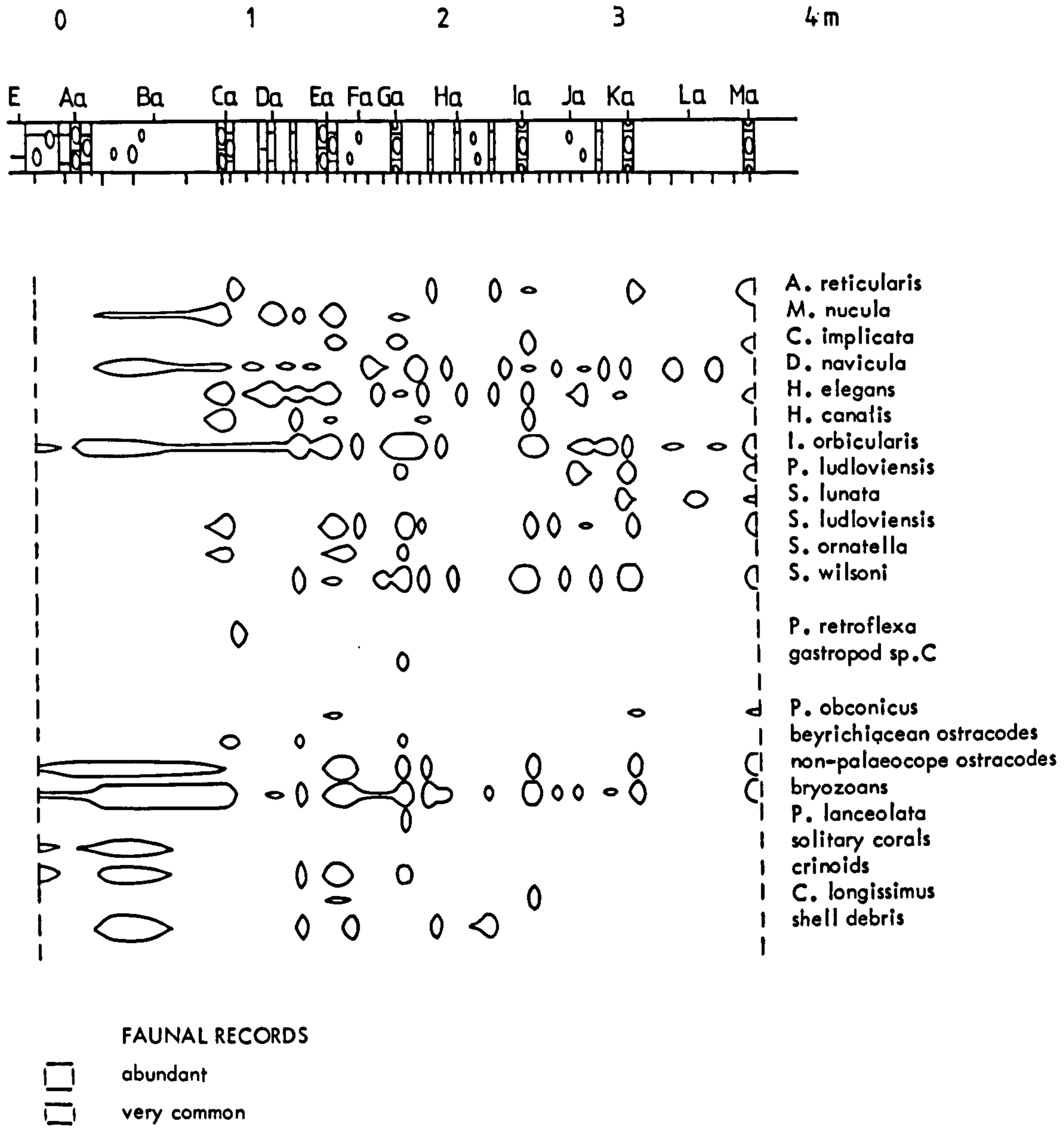


Fig. 3.12 : Chances Pitch; Detailed section Aa-Ma.

others are largely unfossiliferous. The conglomeratic limestones have more varied faunas than individual bedding-plane assemblages, and have several species all very common. Qualitatively, their faunas are similar to those of the other beds, however. The faunas of beds Aa to Ma are plotted in detail in Fig 3.12 (p 89). This diagram shows the higher number of common species of the conglomerates (eg. Ea and Ia) compared with the assemblages of other beds (eg. Ha). It illustrates the increases in abundance and species diversity that take place over the lower part of the succession. The faunas above Aa are brachiopod-dominated; below that level (beds A-E), the fauna, although sparse, is more varied, with corals and gastropods being relatively important constituents.

The distribution pattern of frequent plane-assemblages and shell bands separated by beds containing few fossils continues up to the top of the sequence. The lithology changes little, except that the proportion of laminated siltstones increases and conglomeratic limestone beds are uncommon in the upper half of the LLB. Faunally, there is a marked increase in the occurrence and diversity of bivalves, which are mostly concentrated in siltstone beds. Gastropods and trilobites become fairly common in many of the fossiliferous limestones of the higher strata. These limestones often have several species that are all very common (as in the conglomeratic limestone beds), in close-packed, debris-rich, shell accumulations. Such faunas contrast with the virtually monospecific assemblages of many other beds.

The top laminated siltstones are very calcareous, with smooth bedding plane surfaces which are sometimes gently undulating. There are numerous minor sedimentary discontinuities in the lamination. Thin, shell horizons of convex-up brachiopod valves and planes of fine shell debris occur in these beds. Well-burrowed beds are seen at some levels. Interbedded with the laminated beds are thicker-bedded siltstones, and thin limestones with monospecific faunas. There is a marked increase in faunal diversity in the topmost LLB strata. Fossils are still mainly in bedding-plane concentrations, however.

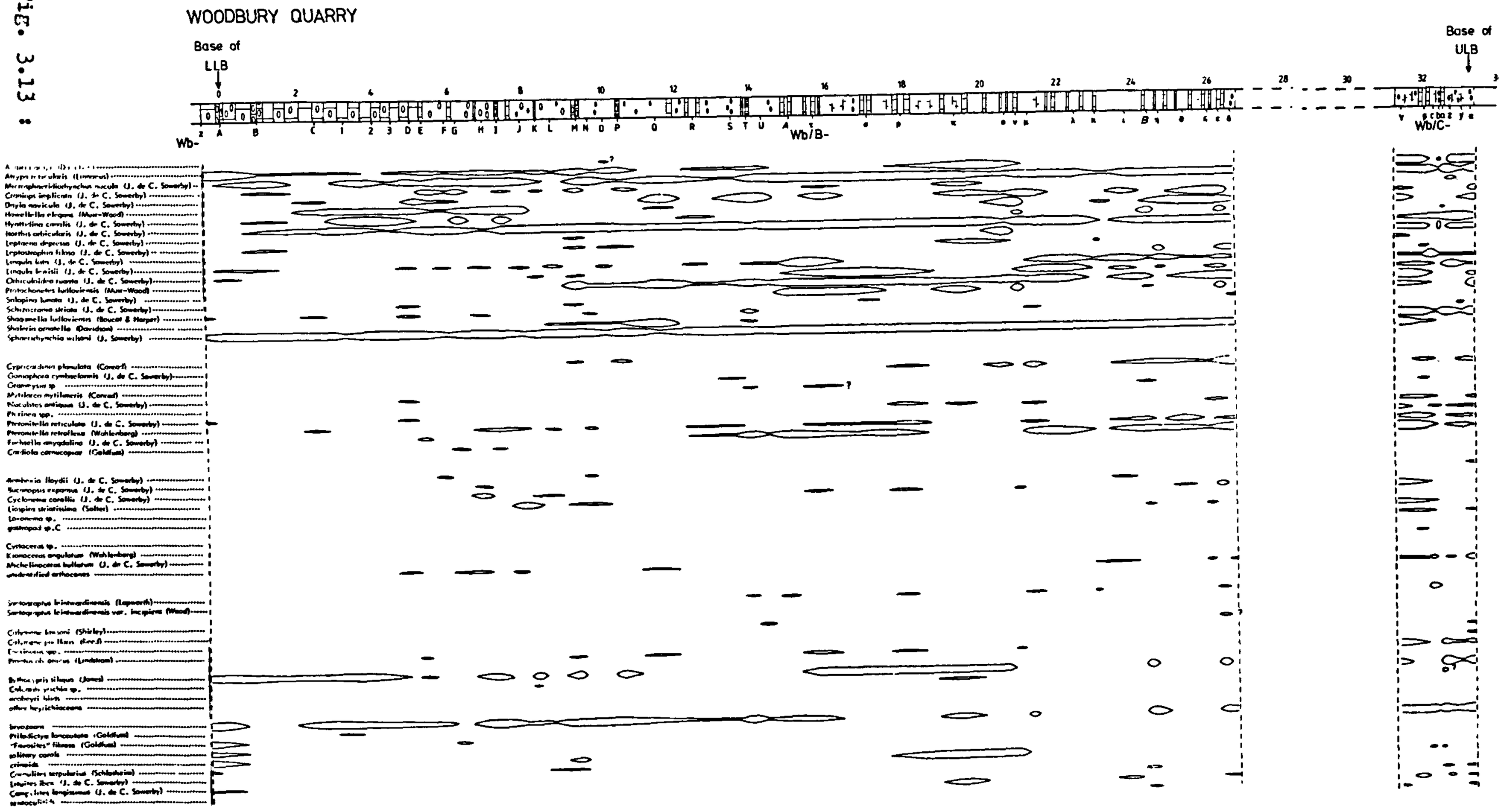
B. <u>Woodbury Quarry - LLB succession</u>:

(SO.743.637) Fig 3.13

The whole of the LLB is exposed in the quarry, and much of the succession is accessible. The LLB thickness here is 33 m. The Aymestry Limestone

Fig. 3.13 :

LLB succession at Woodbury Quarry



facies extends up into the LLB, over the basal 4-5 m of the succession. Above this, the lithology is dominantly composed of interbedded calcareous siltstones and shelly limestones.

The Aymestry Limestone facies is massive, nodular, muddy limestones with thin shaly and muddy siltstone bands. The siltstones indicate the bedding, which is otherwise poorly-defined. Nodules vary greatly in size, up to 15 cm across. They are well-rounded, ovoid to elongated, and are composed of hard, muddy limestone. Lenses and irregular bands of crystalline limestone lie within muddier calcareous facies. The silty partings are laterally impersistent. The sediment wraps around nodules, and beds often thin out between massive limestone units. These facies continue above the faunal change at the UBB-LLB junction, grading into less calcareous and thinner-bedded strata about 5 m above the boundary.

The base of the LLB was taken at Wb/A-A, a massive, muddy limestone bed with a few dark-rimmed lithoclasts of a similar limestone to the matrix. Faunally, the UBB-LLB changes are transitional over a few metres. A lower limestone bed, 2 m below A, also contains lithoclasts, but its fauna includes many UBB fossils. Therefore, the boundary here was not defined at the lowest conglomeratic bed (as it had been at Perton and Chances Pitch), but at a level where the majority of characteristic UBB fossils have disappeared.

Fossils in the top of the Aymestry Limestone occur both concentrated into thin shelly bands, and also widely-scattered through the sediments. The bottom beds, Wb/A-z, have numerous large, articulated individuals of A. reticularis at some levels, while other bands have mostly single and broken valves. "F." fibrosa has comparable distributions; there are very many mushroom-shaped specimens lying convex-surface up, on some bedding surfaces, but randomly-orientated scattered ones are found in other beds. Solitary corals are abundant, S. euglypha very common, and Gypidula lata and P. globosa both common. These fossils are usually patchily distributed. Big brachial valves of S. euglypha are sometimes enclosed within nodules. Broken shell material is common in some crystalline limestone bands in which large smooth ostracodes and crinoid columnals are abundant. Beds Wb-z include 2.25 m of strata, in which there are several thin shale units. One has a fauna of small

A. reticularis and S. wilsoni, but the others are unfossiliferous.

Bed A marks the level at which S. euglypha and G. lata disappear from the fauna, and where solitary corals and "F." fibrosa have begun to decline rapidly in numbers. A. reticularis is still abundant, and bands of small S. wilsoni and of M. nucula are quite frequent. Slightly below A is a band rich in biotite - possibly indicating a bentonitic horizon (cf. LLB stratotype and other shelf inliers at this level).

Above A, few UBB fossils (S.euglypha, P. globosa) were found. The fauna is initially dominated by rhynchonellids, occurring in almost monospecific bands. A. reticularis becomes much less common. Other brachiopod species appear and increase rapidly in abundance. H. elegans, H. canalis and I. orbicularis are prevalent in assemblages of the top part of the Aymestry Limestone facies. Fossils are mainly concentrated in bands and on planes, with few in the intervening beds.

Limestone horizons (up to 15 cm thick) which include muddy limestone lithoclasts, occur at several levels in the massive nodular Limestone sequence (eg. Wb/A-B, Wb/D-1 are both conglomeratic beds). The clasts are mostly flattened and elongated with well-rounded edges, and lie roughly parallel to the bedding (Fig 6.8 p 322). Their length ranges up to 10 cm, but is usually less. A few of the clasts are rounder in outline. The lithology of matrices and clasts is often very similar, of a fine muddy, and sometimes shelly, limestone. Other beds have crystalline shelly matrices, largely composed of fragmental shell material and bryozoans, but with levels containing a higher proportion of unbroken shells. Rhynchonellids, smooth ostracodes (and a few large Calcaribeyrichia sp. ostracodes (DJS)) and branching bryozoa are important faunal constituents of the lower conglomeratic horizons.

The proportion of siltstones increases over the top part (Wb-C and D) of the Aymestry Limestone facies, and bedding becomes thinner, although still irregular. Above D, the lithology is dominantly composed of silty and shelly limestones, nodular calcareous siltstones and fine muddy siltstones. Conglomeratic beds are fairly common over the lower 14 m of the succession, but infrequent at higher levels. The thickness of such deposits decreases upwards in the sequence (above D, conglomerates are mostly less than 8 cm). Fossils are concentrated into

bands. Many assemblages are monospecific, but the conglomeratic beds and some richly fossiliferous limestones have more varied faunas, in which several species are all abundant.

The lower half of the succession (Wb/A-A to U, Wb/C-A, Wb/B-r) is generally more calcareous and less well-bedded than the upper, where more regularly flaggy siltstones and calcareous siltstones become common. Laminated units, with calcareous and siltier layers 1-2 mm thick, are found in the upper half of the sequence. These beds have minor erosion planes and some small scale cross-bedding; they appear unfossiliferous. Irregularly-bedded siltstones and nodular beds remain common at levels throughout the succession, but massive uneven silty limestone beds diminish in frequency upwards. Thin and thicker fossiliferous limestone beds are intercalated among the other sediments. They are more common in the upper half of the LLB.

There is no lithological change at the LLB-ULB boundary, which was defined on faunal criteria. Higher in the ULB, there is a transitional change to the more thinly flaggy, calcareous siltstones typical of the overlying Whitcliffe Beds.

Throughout the succession in Woodbury Quarry, fossils are characteristically found concentrated in bands. Many of the thin plane-assemblages and close-packed, shelly limestone faunas are each dominated by only one or two species. In the basal beds (-in the Aymestry Limestone facies), faunas are brachiopod-dominated, but in the siltier beds above, the diversity and abundance of molluscs increases markedly. Bivalve assemblages intercalate with brachiopod ones throughout the upper 20 m of LLB, with F. amygdalina, P. retroflexa, and G. cymbaeformis (in the higher beds) common in bands, usually, of muddy siltstone. In the topmost LLB, the abundance and diversity of trilobites, gastropods and bivalves are fairly high. C. serpularius, C. longissimus and tentaculitids are present as minor constituents of some faunas at this level. Monospecific fossil beds are still found alternating with horizons bearing rich, varied faunas.

There is little qualitative vertical change in the brachiopod fauna through much of the LLB succession, although quantitative fluctuations are rapid and numerous, occurring from bed to bed. Rhynchonellids M. nucula and S. wilsoni, which are often articulated,

and valves of I. orbicularis remain prevalent throughout. P. ludloviensis and S. lunata (higher in the LLB) enter the fauna, and increase in abundance upwards in the succession. Near the LLB-ULB boundary there is an acme of L. depressa (- large valves, with trails) and A. reticularis; these two species are commonly irregularly scattered in nodular beds of calcareous siltstone. S. ornatella is abundant in some beds of the top 2 m of section, while S. wilsoni disappears in the upper metre.

The appearance of C. puellaris and E. stubblefieldi in the topmost bed (Wb/B-α) was taken to indicate the LLB-ULB boundary in this section. No A. gravi nor N. lauensis were found, and neither were beyrichiacean ostracodes recorded from the higher LLB strata, although smooth ostracodes occur abundantly in many faunas. The Woodbury Shale Member of Phipps and Reeve ('67), defined on an abundance of S. ornatella, here corresponds closely to the LLB-ULB boundary.

Lingulids:

L. lewisii individuals (including many large specimens over 2 cm long), were found perpendicular to the bedding - apparently in situ - at numerous levels throughout the succession. Individuals are concentrated in some bands, but also occur consistently in smaller numbers in many other beds. Most specimens are found in calcareous and muddy siltstone beds.

Bioturbation: ~~(See Figs Wb 1, 2, 3, 4)~~

Occasional irregular and diffuse burrow traces were recorded from beds of the first 2 m (Wb/A-D to H) above the Aymestry Limestone facies, together with fragments of K. squamosus. The latter species, including one specimen from Wb/B-ν which is possibly in situ perpendicular to the bedding, was found in burrowed beds at several levels through the LLB. Traces of bioturbation are common in beds through the upper half of the succession. In Wb/C-A, silt-filled traces, 2-3 mm wide, were seen descending steeply into a limestone-bed from the overlying siltstone. In the laminated calcareous siltstones of Wb/B-ε and μ, silt-filled traces showed up clearly; these were mainly concentrated on planes. The intensity of traces increases on some planes of the topmost flags of the section.

Only in the top beds of the sequence are fossils of possible burrowing organisms, such as tentaculitids and C. longissimus, fairly

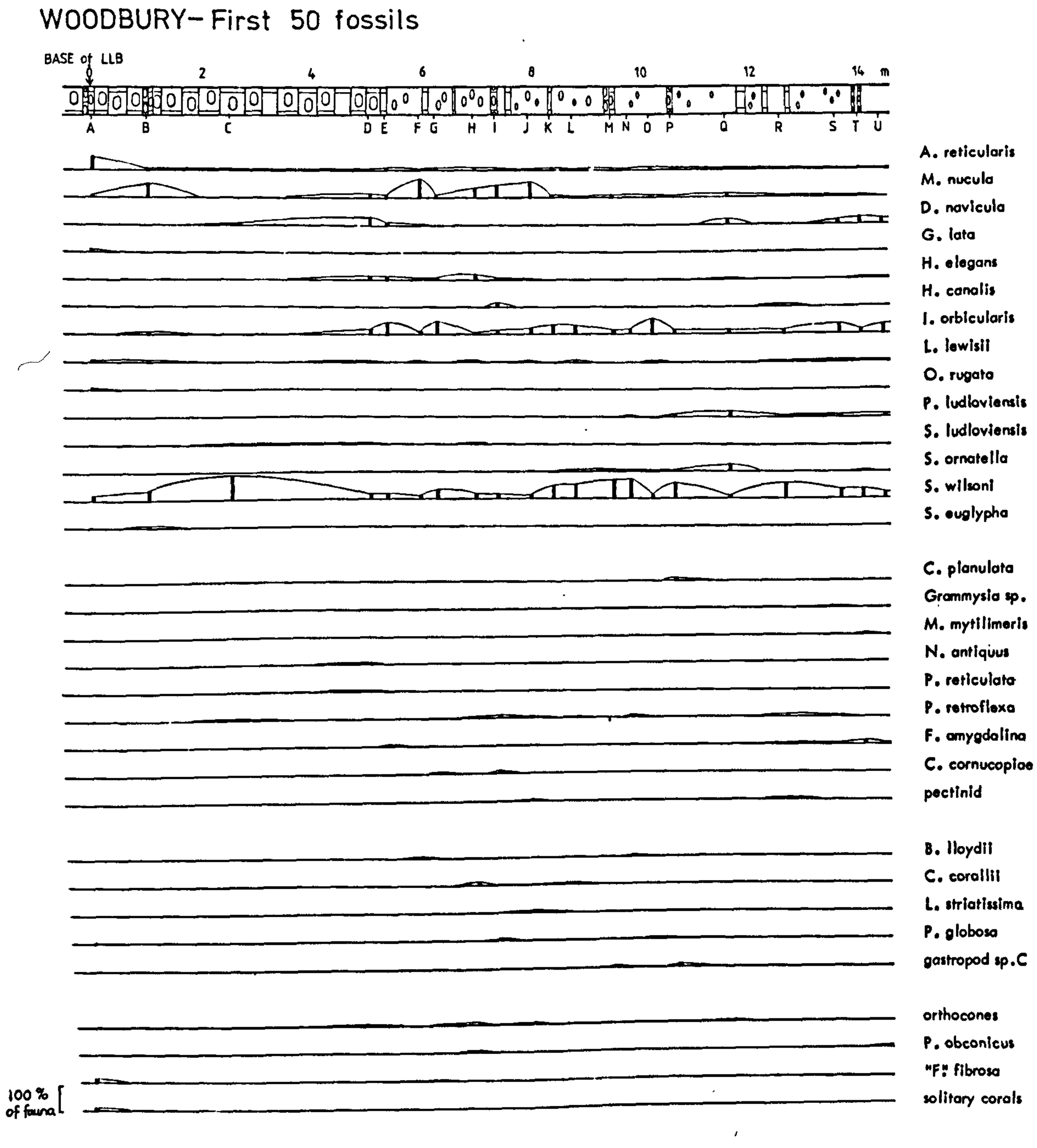


Fig. 3.14 : LLB succession at Woodbury Quarry - first 50 fossils counted.

common - below this, fossils of animals that might have produced the burrow traces are rare. Of the bivalves, F. amygdalina may have been a shallow-burrowing type (see p 257).

Faunal records:

From collections of Wb/A-A to U, the first 50 macro-fossils (excluding bryozoa) counted in each were recorded separately; These results are plotted as species percentages of these faunas, in Fig 3.14 p96 . The diagram illustrates well the rapid changes in quantitative composition of faunas from band to band; it also indicates the dominance of brachiopod species in these lower beds. However, some of these faunas are less diverse than those recorded using the standard collection method employed in this study (Fig 3.13 p91). This suggests that a sample size of 50 fossils was not large enough to be as adequately representative of the fauna as the normal collections.

Various collection techniques are discussed in Chapter 6 p380.

MAY HILL:

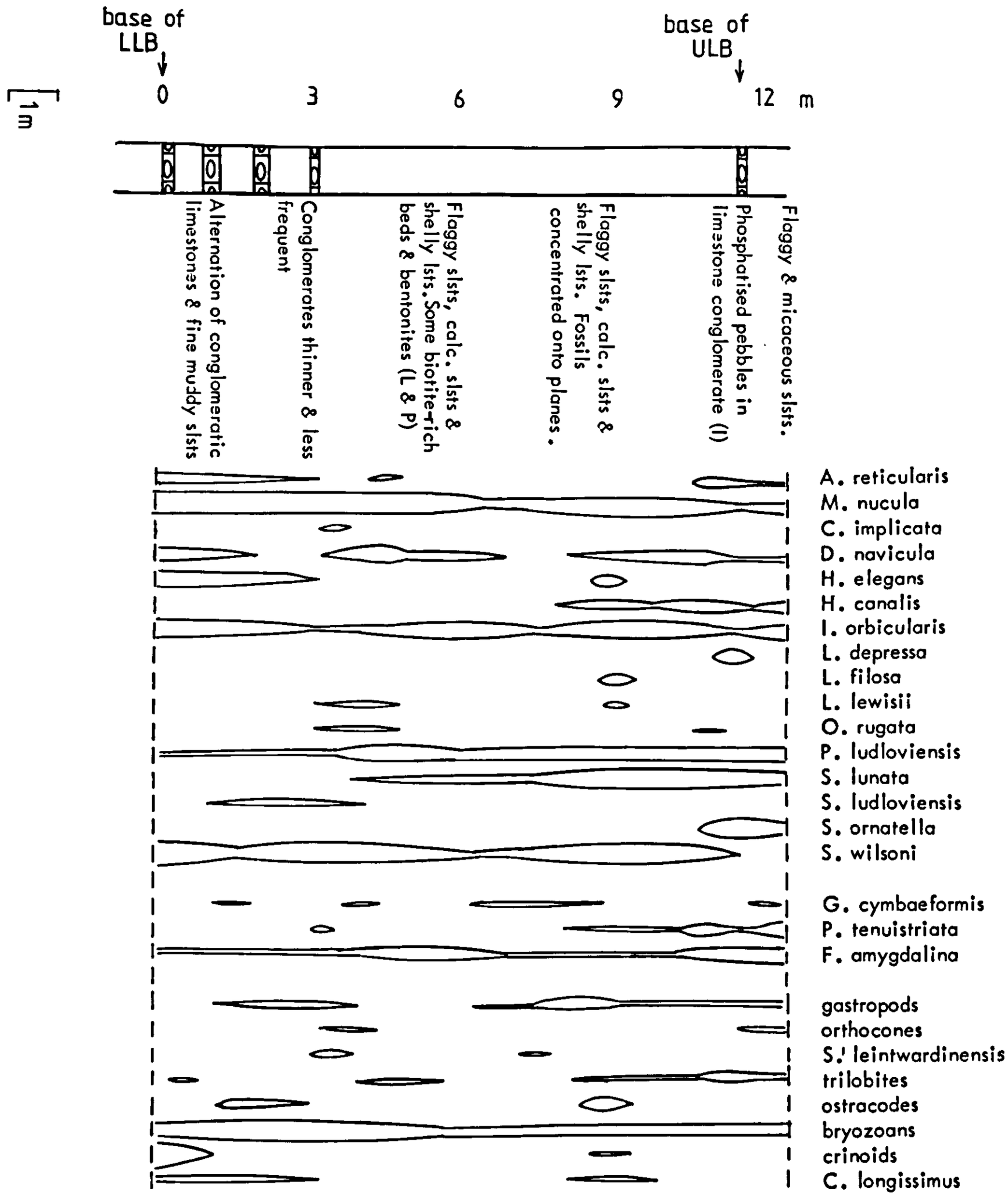


Fig. 3.15 : Summary of succession, May Hill.

PERTON :

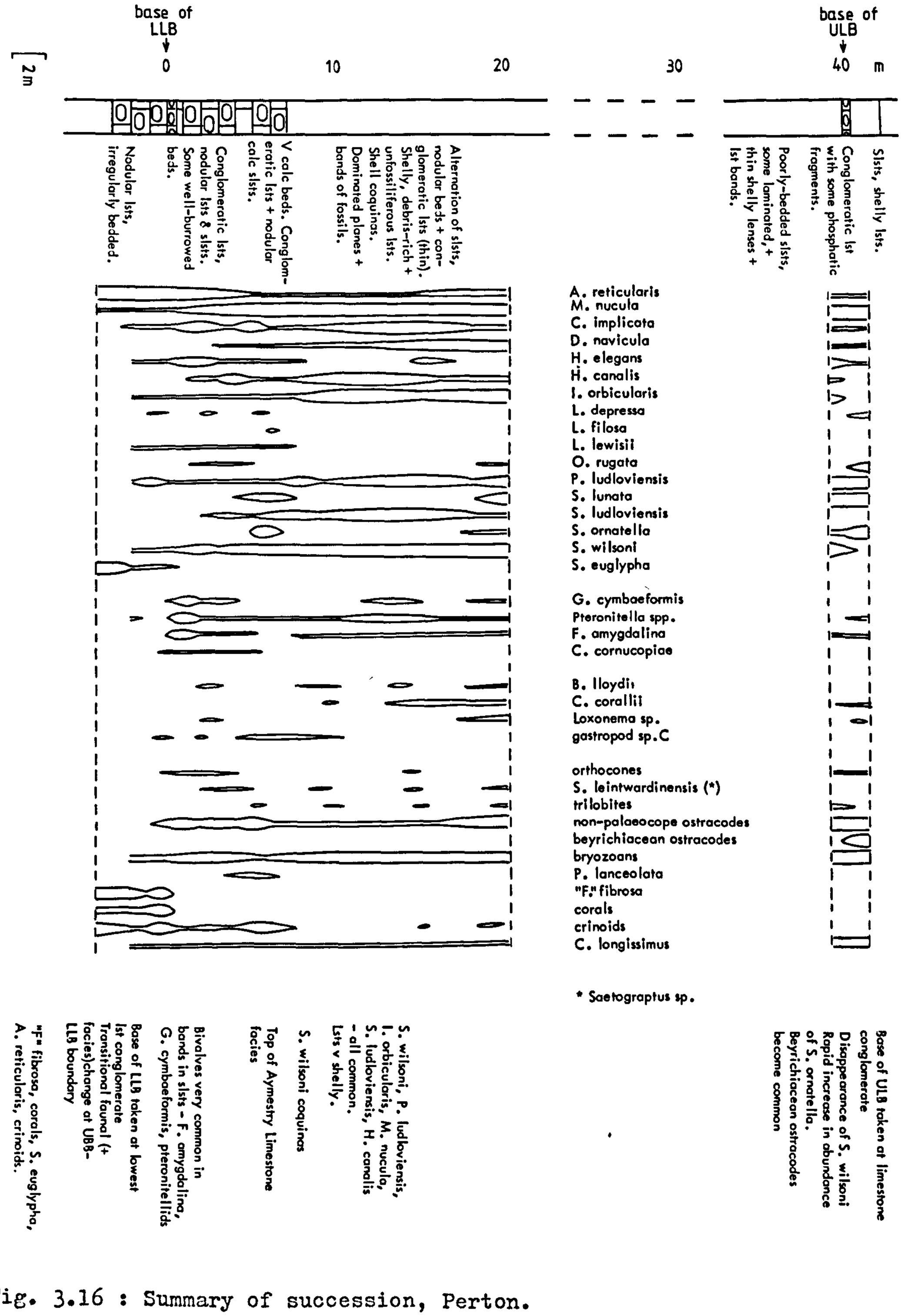


Fig. 3.16 : Summary of succession, Perton.

CHANCES PITCH:

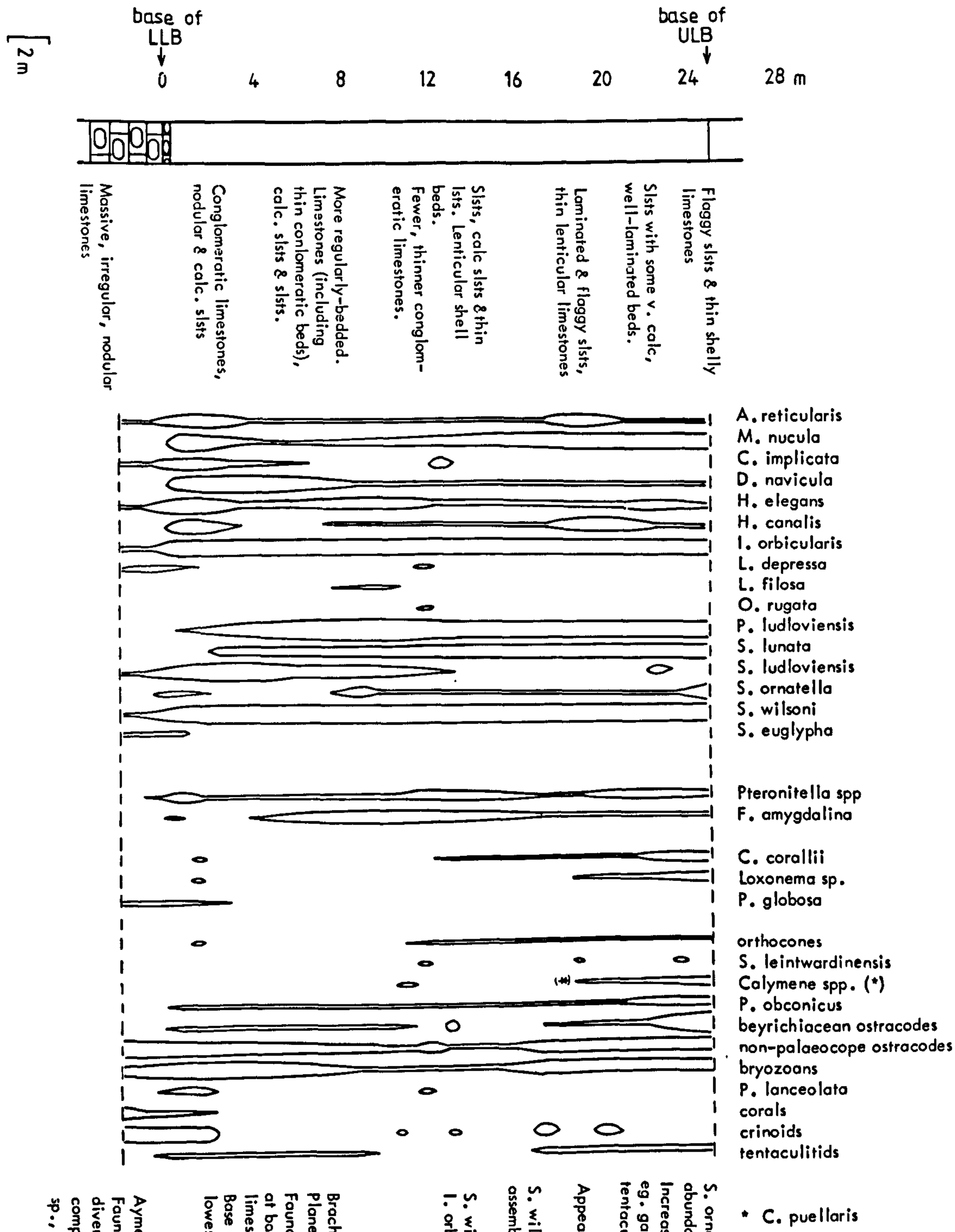
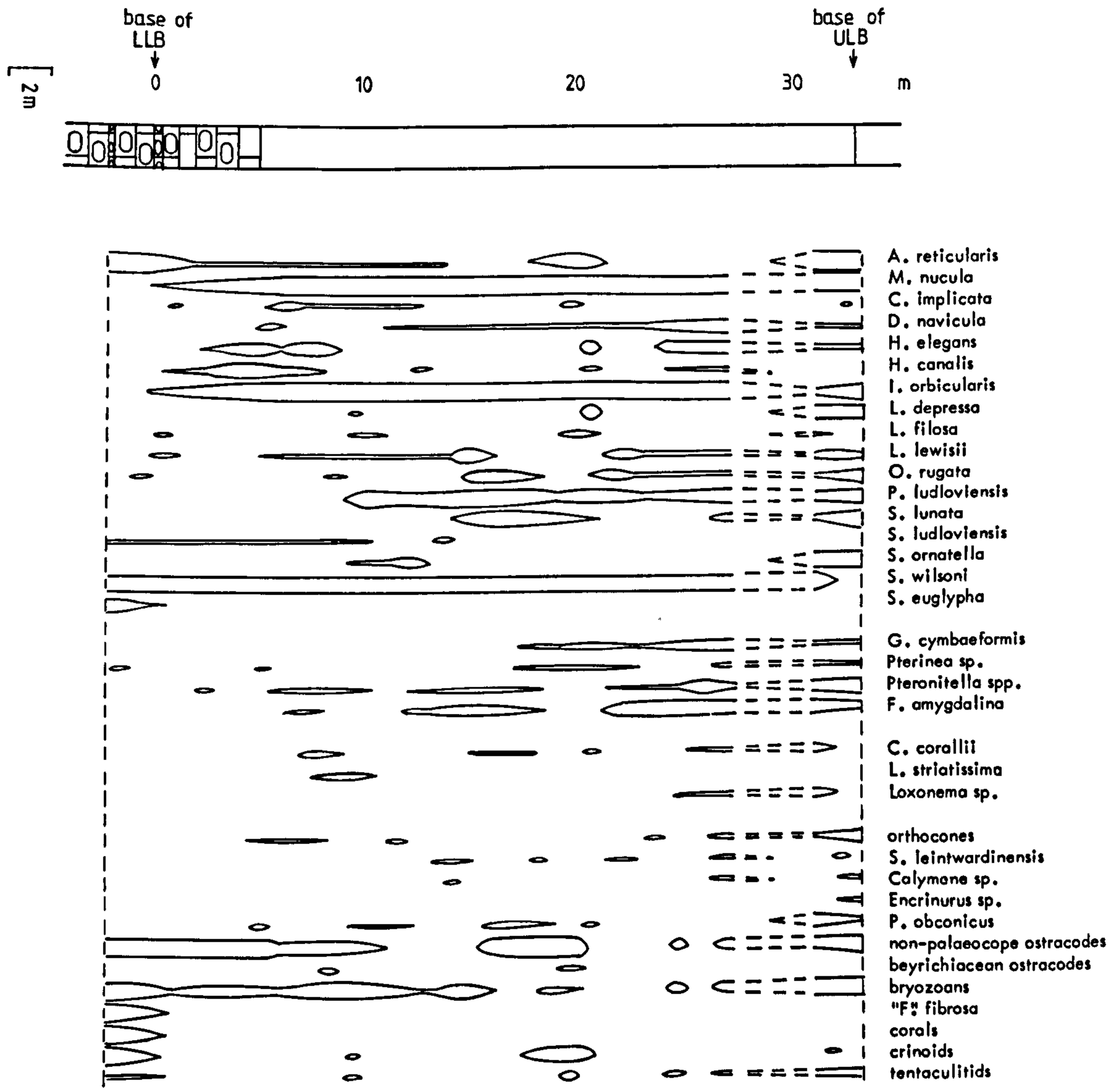


Fig. 3.17 : Summary of succession, Chances Pitch.

WOODBURY:



Appearance of E. stubblefieldi
S. ornatella becomes abundant
Disappearance of S. wilsoni
A.reticularis - L. depressa acme

Increase in faunal diversity. Trilobites, gastropods, bivalves, tentaculitids, cornulitids become more common

S. wilsoni, M. nucula abundant. Bivalve-rich assembloges - F. amygdalina very common

L. lewisii , perpendicular to the bedding, common

S. wilsoni, M. nucula, I. orbicularis & P. ludloviensis - all abundant

Increased diversity of molluscs

Aymestry Limestone facies
Brachiopod-dominated faunas

Base of LLB - disappearance of UBB fossils eg. S. euglypha, corals, P. globosa, "F" fibrosa. Boundary not taken at lowest limestone conglomerate because fauna is clearly UBB.

Fig. 3.18 : Summary of succession, Woodbury.

CHAPTER FOUR

THE LLB STRATIGRAPHY IN AREAS WEST OF LUDLOW

The succession was studied in detail in the shelf edge regions of Leintwardine and Aymestrey, where the fauna and facies are intermediate between those of the shelf and the basin. A stratigraphical break in the LLB succession at Aymestrey is interpreted to indicate the site of a former submarine channel, comparable with those described at Leintwardine by Whitaker ('62).

The leintwardinensis beds of normal and slumped sequences in the Kerry district were examined. The fauna here is sparse and dominantly graptolitic. In order to aid correlation of the shelly and graptolitic faunas, a brief survey of the succession in the Brecon Anticlinal region was made. Additional localities from the Knighton area (Cwm Jenkin) and Llandovery (Clawdd British) were visited to examine small parts of the LLB.

Syntheses of the succession in the Leintwardine and Aymestrey, Kerry and Brecon areas are given at the end of these sections.

A. LEINTWARDINE:

The Ludlow rocks of the Leintwardine area were mapped and described by Whitaker ('62). The LLB here range from 30 - 67 m thick compared with 27 m at Ludlow, while the ULB attain a thickness of 0.3-6 m, similar to the 1.5-7.5 m recorded at Ludlow. The LLB were subdivided by Whitaker ('62 - p 326) into basal (bLLB) and higher (hLLB) units, which were often separated by an unconformity. He described six ENE-WSW trending submarine channels, which deepened from the shelf area towards the basin. In each, the hLLB rested unconformably upon older rocks, with the break becoming more pronounced towards the WSW.

Parts of the LLB succession were studied at localities shown on the map - Fig 4.1 p103. Several sections included the junction with the underlying UBB, and others the LLB-ULB boundary. The localities were selected to give a fairly complete coverage of the succession in this area.

LLB OF LEINTWARDINE

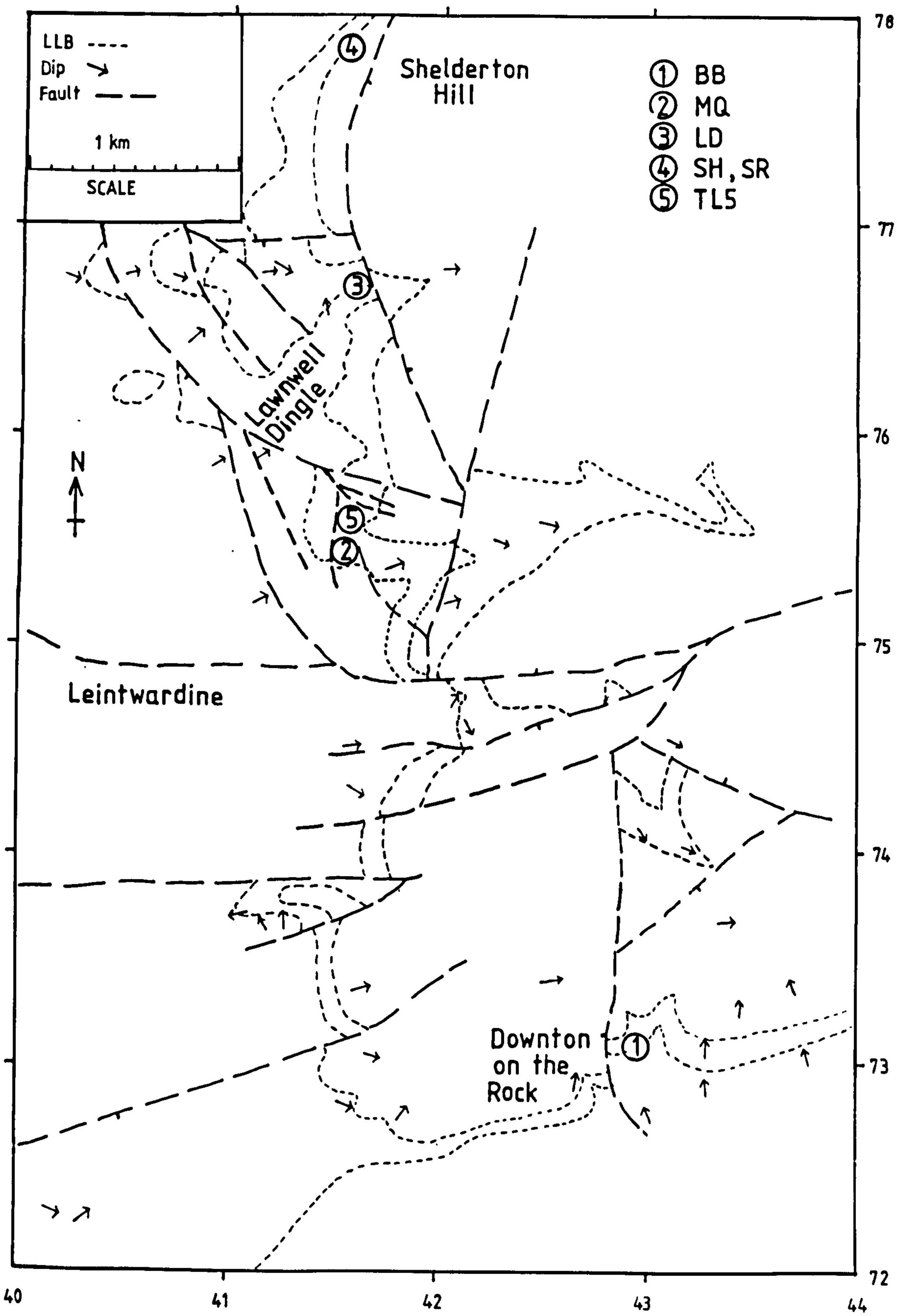


Fig. 4.1: Map of the LLB of Leintwardine showing the sections studied. (Map taken from Whitaker '62).

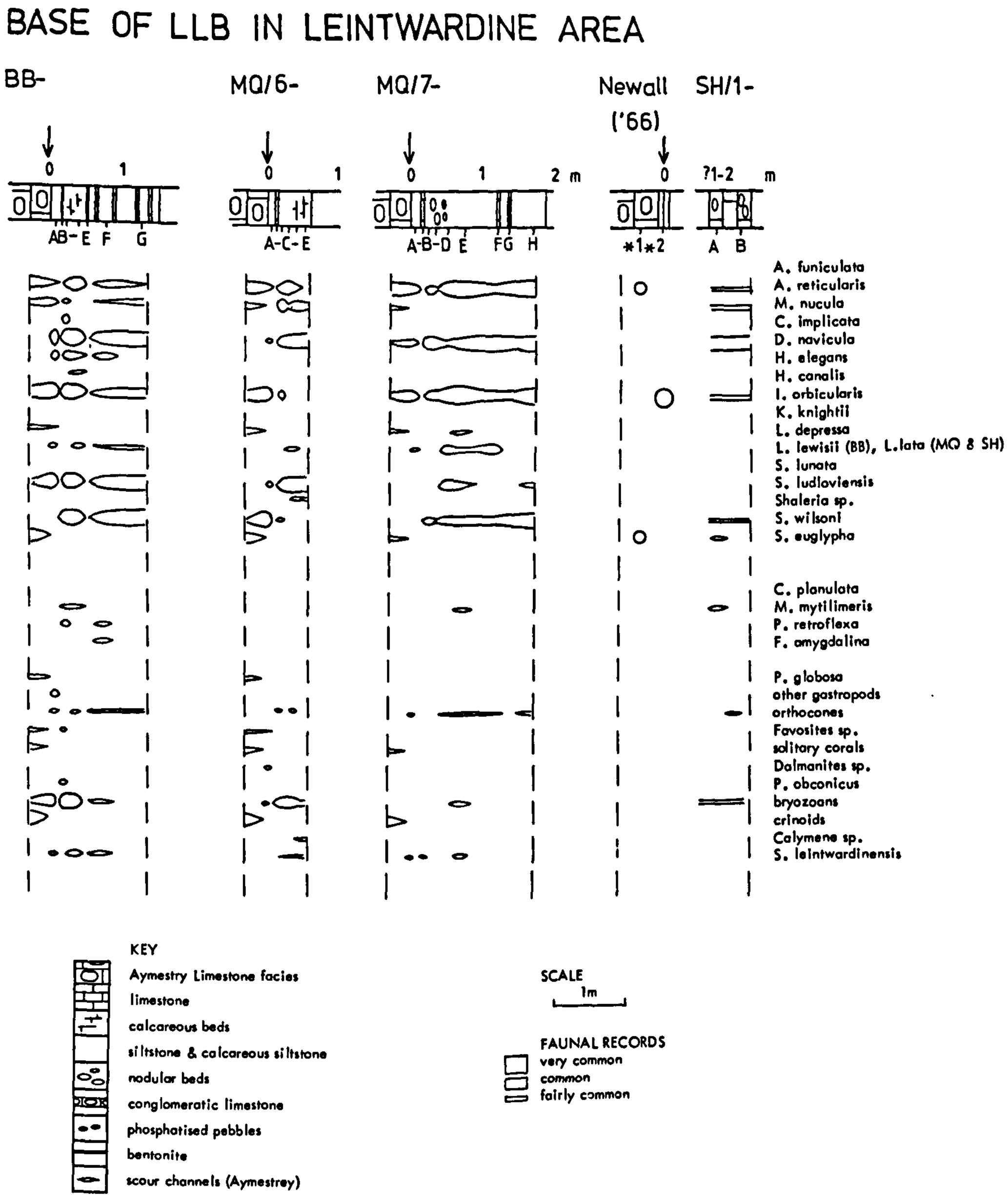


Fig.4.2 : The base of the LLB in the Leintwardine area.
(Faunal list as in Fig. 2.9 for Ludlow for comparison).

1. The base of the LLB:	a. Bow Bridge	SO.430.732)	
	b. Mocktree Quarries	SO.417.754)	Fig 4.2 p104
	c. Shelderton	SO.416.778)	
	d. Lawnwell Dingle	SO.416.768	Fig 4.3 p110

a. Bow Bridge (BB-)

The locality lies approximately 4 km west of the Bringewood Chase section MF/C-. A small quarry face, directly west of Bow Bridge, exposed the UBB-LLB boundary. Here, thinly flaggy, shaly and calcareous siltstones rest with sharp contact on massive nodular limestones. The faunal change corresponds to the lithological one, so that the base of the LLB was taken at the bottom siltstone bed of BB-A.

The uppermost rubbly limestone strata of the Aymestry Limestone facies contain irregularly scattered fossils, with large valves of S. euglypha and A. reticularis, I. orbicularis, crinoid columnals and solitary corals all fairly common. A small inverted colony of Favosites was found too in these beds which have a fauna typical of the top UBB. The overlying, thinly but irregularly-bedded, calcareous siltstones of BB-A are, in contrast, richly fossiliferous, but without characteristic UBB forms. They lie directly upon the uneven top surface of the Limestone. Fossils and shell debris are concentrated in some bands as well as commonly distributed throughout other beds. In these basal flags, D. navicula is often prevalent in closely-packed accumulations of shells; there were a few articulated specimens but most assemblages were of single pedicle valves. The calcareous matrices of these bands were probably secondarily derived from the shells. I. orbicularis (disarticulated valves) is also abundant, occurring almost monospecifically on some planes.

Two thin units of reddish-brown shaly clay (BB-B, and BB-E) are present in the bottom half-metre of LLB. Samples elutriated in water, so that these are probably bentonites (Marsh '75). Their position in the succession compares closely with that of the bentonite (SY/A-g) at the stratotype.

Above the lower clay horizon is 10 cm of thinly flaggy, highly fossiliferous, fine muddy siltstones (BB-C). The fauna is similar to BB-A, but I. orbicularis is particularly abundant in closely-packed layers. S. ludloviensis and S. wilsoni are very numerous at some levels. A broken piece of a Favosites colony was found in one shelly band.

The following beds (BB-D) are more evenly-bedded and less fossiliferous, with the fauna restricted to discrete shell horizons. Some of the intervening siltstones are laminated, with alternating calcareous and siltier layers. A number of small calcareous lenses around which the laminae curve and which are associated with minor cross-bedding in some units, are intercalated within these beds. Fossils are uncommon except in the shell bands, where S. wilsoni, A. reticularis (some articulated specimens) and D. navicula are the dominant species.

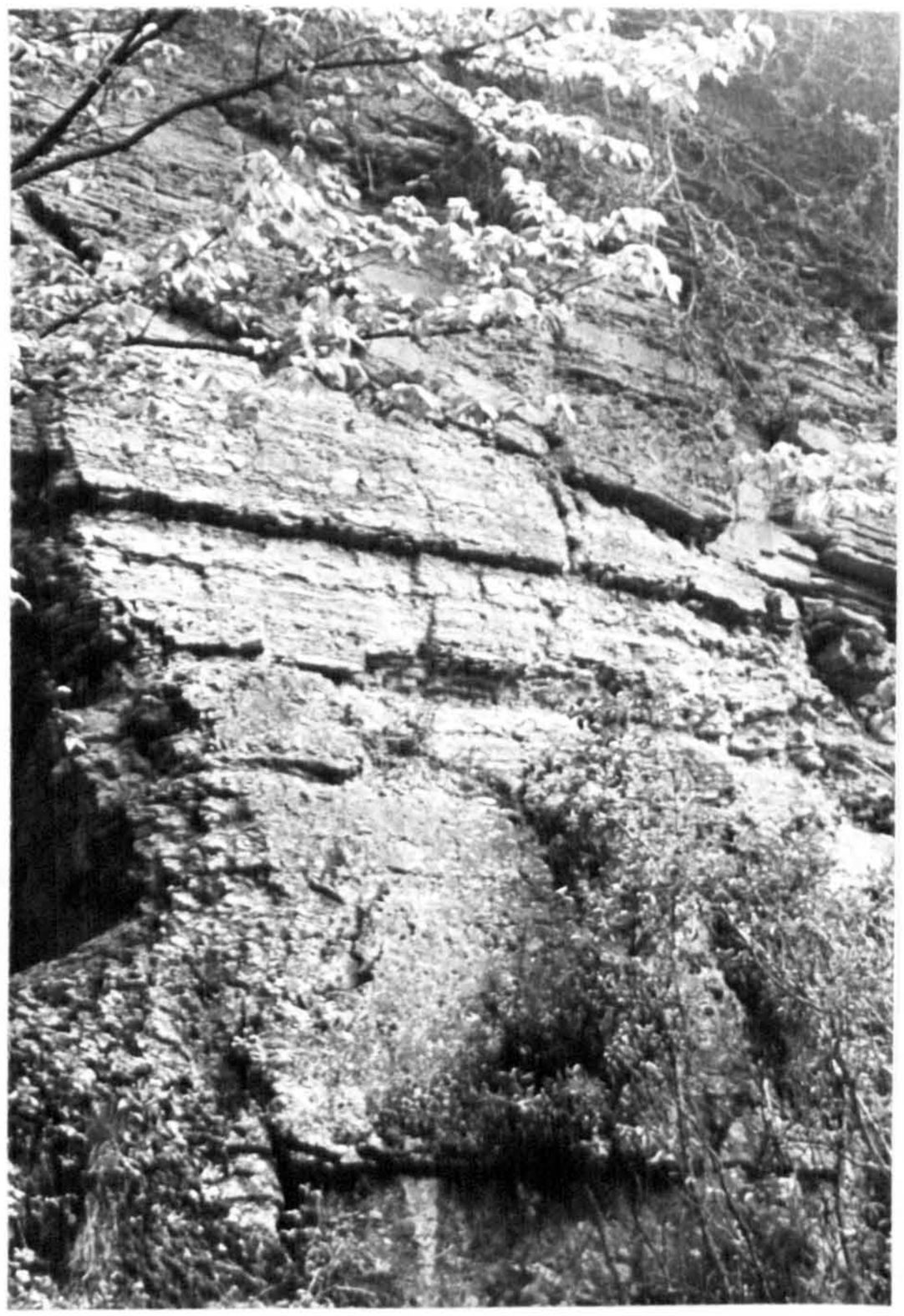
The metre of beds above the second clay horizon (BB-F and G) are regularly-bedded, thin siltstones and calcareous siltstones, interbedded with thicker limestone bands. Many beds are laminated; these are also unfossiliferous. The fauna is concentrated onto planes in the thicker-bedded siltstones. The limestones are massive and contain few fossils; articulated S. wilsoni and D. navicula occur sporadically in these beds.

Graptolites from bed F were identified as S. leintwardinensis (RBR). Drifted single valves of L. lewisii were present on several shell planes and, in addition, specimens perpendicular to the bedding, possibly in situ, were found in beds A and D. Lingulid valves similar to Lingula cornea (LC) occur rarely. Diffuse traces of bioturbation were seen in some beds of the basal 1.5 m of the LLB.

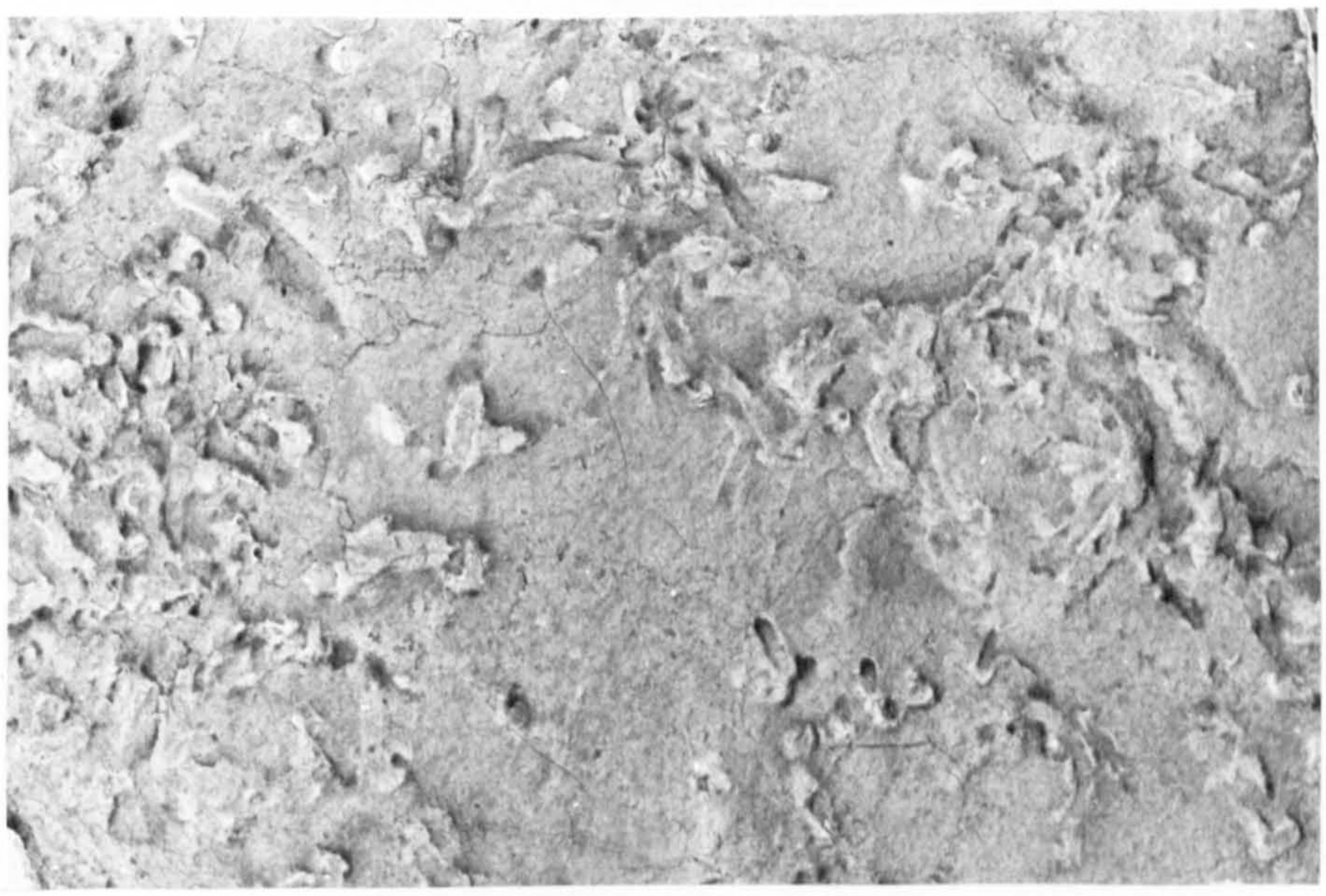
b. Mocktree Quarries (MQ/6-, MQ/7-) Fig. 4.4-a, p107

The two sequences were taken from the quarry face below the shallow channel section (-originally figured and described by Lightbody - 1863). MQ/6- is situated where the channel cuts down most deeply, when only 60 cm of bLLB are present. MQ/7- is 6-7 m away laterally, and here 4.3 m of bLLB lie beneath the hLLB of the channel.

The upper beds of the Aymestry Limestone, which are massive, irregular, nodular limestones, have an UBB fauna. S. euglypha valves, A. reticularis, L. depressa, M. nucula, crinoid columnals (including pentacrinoidal ones), Poleumita spp., and corals, both solitary and compound (Favosites) forms, are among the more common fossils. The fauna is distributed sporadically through the strata, and is not numerically very common. The uneven top surface of the limestone appears to be due to the nodular nature of the beds; it is similar to that at Bow Bridge, with no evidence of erosion.



a - Channel section : hLLB cutting through bLLB.



b - MQ/7- : Burrows on plane, basal LLB. (x 2·5)

Fig. 4·4 - Mocktree Quarries.

The overlying, thinly flaggy dark siltstones rest with sharp contact on the Limestone. The lower 10-15 cm are irregularly-bedded, shaly, calcareous and nodular bands, with a fauna dominated by disarticulated valves of I. orbicularis occurring almost monospecifically. A small broken compound coral was found in the basal layers of MQ/6-A. Broken shells and fine debris are very common in the closely-packed assemblages.

A massively-bedded, unfossiliferous limestone bed (5 cm thick: MQ/6-b and MQ/7-B) overlies the basal flags. It is followed by siltstones, some of which have a fine lamination of calcareous, silty and micaceous layers. Small calcareous lenses, around which the laminae can be seen to curve, are common. Bedding plane surfaces are smooth, and often gently undulating. Fossils are uncommon in the laminated beds except for occasional planes of scattered valves together with much shell debris. Fine siltstones, beds with elongated flattened limestone nodules, and thin unfossiliferous limestones are interbedded with the laminated strata. Fossils are mostly concentrated in thin horizons in the siltstones. Assemblages are dominated by different species; S. wilsoni, M. nucula, I. orbicularis, D. navicula, S. ludloviensis and A. reticularis are all very common in some bands.

Graptolite fragments and some S. leintwardinensis (LC), were found occasionally in these basal beds. Lingulids, here represented by L. lata, are fairly common, mostly as single, drifted valves, but including a few articulated specimens apparently in position of growth within the sediment. MQ/7-C included a plane with numerous narrow burrow traces - Fig 4.4 p107. No other distinct evidence of bioturbation was found, although many flags have small diffuse patches of fine muddy siltstone within coarser or more calcareous facies, probably resulting from biogenic reworking.

c. Shelderton

The succession of the Aymestry Limestone and overlying beds at Shelderton was described by Newall ('66). He noted that the top massive, nodular beds of the Limestone had an UBB fauna, of which S. euglypha and A. reticularis were common elements. Directly above was a 15 cm band of siltstone containing abundant I. orbicularis. This was overlain by flaggy calcareous and nodular siltstones, which became less calcareous upwards in the next 5 m of the section. These

beds were very fossiliferous, and particularly rich in D. navicula.

Shelderton (SH/1-)

Some basal LLB were exposed in a small quarry on the south side of the Clungunford-Onibury road above the main quarry. The junction with the Aymestry Limestone was not accessible (but was not very much (?1-2 m) below the rocks examined). The rocks are a series of irregularly-bedded, flaggy, calcareous siltstones and limestones, with dense accumulations of D. navicula.

Shells are commonly distributed throughout beds in the siltstones, as well as being concentrated onto planes and in bands. Assemblages of D. navicula are virtually monospecific, with only a few rhynchonellids (S. wilsoni and M. nucula), I. orbicularis, occasional valves of Mytilarca mytilimeris, and pieces of bryozoans. The majority of Dayia shells are disarticulated pedicle valves, although some articulated individuals are present. More bands of shells are dominantly convex-surface up, but assemblages of irregularly-orientated, and concave-up shells are quite common. The amount of fragmental material, and proportion of broken and chipped shells varies considerably; both are generally high.

In the limestones, which include impersistent lenses and more continuous beds, shells are again abundant. Their orientations are often highly variable and some, though not all, of the carbonate horizons include many articulated shells. The lateral gradations of limestone and siltstone in several densely shelly beds indicates the secondary origin of much of the carbonate matrix in these layers. Other limestones, however, particularly those with less closely-packed fossils, may represent primary deposits.

d. Lawnwell Dingle (LD-)

Fig 4.3 p110

This section covered approximately 7 m of the bLLB. The boundary with the UBB was not exposed but was probably not far below the section (?1-2 m). The sequence includes Dayia-rich strata such as those seen at Shelderton (SH/1-). The rocks are a series of fairly thinly-bedded, calcareous and nodular siltstones, and limestones. They are highly fossiliferous.

LAWNWELL DINGLE

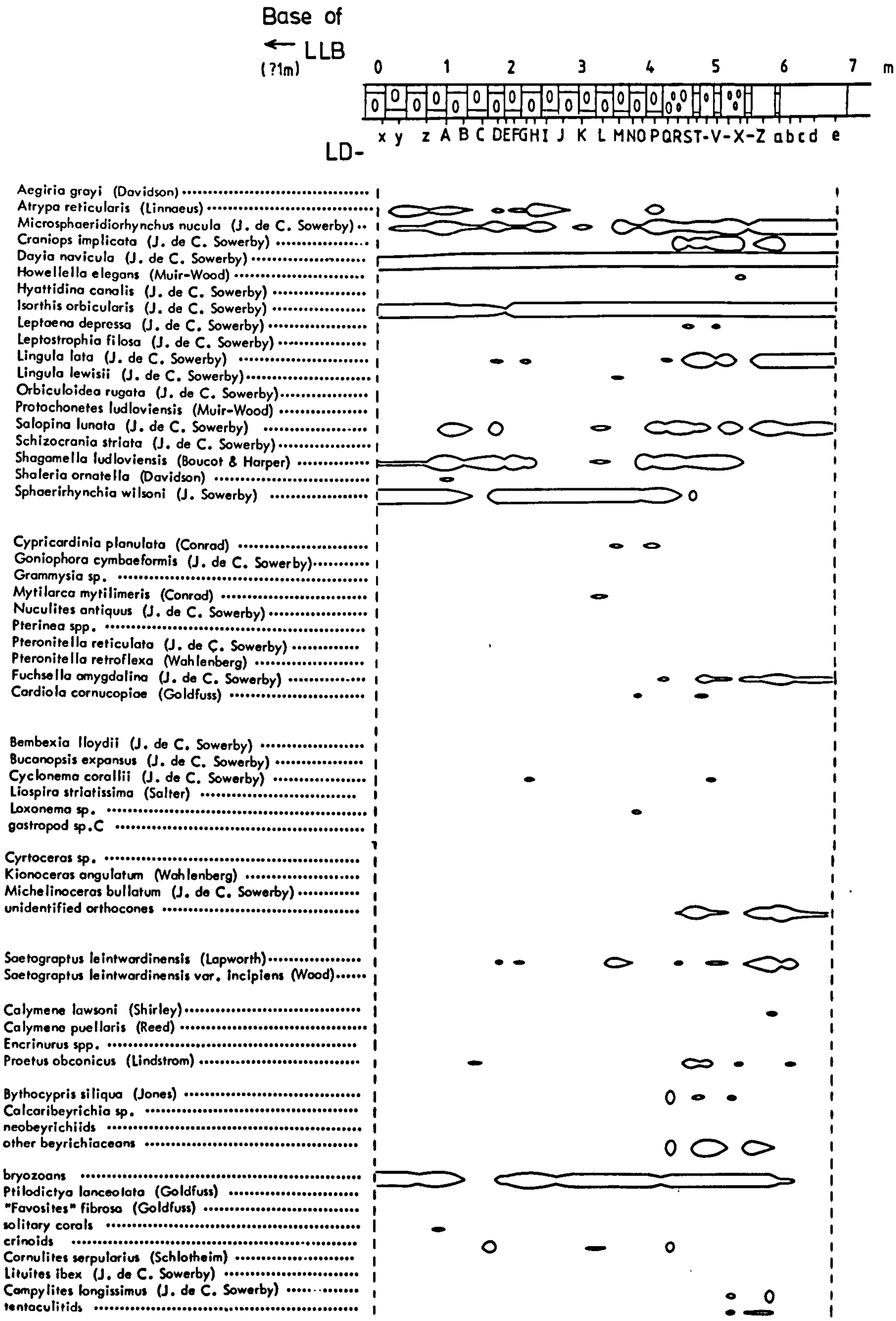


Fig. 4.3 : LLB succession at Lawnwell Dingle.

In the lower 4.2 m of the sequence (x-P), many beds include numerous small, elongated limestone nodules, which weather out to give a honeycombed appearance to the rocks. The facies of the lower 2 m (x-E) are dominantly more calcareous than the higher strata, consisting of irregularly-bedded limestones and very calcareous nodular siltstones. The limestones include both richly shelly and unfossiliferous bands, and although some are laterally extensive, other beds thin and die out over short distances. Many lenses of limestone are only 1 to 2 m wide, with a maximum thickness of up to 3 cm, other, more consistent, limestone beds are up to 10 cm thick. The siltstones vary in carbonate content from thin, fine muddy bands to thicker and highly calcareous flags; the former, being less resistant, weather back in hollows on the quarry face. Beds F-P, include a greater proportion of less calcareous siltstones. The beds are still irregular, but generally more thinly flaggy.

At the top of P, some shaly and fine siltstones have been eroded back to leave a prominent hollow groove. Above this, nodular horizons are much less common among the interbedded calcareous siltstones and limestones, and the bedding is more regular. Some of the siltstones are finely laminated, with small, thin calcareous lenses around which the laminae curve. Many of the higher siltstones are very thinly flaggy, but the lower ones are mainly thicker-bedded. Limestones are infrequent in the top metre (LD-a to e) of section, but common below; they include massive shelly beds and thinner impersistent lenses.

The faunas may be conveniently divided into two groups: those of beds x-K, and those of higher beds. The former group comprises beds in which D. navicula is consistently the prevalent fossil, while the latter includes strata where other species dominate some assemblages.

The faunas of the lower 3.15 m (i.e. x-K) of the sequence are composed almost entirely of brachiopods and bryozoa. Shells are concentrated, often very closely-packed, in bands, but also more evenly distributed through many beds. D. navicula is extremely abundant; other species are occasionally dominant in thin bands, but more usually occur with D. navicula in assemblages. A. reticularis, I. orbicularis, S. ludloviensis and S. wilsoni are the most common associated forms. Some assemblages of S. wilsoni are of a large flat variety.

The orientation, and degrees of disarticulation and breakage, of shells changes considerably from band to band. Rhynchonellids are commonly articulated. Some limestones have many complete individuals of A. reticularis (e.g. LD-H), and the majority of I. orbicularis are articulated in a few bands. However, usually these species, and typically S. ludloviensis, occur as separate valves. D. navicula assemblages are very variable, with faunas of mostly complete individuals closely interbanded with disarticulated accumulations. Shell orientations of populations range from random to fairly uniform. Populations are heterogeneous, and lateral changes along beds of D. navicula are as considerable as vertical ones (see Dayia ecology section p337). Among the disarticulated assemblages, there is a general shortage of the smaller, brachial valves.

Although the boundary of the UBB-LLB at the top of the Aymestry Limestone is not exposed, it is probably not far below: a specimen of a stunted, flat Favosites colony was found in LD-A, and occasional valves of S. euglypha and G. lata occur in the bottom metre of beds. Bryozoans of the lower beds are branching forms, but small nodular colonies, with concentric growth structures, also become common in beds F to K.

Above K, D. navicula, although still abundant in very many beds, is much less common in others where different species become prevalent. (The species remains abundant in all the collections so that Fig 4.5 does not show this change). The metre of rocks from K to P (ie. to the top of the dominantly nodular lithologies) covers this overall relative decrease in the abundance of D. navicula. It precedes a transition from the faunas with few species of the lower, "Dayia" beds to the more diverse faunas of higher beds. I. orbicularis, S. wilsoni and M. nucula are abundant in a number of the assemblages, but A. reticularis declines in occurrence. Bivalves begin to appear at this level.

The rocks following P show several qualitative and quantitative faunal changes. C. implicata, L. lata, S. lunata and M. nucula (and S. ludloviensis again) are all abundant, but S. wilsoni declines rapidly above R. F. amygdalina, orthocones, beyrichiacean and smooth ostracodes, graptolites, trilobites (mostly proetids), and tentaculitids are all constituents of the much more diverse fauna. D. navicula, I. orbicularis and bryozoa remain abundant throughout the section.

Up to W, fossils are very closely-packed throughout the majority of beds, with some stratification of different species-dominated bands, and large quantities of associated shell debris. The laminated beds, however, and many of the higher beds, have fossils restricted to discrete horizons. The density of shells in the upper beds is therefore less, although the assemblages themselves are still very fossiliferous. With the transition in distribution pattern of the faunas, shell populations of D. navicula are more commonly orientated with the pedicle valves convex-up: the assemblages are more uniform than is typical of the lower beds.

Some shell-bands are largely monospecific, others have a wider fauna. I. orbicularis, D. navicula and M. nucula are found together on many planes, in varying proportions; many of the shells are large and articulated. Thick, branching bryozoa are very common in some beds. Between shell horizons, L. lata specimens apparently in situ were frequently found, as well as planes and patches of single valves. Orthocones and graptolite fragments are also occasionally obliquely through the bedding, other times lying on bedding surfaces. In the flags with thin fossiliferous horizons, relatively few shells lie in the intervening sediments, but those present are the same species as are common in plane assemblages.

Bioturbation:

Distinct burrow traces were not noted from these beds, and the well-laminated beds show no evidence of bioturbation. However, a "mottled" texture seen in a few of the less fossiliferous, unlaminated siltstones may indicate that extensive bioturbation has affected some bands.

2. The top of the LLB and the LLB-ULB boundary

a. Shelderton Road Section: (SR-, SR/1-, SR/2-)

Fig 4.5 p113

The section, on the N. side of the Clunguhford-Onibury road, comprised the top 7.75 m of the LLB, and included the faunal transition at the LLB-ULB boundary.

The lowest metre of beds (SR/2-A and B) are very thinly-flaggy, dark calcareous siltstones, laminated in parts (with alternating more calcareous and silty layers). The shelly fauna is distributed on

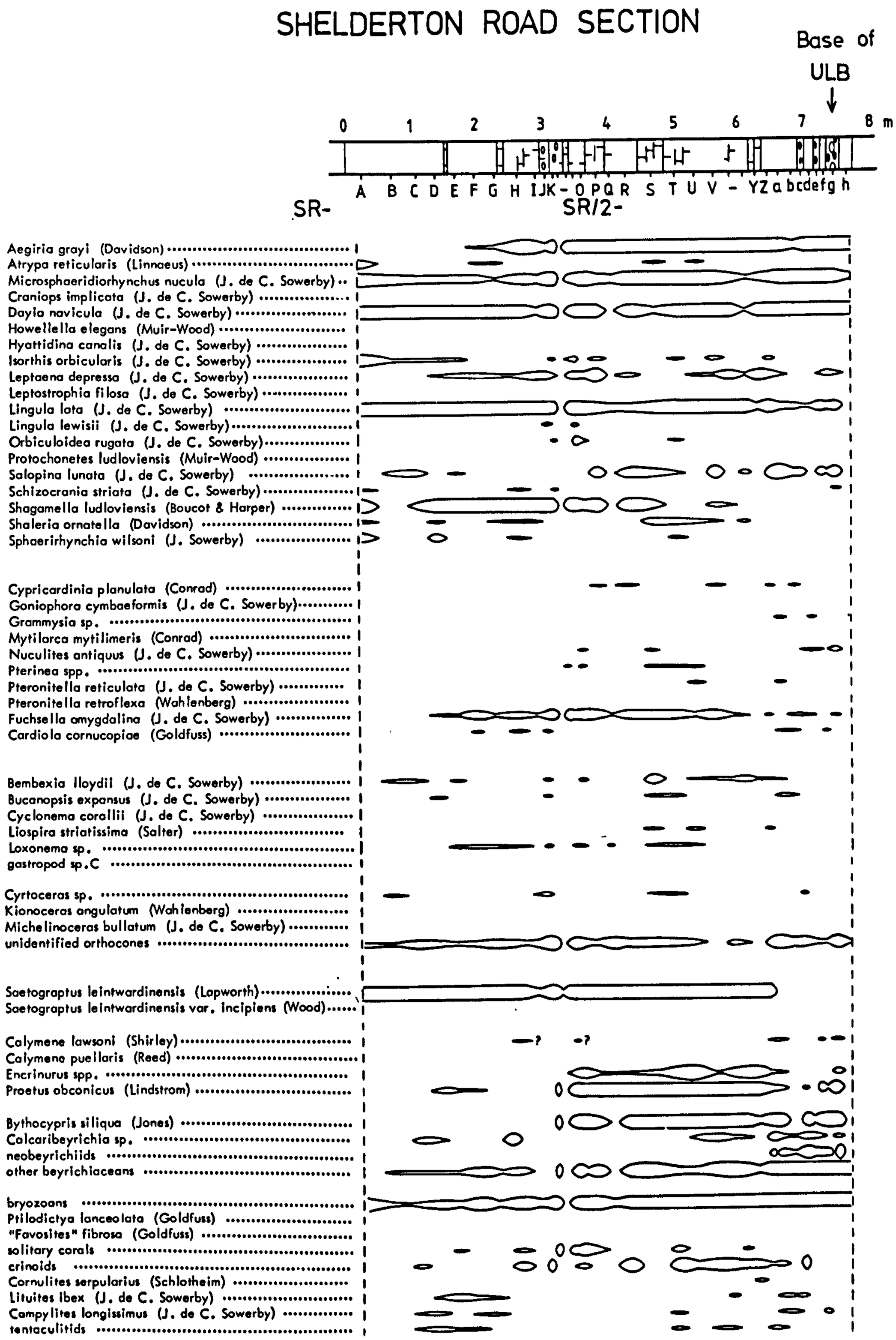


Fig. 4.5 : LLB at Shelderton Road Section.

bedding planes, and is dominated by disarticulated, pedicle valves of D. navicula. L. lata valves and graptolites of S. leintwardinensis S. leintwardinensis cf. primus (RBR) are found commonly among the shell assemblages, as well as in separate horizons.

Over the next 2 m (SR/2-C-I), the strata are often slightly thicker-bedded. There is an alternation of siltstones and calcareous siltstones, some of which are laminated, interbedded with some more massive, very calcareous units. The carbonate in the latter beds is apparently largely inorganic; there are very few fossils in such bands. Several of these horizons are nodular. The more flaggy siltstones are fairly heterogeneous. Faunal distributions correspond closely to the lithology. Well-laminated beds have discrete planes of fossils, while the thicker siltstones and wispily-laminated beds have more evenly-scattered faunas.

In the shell assemblages, D. navicula is much less abundant than in the lower beds, occurring with S. ludloviensis, M. nucula and bryozoan fragments on planes rich in shell debris. The total fauna of these beds is quite diverse. L. lata, which is commonly perpendicular to the bedding (-probably in situ), A. grayi and graptolites are abundant in siltstones between the shell horizons, with orthocones, occasional gastropods, beyrichiacean and smooth ostracodes, proetids, tentaculitids and rare C. cornucopiae, F. amygdalina valves are consistently fairly common, mostly in assemblages separate from the rest of the fauna. L. depressa becomes fairly common in the more calcareous beds.

The lower 10 cm of J is a highly calcareous siltstone containing nodules of limestone, and very large, worn, bryozoan-encrusted orthocones. 5 cm of siltstone, which includes a plane with numerous, aligned graptolites, is intercalated between this and an overlying, similar, nodular horizon in K. There is a marked faunal change above this level in the succession, with a rapid increase in the abundance of trilobites (- proetids, warburgellids and encrinurids mainly), and ostracodes. Small, conical solitary corals and L. depressa have acmes over the next metre (K-Q). The faunas of beds above J are very diverse, and numerically rich. L. lata specimens are not as commonly found perpendicular to the bedding in higher beds (except for a few bands), but single valves remain abundant. L. lewisii, including a specimen

apparently in situ, was present in J and M. Graptolites are widely distributed but, as well, occur in large numbers on some planes.

The beds from K to Y, which extend up through 3 m of succession, are similar in lithology to those below. Laminated units are more common in the higher part. They include some very finely-banded flags in which minor sedimentary discontinuities are common, and beds of very calcareous siltstone with thicker, more even, layering. Fossils in the latter are infrequent except for certain planes; graptolites are the main fauna in beds between these horizons.

The majority of shells of D. navicula, M. nucula, and S. lunata are found in plane assemblages. A.grayi and ostracodes tend to occur together in "nests" and on planes, separate from bands with other fossils. The rest of the fauna is found both in layers and scattered through beds. The abundance of various faunal elements fluctuates from bed to bed. Bivalves and gastropods, which are more diverse above K, are frequent minor constituents of faunas. S. ornatella (small valves) becomes fairly common in assemblages from S to X.

The top part of the section, from Z upwards, is more thickly-bedded siltstones with numerous horizons of fossils. The concentration of these shelly layers increases at intervals to form thick bands composed almost entirely of shells and broken debris. Many of the fossils in these beds are worn and limonitised, and phosphatised fragments and pebbles are common (SR/2-c,e,g). The beds between these conglomeratic horizons have comparable faunas, largely concentrated into thin fossiliferous levels.

The lithological transition corresponds to faunal changes. Graptolites disappear rapidly above Z, and S. ludloviensis, which has dwindled in abundance above S, is not found in these beds. D. navicula, in contrast, becomes much more numerous, dominating the shelly faunas. Trilobites are less prevalent, but beyrichiacean ostracodes become extremely abundant; and increasingly diverse. Beds of close-packed A. grayi, ostracodes, small M. nucula and shell debris are found at many levels. Neobeyrichiid ostracodes first appear in Z, and are common in higher beds. Specimens from Z were identified (DJS) as Neobeyrichia? sp. 1, followed in beds a to e by N. nutans; with N. lauensis, N. confluens and N. scissa entering the fauna in g.

Bed g is the thickest conglomeratic horizon (15 to 18 cm), and contains large, irregularly-shaped pebbles of shelly limestone, as well as numerous smaller, and phosphatised clasts. Worn shells and big bryozoan-encrusted orthocones are also common.

The positioning of the LLB-ULB boundary in this section is difficult because the faunal indices of the stratotype appear at widely different levels. S. ornatella is not common at any level, and C. puellaris was not recorded from this section (Calymene lawsoni was identified (DJS, and LC) from several levels, including specimens in a and g). A. gravi and encrinurids (which include both E. stubblefieldi and Encrinurus rosensteinae(RTT)) first appear 5.5 m and 4 m respectively below the horizon where N. lauensis was found (SR/2-g). The appearance of N. lauensis was taken to indicate the base of the ULB (-the stratigraphical use of various fossils is discussed in Ch.6).

Bioturbation:

Burrows were only recorded from bed SR/2-c, where a trace filled with shell debris and tapering from a maximum width of 4 mm extended down perpendicular to the bedding through more than 3 cm of a siltstone flag. However, the "patchy" lamination of some bands, and apparent lack of bedding in others in which fossils are evently distributed, suggests that bioturbation has been fairly extensive.

b. Lawnwell Dingle (LD/A-): High in the LLB (SO.416.768)

The quarry face to the east of the section LD-, which lay across a fault gully, exposed some strata high in the LLB. The fauna correlates closely with the top LLB of the Shelderton Road section.

The lowermost beds are dark, thinly flaggy calcareous siltstones. Planes of scattered valves of D. navicula, I. orbicularis and M. nucula occurred at intervals, while graptolites (S. leintwardinensis (LC)) and L. lata valves are found abundantly on bedding planes, and also in patches through the sediment.

The flags about 1.5 m higher in the succession are thicker-bedded siltstones and calcareous siltstones. In some, fossils are concentrated onto planes, but commonly they are distributed through beds. L. depressa is very common at this level, especially in more calcareous bands, and often with some A. reticularis valves. Proetids (including warburgellids)

are abundant, while encrinurids and calymenids (C. lawsoni (LC)) are fairly common. Bands of A. grayi and ostracodes (mainly beyrichiaceans but also Bythocypris siliqua), together with finely comminuted shell debris, crinoid columnals, and bryozoans occur often. Graptolites and L. lata remain very numerous in these beds, but shell planes of D. navicula are less frequent.

The top beds, about 2 m above, have a similar lithology and fauna to those just described. "Nests" of small ostracodes occur in many beds, as well as the more extensive bands of abundant specimens, associated with A. grayi. A. reticularis is quite common in this part of the sequence.

c. Small quarry NE of Wassell Barn (TL5-)
(SO.416.756)

The section covered almost 1.5 m of beds. It includes the unconformable junction of LLB and ULB.

The bottom 1.25 m (TL5-P to R) is a series of very thinly flaggy, calcareous siltstones. Some are finely laminated, with smooth, even bedding surfaces, others are more thickly bedded. The lamination, which is not very distinct, is of more calcareous, silty and micaceous layers. Thin shell and debris-rich horizons occur at frequent intervals in these beds. Some flags have narrow (2-3 cm), shell-filled, shallow scour grooves, which trend ENE-WSW. The lengths of these structures were difficult to measure (because it was not possible to extract sufficiently large pieces of rock to expose the complete grooves). Two were estimated to be 30-50 cm long; the scours are long compared to their widths. The grooves are filled with disarticulated and broken, tightly-packed shells. Prod-casts have similar trends to the grooves, but fine crinkle-marks on some planes are aligned ESE-WNW. The shell-filled grooves occur at many levels, often not much separated vertically.

The faunas (LLB) of these beds are fairly diverse, but planes are dominated by different species in turn. Disarticulated valves of D. navicula, S. ludloviensis and L. lata, S. wilsoni (large individuals of a flat variety) and H. nucula are prevalent in several plane assemblages. Amounts of shell debris, pieces of bryozoa, beyrichiacean ostracodes (Hemsiella sp., Calcaribeyrichia sp. 1-DJS), small trilobites

(Proetus obconicus (LC), Warburgella ludlowensis, and Otarion cf. diffractum (RMO)), and graptolite fragments are the common minor constituents of faunas. Shells on planes are mostly convex surface-up, and occasionally appear to be preferentially orientated - umbones of D. navicula pedicle valves in one assemblage were mainly pointing northeastwards, while the long axes of many L. lata valves on one plane were aligned NE-SW. The faunas of the shell grooves are similar to those of the other beds, with S. ludloviensis and D. navicula the most common constituents in many cases.

Bed S is a massive, highly calcareous siltstone (10 cm thick), which has an uneven, partly eroded top surface. The lower part is well-burrowed with narrow silt-filled traces oblique to the bedding. Small phosphatised fragments are present at the top of the band, and a few fossils which include a neobeyrichiid (LC) ostracode, A. gravi and a proetid pygidium.

Directly overlying S, T is a very shelly conglomeratic band (8-10 cm thick), with irregular rounded pebbles of limestone and numerous phosphatised nodules in a fine siltstone matrix. Large bryozoan-encrusted orthocones are fairly common. The fauna is rich and diverse. Abundant A. gravi, D. navicula and M. nucula are distributed through the band, with calymenids, proetids, beyrichiacean and neobeyrichiid ostracodes (including N. confluens - DJS), smooth ostracodes, and pieces of branching bryozoans, and small internal moulds of orthocone chambers. Large quantities of shell debris are associated with the more complete fossils.

The conglomerate and overlying beds (U) lie with an angular discordance (of 3-4°) upon the eroded top of S. Beds in U are thickly flaggy siltstones, which are not very fossiliferous. Small patches of closely-packed A. gravi valves are found within some of the beds.

3. Mocktree Quarries: MQ/A- (SO.4165.7540) and MQ/B- (SO.4163.7531)

These two localities showed parts of the Mocktree channel (Whitaker '62 - p 330) where topmost LLB and ULB rest directly upon massive nodular UBB Aymestry Limestone. MQ/A- was a small bank exposure at the top of the main quarries. MQ/B- was on the north side of the main road (A4118) outside the quarries, where the channel-fill beds are banked against the Aymestry Limestone (-Whitaker estimated a high

original dip for the hLLBbeds of 23° at N/40°W).

MQ/A includes 1.40 m of strata lying directly over the Limestone. (The dip of the former is approximately 20°SE, while the main quarry dip for the limestone is about 5° northwards). The top beds of the Limestone are rich in crinoid columnals. The overlying flags are calcareous siltstones, fairly thinly-bedded, but often splitting irregularly. Some are laminated, with an alternation of micaceous, silty and calcareous layers. Many of the beds are very poorly fossiliferous. However, beds B and C (each 5 cm thick) have abundant faunas. The lower band (B) is packed almost exclusively with skeletal elements of C. lawsoni (LC), of widely differing sizes. Small beyrichiacean ostracodes, mainly concentrated into one "patch", form the only associated fauna. In the band above (C), shelly fossils - D. navicula and M. nucula - are found in addition to the trilobites. Higher beds are again fairly barren. In E, approximately half a metre up from C, a large neobeyrichiid ostracode was identified as N. lauensis (DJS). Beds in F have occasional small "nests" of A. grayi and ostracodes, which included N. cf. confluens (DJS). The appearance of N. lauensis is taken to indicate the ULB here.

MQ/8- has a similar band (3 cm) of abundant C. lawsoni skeletal elements. It thins out laterally to a single plane within 1.5 m. The rest of the calcareous siltstones appear unfossiliferous. The trilobite band is followed closely (3-4 cm) by a second, thin, decalcified seam of broken shell debris, A. grayi, ostracodes, C. lawsoni, D. navicula and M. nucula, together with rare phosphatised fragments. The ostracodes, which are mainly beyrichiaceans, include some neobeyrichiids (LC). Higher beds have infrequent planes of broken shell fragments, and clusters of A. grayi. The presence of neobeyrichiid ostracodes indicates a level in the ULB or topmost LLB.

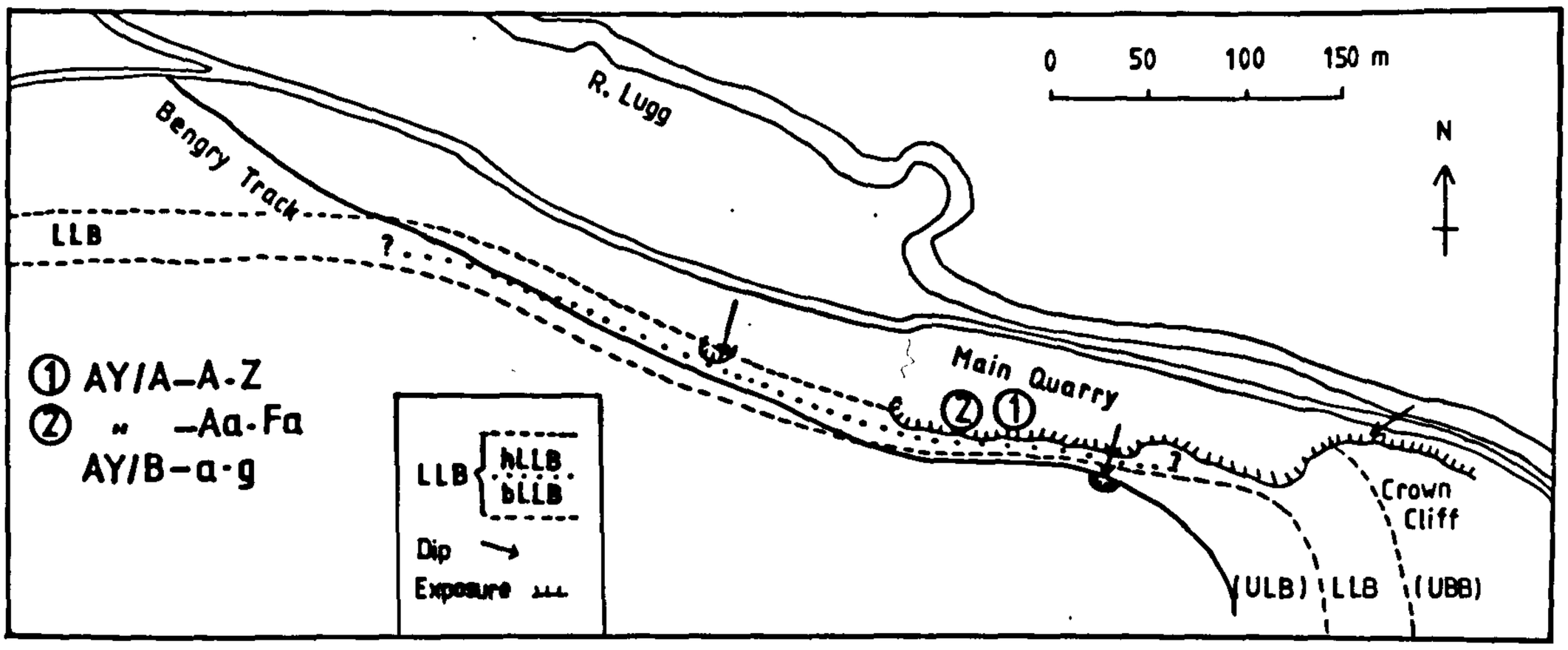


Fig. 4.6 : Locality map for the Aymestrey sections.
(Map taken from Lawson '73(a)).

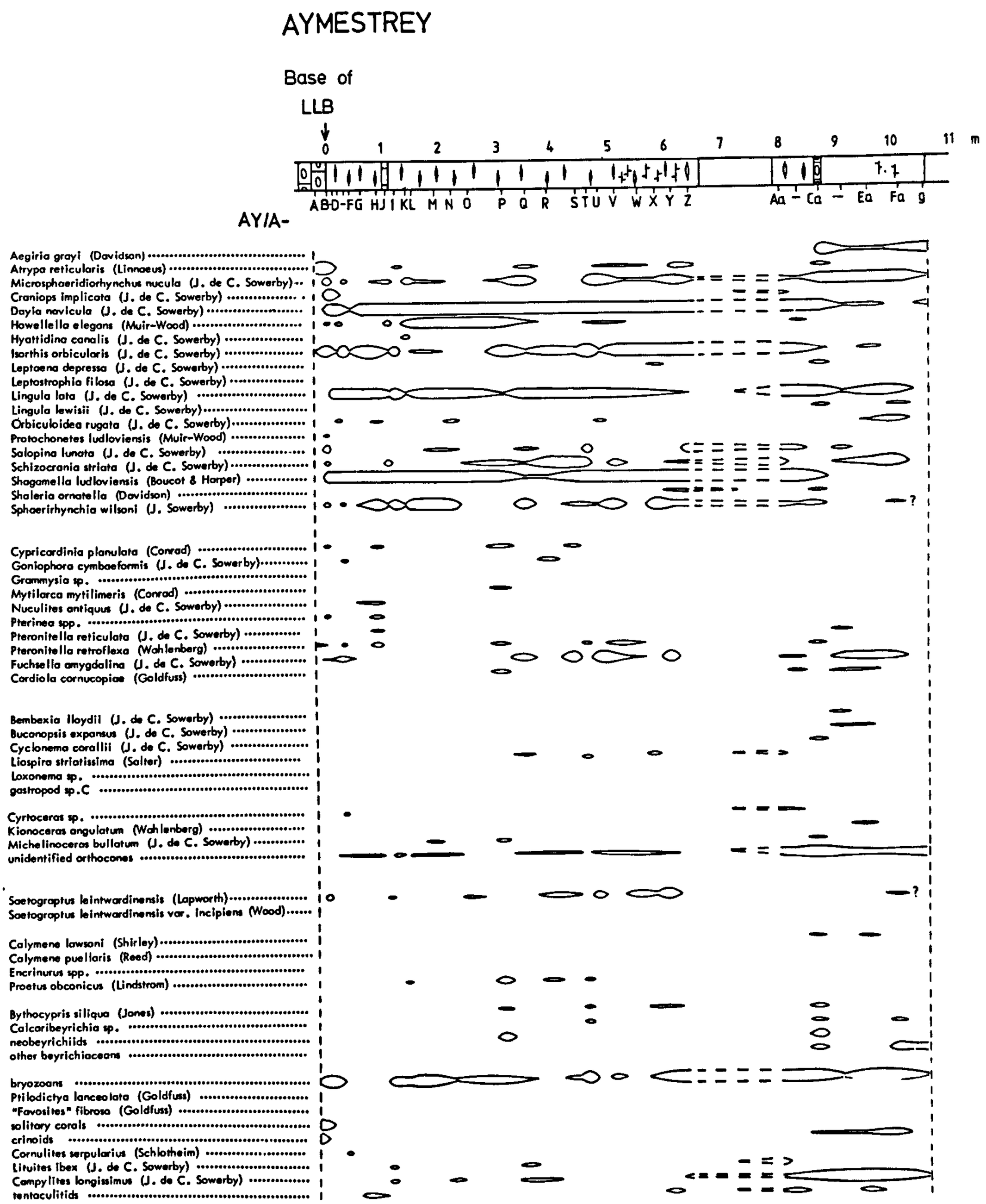


Fig. 4.7 : LLB succession in Main Quarry, Aymestrey.

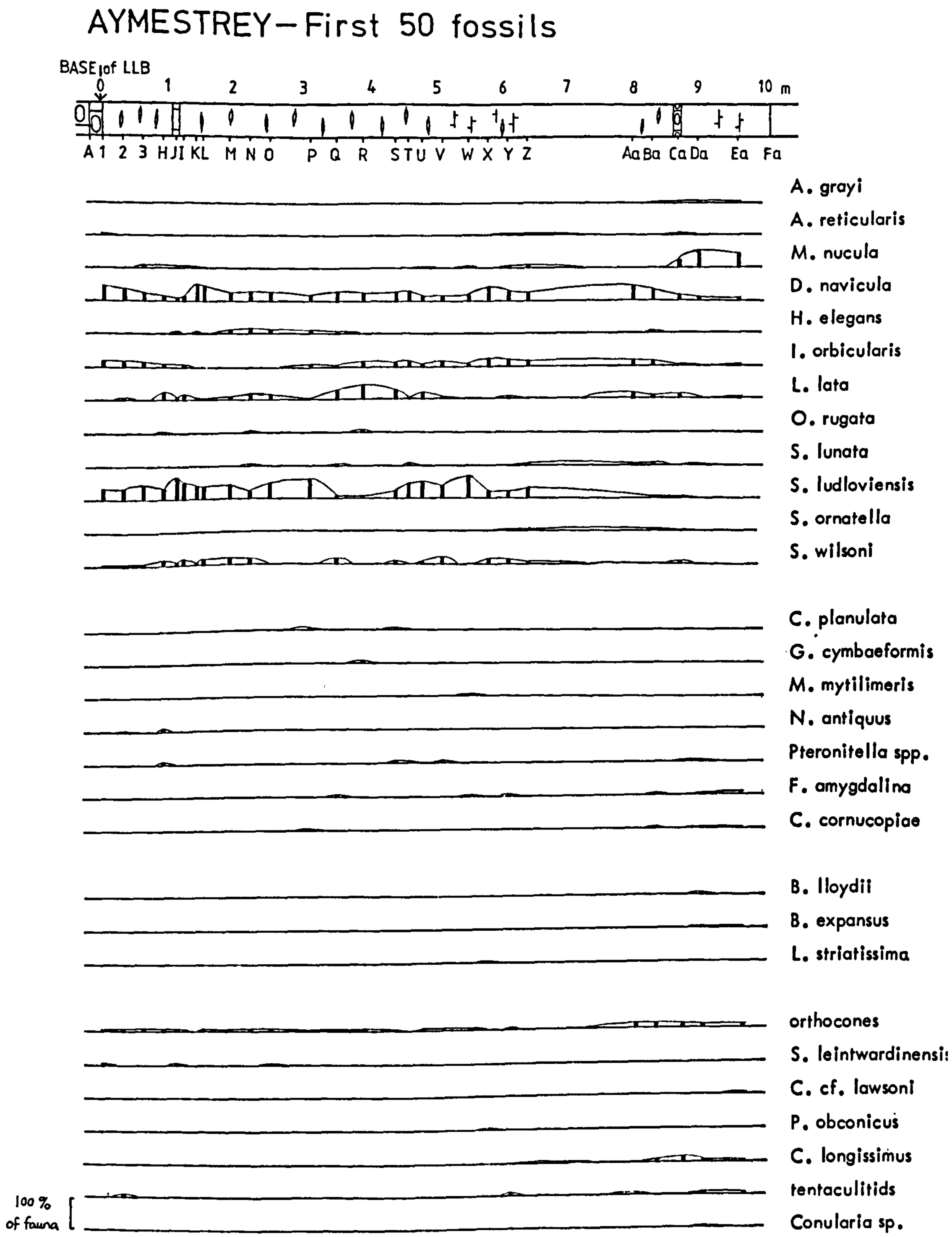


Fig. 4.8 : LLB succession in Main Quarry, Aymestrey-first 50 fossils counted.

B. AYMESTREY

The Ludlow rocks of the Aymestrey area were recently mapped and described by Lawson ('73(a)). The LLB succession was examined in the present study in sequences in the Main Quarry and the Bengry track above the quarry at Aymestrey (Fig 4.6 p121).

1. Main Quarry, Crown Cliff AY/A-, AY/B- (SO.424.655)

Fig 4.7 p122. Fig. 4.8 p123.

Thinly flaggy, dark calcareous siltstones lie with sharp contact on the Aymestry Limestone in the main quarry. The limestone is massive, nodular, and irregularly-bedded, with a characteristic UBB fauna. S. euglypha, A. funiculata, A. reticularis, L. depressa, solitary corals, Favosites and crinoids are the most common fossils of the upper beds. The fauna is widely distributed through beds, and is numerous in comparison with the equivalent beds at the stratotype. The siltstones above are very fossiliferous, with a fauna typical of the LLB. The diagnostic forms of the UBB are absent from these basal siltstone faunas.

The junction of the Limestone and overlying beds can be traced in relation to the top Kirkidium band and a higher thin shale band in the Limestone. The contact is irregular, but does not transgress the bedding planes of the lower formation. The top surface of the Limestone is fairly uneven, probably largely due to its nodular lithology, but in one place, a large favositid coral colony was planed-off along the contact (Fig 4.9 p125). (The colony is overturned, so that this is its basal region). Next to the coral, very fine, shelly siltstones fill in hollows in the limestone topography of up to 10 cm thickness. Worn, corroded nodules of limestone and UBB fossils are enclosed in this matrix, with a few small phosphatised fragments, broken shell material and abundant small D. navicula valves. Bedding in the siltstone matrix is unclear. Similar, though thinner, deposits of tightly-packed shells and nodules, with little matrix material, lie over much of the Limestone surface. In one part, a K. squamosus burrow descended down into the limestone, perpendicular to the bedding.

The most common UBB forms in the shelly, conglomeratic layers (AY/A-B: 1 to 10 cm thick) are large valves of S. euglypha. These are mostly very worn and often broken, sometimes "stacked" together. A. reticularis valves are comparably preserved among the numerous

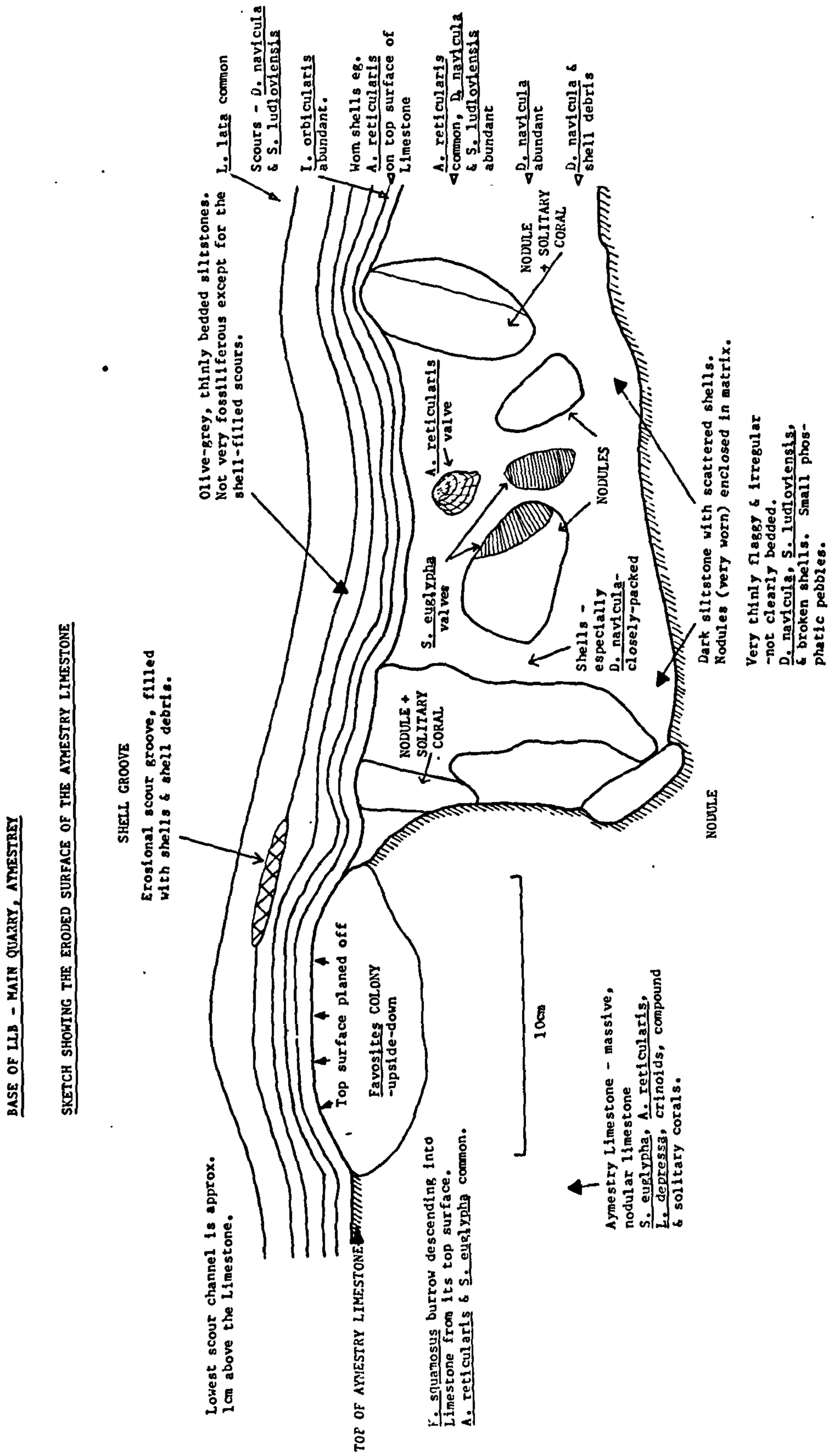


Fig. 4.9 : The base of the LLB in the Main Quarry, Aymestrey.

D. navicula valves. Nodules, also worn, contain the common fossils of the topmost UBB, with large S. euglypha prevalent. Higher up in the band, S. ludloviensis, I. orbicularis and C. implicata are common in the shelly matrix, and one cluster of poorly preserved monograptids was found. The top layer has a marked abundanceof I. orbicularis.

The calcareous and shaly siltstones overlying the basal shelly deposits are thinly-bedded. The lowest flags undulate gently over the uneven surface below. Many of the siltstones are finely-laminated, with an alternation of silty, muddy and calcareous layers. Interbedded with these are thicker, more massive, calcareous flags, up to 5 cm thick, and shelly and unfossiliferous limestones. Some flags split evenly along smooth bedding surfaces, others fracture irregularly. Fossils in the siltstones are confined to bedding-plane accumulations, and to shallow, scour grooves. Shells are variably distributed on planes, widely dispersed, in small patches, or highly concentrated over wide areas. Large quantities of fragmental material are associated with shell horizons and, commonly, bedding surfaces are covered with finely comminuted shell debris.

The scour channels, which occur at many levels from the base of the siltstones upwards (the lowest were 0.5 - 1 cm above the shell layer B), are narrow elongated structures, trending ENE-WSW. They are very similar to those seen in the quarry NE of Wassell Barn (p118). The widths of the grooves are usually 1-5 cm, by a few millimetres depth. Lengths observed were often less than 30 cm, but the persistence of larger structures was difficult to determine. The scours are mostly filled with shells and bioclastic debris, with finer material in the top layers. Some thin channels have a single large shell spanning their widths at the end (Fig 4.10 p129). Small, anhedral flakes of biotite mica were commonly associated with the shelly deposits. Calcareous sandstone, rich in biotite, and with some fragmented shells, filled one large (5 cm width), deep (2.5 cm) channel. The structures can sometimes be seen to cut down into the underlying beds, but more generally, the lamination appears to curve beneath the shell lens; this is probably due to post-depositional compaction of the sediment. The erosional channels were described by Newall ('66) in his thesis on the Aymestry Limestone. Although they are smaller in size and in much

finer sediment, they appear to be comparable to the 'separated gutter casts' of Whitaker ('73).

The sequence AY/A-C to Z extends up through 6.4 m of the thinly flaggy siltstones. There is little change in facies through this thickness. The scour channels become less frequent in the higher beds, where micaceous layers and planes of finely disseminated carbonaceous material are more common.

The fauna of the lower siltstone beds is dominated by the brachiopods S. ludloviensis, D. navicula, L. lata, I. orbicularis, S. wilsoni, and H. elegans, with bryozoa and orthocones. Many horizons have small aggregations of randomly orientated shells. However, the surfaces with erosional grooves often have parallel prod-casts, and aligned shells among a layer of fine debris. S. ludloviensis valves fill numerous scour channels. Lenticular shelly limestone beds have similar faunas to the siltstones. One of these - AY/A-K - was up to 3 cm thick, by 35 cm wide in section, and more than 55 cm long; it had abundant D. navicula valves, with S. ludloviensis and H. elegans.

In the beds above M, assemblages of evenly distributed shells, dominated by different species in turn, become more common. H. elegans declines in abundance above P, when small Schizocrania striata valves become very common on some planes, often associated with disarticulated L. lata. The proportions of the various prevalent species fluctuates through the succession, from band to band. In the upper part of the sequence, planes of F. amygdalina and G. cymbaeformis valves are frequently found, and M. nucula is increasingly abundant. Graptolites are common on a few planes, sometimes with L. lata valves.

The section AY/A-Aa to Fa, and AY/B- lay approximately 50 m further west along the quarry. The gap between Z and Aa was estimated to be 1-2 m. The lower 0.7 m is thin, muddy siltstone flags, with scour channels and shell planes. The fauna is similar to C-Z, with D. navicula, L. lata, I. orbicularis, S. ludloviensis, and S. wilsoni, all common, with many cyrtocones, orthocones, tentaculitids and bryozoa.

Directly above these beds is a richly fossiliferous, irregular, conglomeratic band (10-15 cm) of calcareous siltstone (AY/A-Ca, AY/B-C) with limestone and siltstone pebbles of assorted sizes, and numerous very large, bryozoan-encrusted orthocones. There are considerable

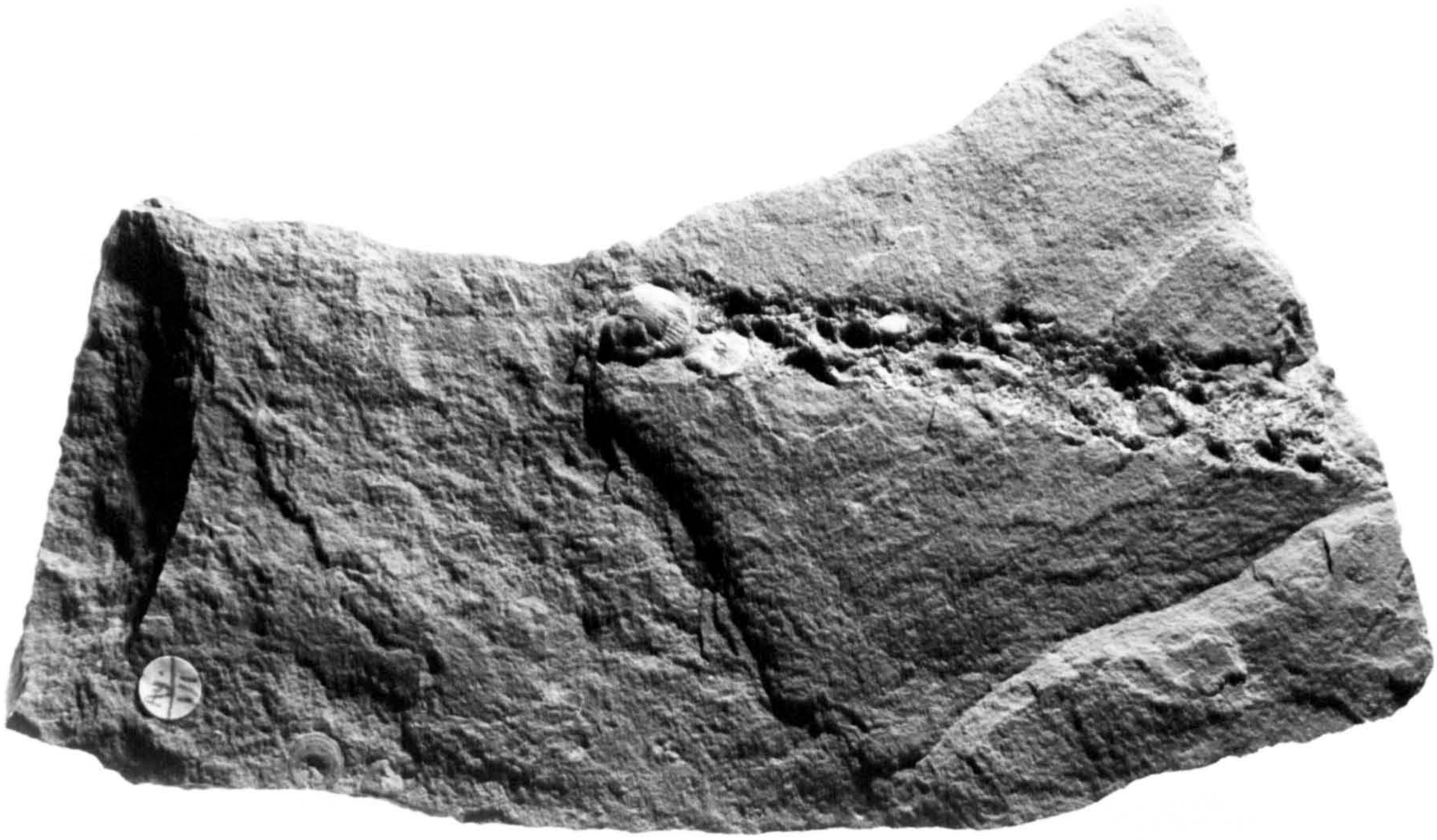
faunal changes at this horizon. A. grayi, beyrichiacean and smooth ostracodes, bryozoan-encrusted shells and large, thick sections of branching bryozoa are abundant with D. navicula and M. nucula in the diverse fauna. Calymenid skeletal elements are fairly common. Among the ostracodes N. nutans and Hemsiella sp. were identified (DJS). Above this band, the common species of the lower beds disappear or are rare; only M. nucula (large, strong-ribbed individuals) is still common in higher beds. No scour channels were found above the conglomerate.

The overlying flags (45 cm) are thicker-bedded, unevenly splitting, calcareous siltstones, some of which are laminated. They have a fairly sparse, unusual fauna. Very long, curved C. longissimus are numerous, particularly in one horizon. Orthocones, conulariids, clusters of big M. nucula, and a segment of an appendage of a large eurypterid (Carcinosoma punctatum (LC)) are associated with the C. longissimus in these beds. (C. longissimus: Fig 4.10 p129).

Higher beds (AY/A-Ea, Fa; AY/B-e-g) are more evenly laminated flags alternating with massive calcareous siltstones. Fossils are rare between the occasional, debris-rich, shelly horizons. The fauna is restricted to a few orthocones, bivalves, M. nucula, and one large C. cf. lawsoni (DJS) (an articulated thorax and pygidium). One plane in AY/B-f (0.7 m above the conglomerate), which had a lot of bioclastic debris, included small pebbles and bryozoan nodules with a fairly diverse fauna. Pieces of C. longissimus, M. nucula, Orbiculoidea rugata, eurypterid fragments, lingulids, S. striata, and bryozoa, together with abundant ostracodes (beyrichiacean and smooth) and a few A. grayi, compose the assemblage. Hemsiella cf. loensis and Calcaribeyrichia sp. 1 (DJS) were among the beyrichiacean ostracodes.

In the top few metres of rocks in the quarry, the siltstones are much thicker-bedded. A few, small decalcified "nests" of A. grayi, ostracodes, crinoid columnals and shell debris occur in these beds, but generally fossils are uncommon.

Above the top of the main quarry, in the small quarry by the path (see map in Fig 4.6 p121), thickly-bedded siltstones with periodic thin biscuit-seams of fossils yield a typical ULB fauna. A. grayi and N. lauensis (together with a rich assemblage of other beyrichiacean ostracodes, including N. scissa and N. confluens (DJS) are abundant,



a : Erosive scour channel with large shell at end. (x 2/3)

b : Slab from beds above the conglomerate Ca, showing many long <u>C. longissimus</u>. (x 1/2)

Fig. 4·10 : Aymestrey.

and encrinurid and calymenid skeletal elements occur commonly.

Bioturbation:

The top beds of the Aymestry Limestone were mottled from extensive biogenic reworking. A few distinct silt-filled traces and K. squamosus tubes were also seen in these beds. The overlying thin LLB siltstones do not appear to have been burrowed; they are often finely laminated.

2. Bengry Track: AY/2-, AY/4-

The track section leading up to behind the main quarries; from west of them, now provides only intermittent exposures through the LLB. Lawson ('73(a) p 262) examined the succession when the section was newly excavated, and estimated there to be 10.5 m of LLB strata in this sequence. He reported the topmost layer of the UBB here to be a 20 cm limestone "containing numerous limestone fragments in its upper part", which was overlain by thinly flaggy calcareous siltstones. The conglomeratic horizon, from its unity with the limestone beneath, was considered to represent erosion during the last phase of UBB deposition.

The fauna and lithology of the succeeding LLB is comparable to the succession in the main quarry. Fossiliferous horizons are numerous, and packed with shells. H. elegans, I. orbicularis, M. nucula, S. wilsoni, D. navicula, L. lata and S. ludloviensis are all prevalent in assemblages. In the higher beds, the last three species are particularly common. Lawson ('73(a) - p 262) placed the junction of the LLB and ULB at the level where L. lata and S. ludloviensis suddenly disappear and S. wilsoni and I. orbicularis also depart from the fauna.

Above this, the flags are more thickly-bedded, and fossils are uncommon. It was observed by Dr. I.E. Penn (in Lawson '73(a) p 262)

> "that the typical layers crowded with A. gravi and N. lauensis do not appear until about 9 m above the base ... (of the ULB) ... where they are accompanied by phosphatised pebbles."

However, among the fauna of the intervening beds, Lawson recorded occasional specimens A. gravi, N. lauensis and C. puellaris.

Collections (AY/2- and AY/4-) were made from the beds between the typical developments of the LLB and ULB. The lithology is dominantly fairly thickly-bedded, calcareous siltstones, laminated in parts, and with some more micaceous bands. Small patches and nests of decalcified

shells and bioclastic debris occur sporadically, but fossils are infrequent. A. gravi, and ostracodes (beyrichiacean and non-palaeocope), with small S. lunata, M. nucula, D. navicula, L. lata and orthocones are the more common forms. C. longissimus fragments, bryozoa and crinoid columnals can be identified among shell debris deposits. Beyrichiacean ostracodes identified (DJS) from these beds did not include any neobeyrichiids.

Re-examination of the collections made by Lawson shows that a calymenid cranidium from these beds was of C. lawsoni (LC). The specific identification of some neobeyrichiids from beds below the incoming of the characteristic N. lauensis - A. gravi seams is uncertain (Lawson '76 - pers. comm.).

At the level of the typical ULB faunas, the siltstones are more thickly and irregularly flaggy than the lower beds. The appearance of N. lauensis has been taken (LC) to indicate the ULB here, so that the poorly fossiliferous beds between this level and that of the disappearance of the characteristic LLB brachiopods (9 m) are considered to be topmost LLB.

The Aymestrey LLB succession:

The marked change in the fauna and facies above the conglomeratic horizon AY/A-Ca (= AY/B-C) in the Main Quarry sequence is interpreted to show that this is the site of a former submarine channel, cut and mainly filled during the LLB period. The position of the break in the succession is similar to that found in the Leintwardine area by Whitaker ('62 p 327), who described six ENE-WSW trending channels that deepened from the shelf area towards the basin. The LLB development at Aymestrey appears very comparable to the Leintwardine succession. The poorly-fossiliferous beds above the break have a restricted and rather unusual fauna including many large C. longissimus tubes, conulariids, and eurypterids; in siltstones that are fairly thickly and irregularly-bedded. They contrast greatly with the thinly-bedded and very fossiliferous siltstones below, which have a brachiopod-dominated fauna. These two sequences correspond respectively to the hLLB and bLLB of Whitaker ('62).

In the Bengry Track sequence no conglomeratic horizon was found at the level of the faunal and facies change (Lawson '73(a)), and this

part of the section is now poorly exposed. However, a similar abrupt transition was noted between the bLLB and overlying strata. The 9 m of beds between this level and the appearance of the characteristic ULB N. lauensis - A. gravi assemblage at the level of a phosphatised pebble-bed (Lawson '73(a) - p 262) are equivalent to the hLLB of the Main Quarry.

The trend of the channel cannot be evaluated from the Aymestrey sequences, but is probably approximately parallel to the Leintwardine canyons, cutting down towards the basinal areas to the west. The comparable palaeogeographical position of the areas is emphasized by the similar development of ENE-WSW trending scour channels in the bLLB of both.

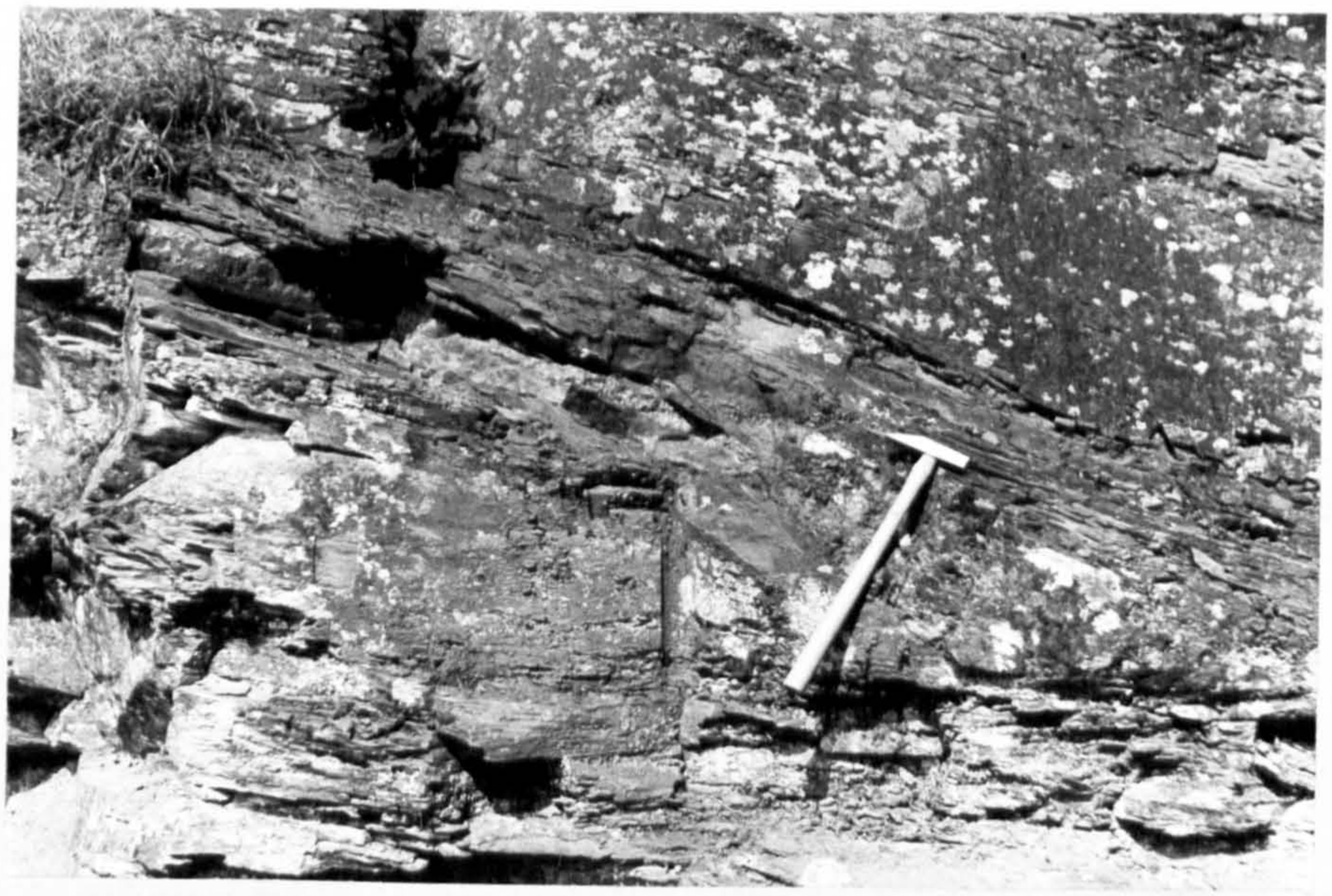
N. nutans (DJS) was found in the conglomerate AY/A-Ca at the level of the bLLB-hLLB junction. The 9 m of channel-infilling hLLB here below the N. lauensis level taken to indicate the ULB correlate with less than 1 m of beds between the N. nutans and N. lauensis horizons at Shelderton Road section (Fig 4.5 p 114).

3. Lyepole Bridge Quarry (LyBr-) SO.4014.6530

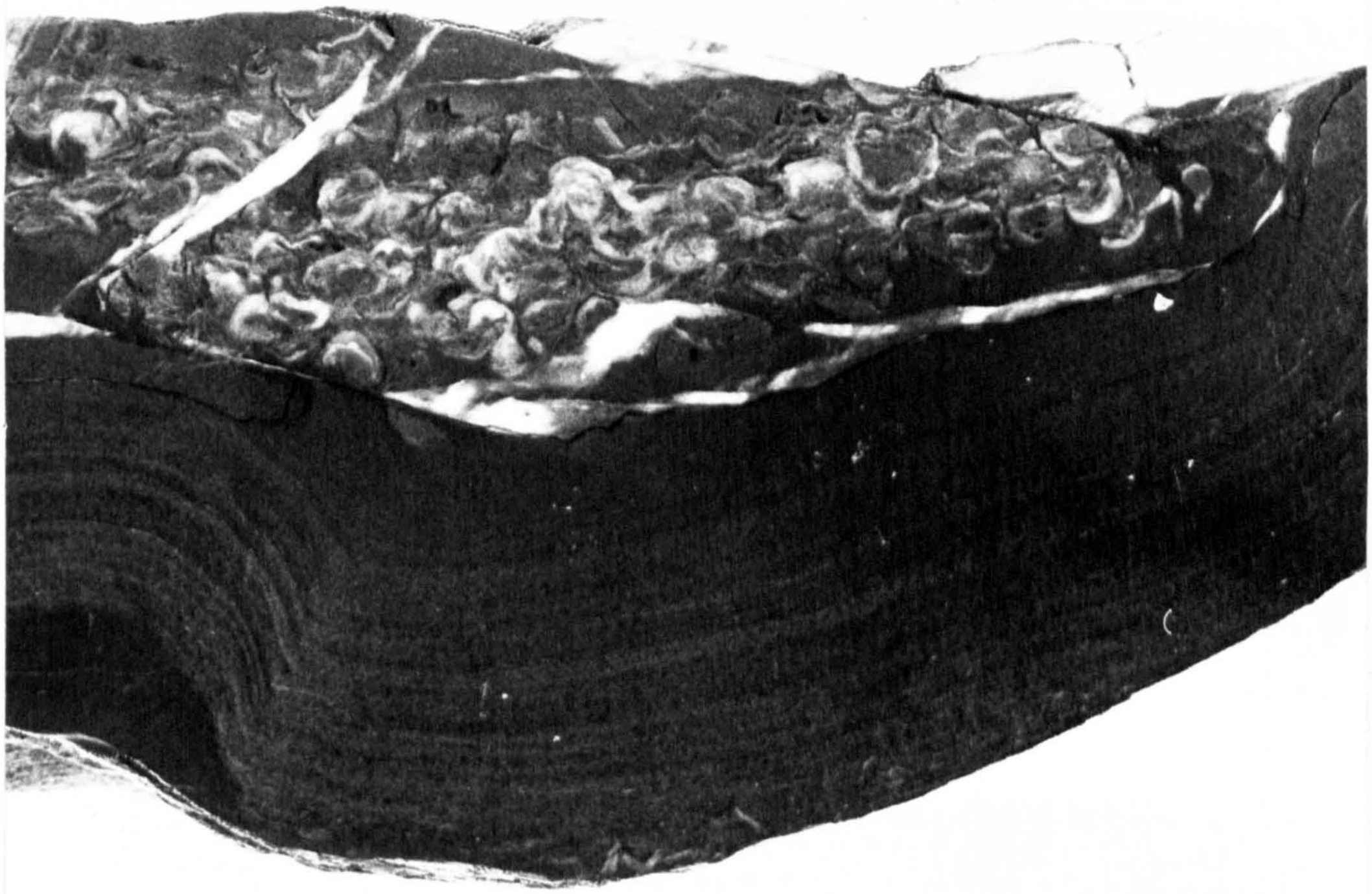
About 18 m of LLB were exposed in the quarry (Lawson '73(a) - p 266). The sequence comprises a series of thinly flaggy and shaly, dark siltstones interbedded with slumped bands. The undisturbed strata are closely laminated and fissile - finer and more thinly bedded than the Aymestrey lithologies. The contorted beds of slumped units have a direction of movement to the NW. The slumps have erosive lower boundaries, and thick, calcareous basal bands mainly composed of shells and shell debris. (Figs. 4.11 a and b).

The faunas of these shell concentrations are dominated by brachiopods. The majority of shells are disarticulated, and large quantities of bioclastic debris are associated with the dense concentrations of valves. D. navicula, S. wilsoni, M. nucula, I. orbicularis, H. elegans and S. ludloviensis are the most abundant elements of the fauna. Pieces of branching bryozoa occur very commonly with the shells.

The regularly-bedded units include some thin bands of similar, poorly-sorted, shells. In other fossiliferous horizons, L. lata valves and graptolites frequently form monospecific assemblages, but also, not uncommonly, occur together on planes. Graptolites from these beds were

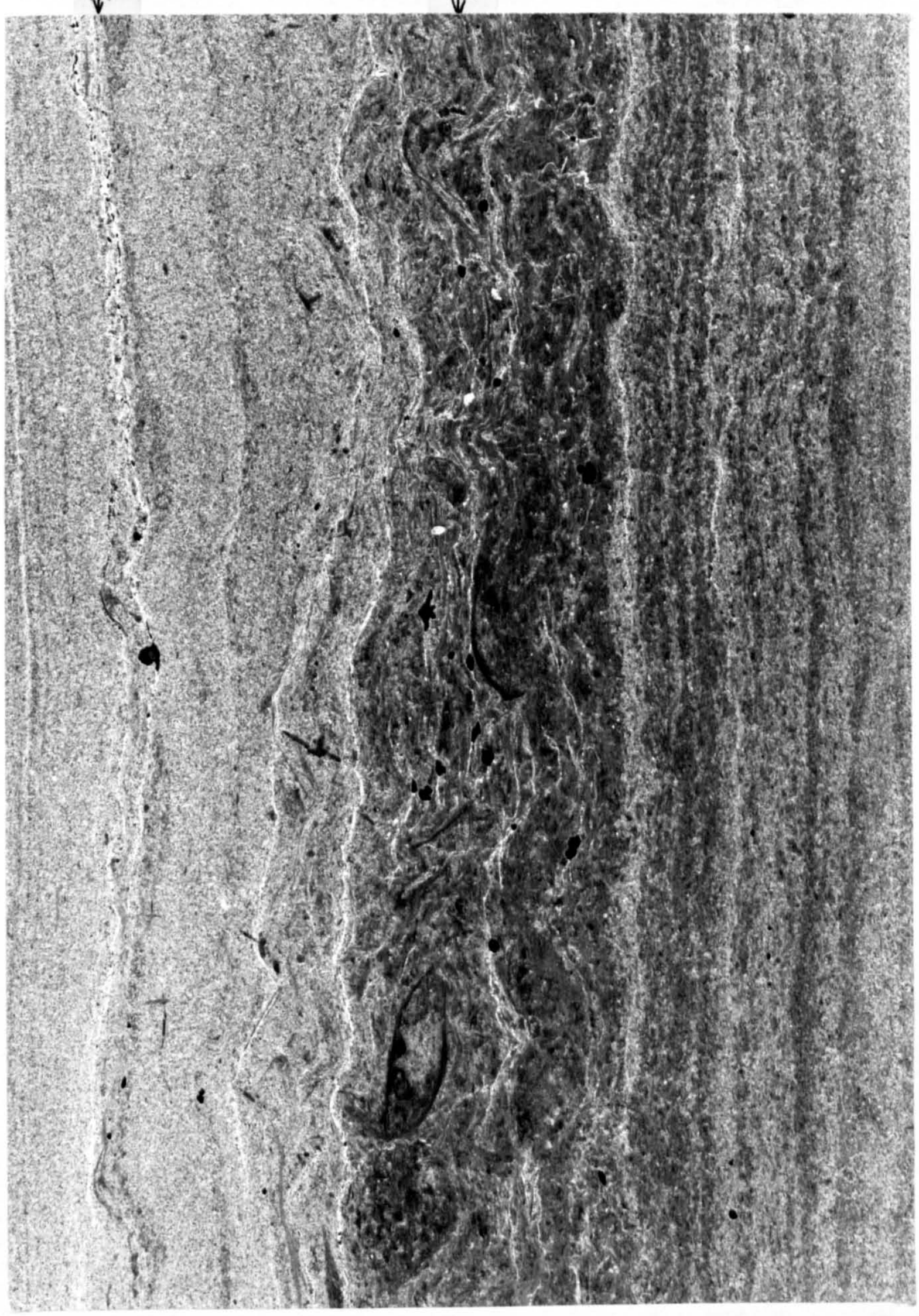


a : Slumped beds, Lyepole Bridge Quarry.



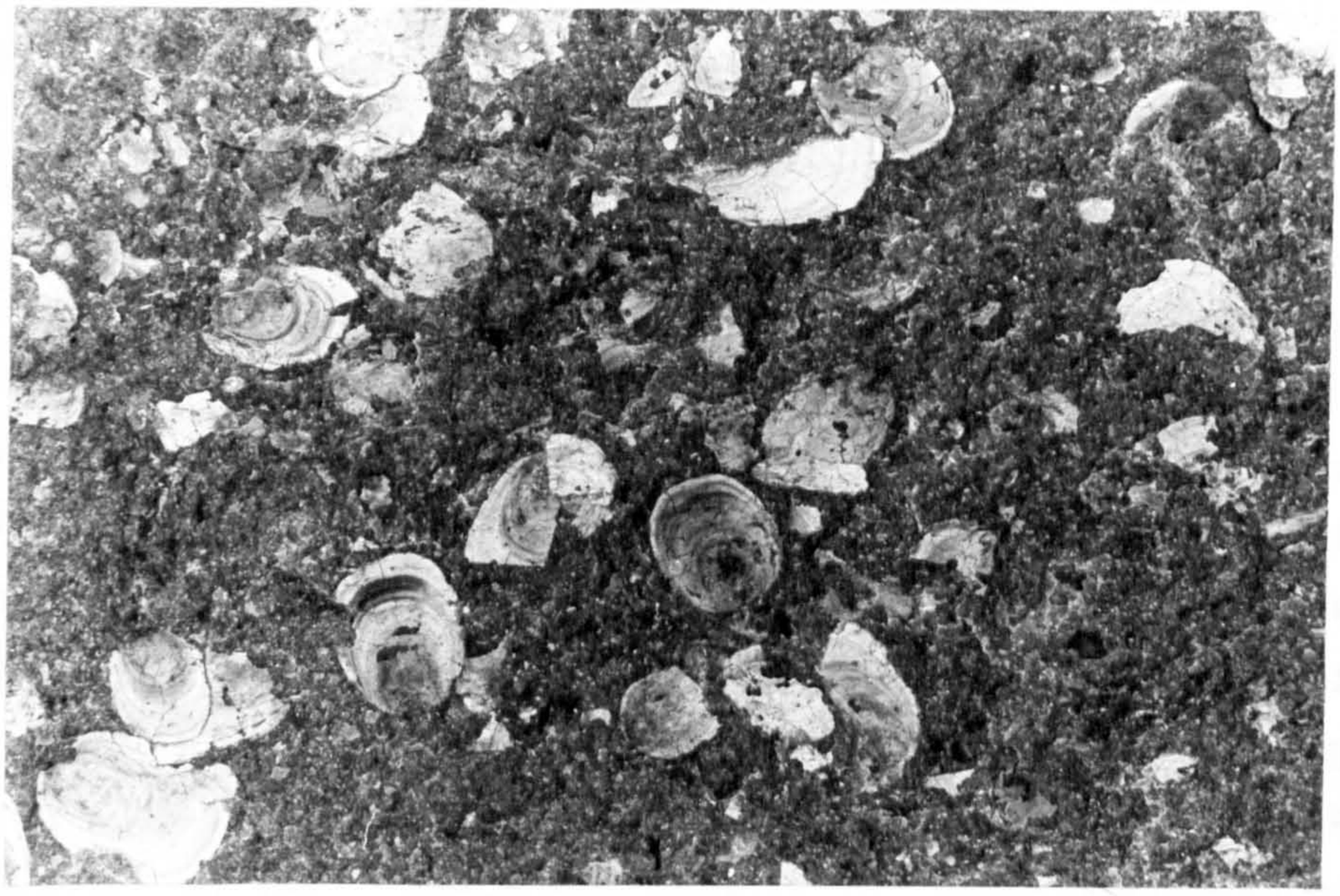
b : Section of slumped beds, showing shell band above finely-laminated siltstones. (x 1·25) (Detail from (a), near hammer).

Fig. 4·11 : Lyepole Bridge Quarry.



Section of graptolite - L. lata siltstones. (x 6)
Layers of L. lata valves and finely-disseminated, lingulid shell meal in thinly-bedded siltstones.

Fig. 4·12 : Lyepole Bridge Quarry.



Planes with L. lata valves; many unbroken (except for compression cracks). (x 3)

Fig. 4·13 : L. lata, Lyepole Bridge Quarry.

identified as S. leintwardinensis and S. leintwardinensis cf. primus or ? S. incipiens (RBR). Planes of aligned rhabdosomes are interspersed with others showing random arrangements, and some with small eddy current patterns.

The L. lata assemblages range from planes of widely-distributed valves to highly concentrated accumulations in layers several shells thick. The degree of breakage of the valves is often fairly low (Fig 4.13 p135) except in the tightly-packed deposits, which include many fragmented shells. Post-depositional compaction commonly appears to be responsible for cracking of valves. However, periodic horizons of finely comminuted shells are found. The lingulid valves, like the graptolites, show alignment in some assemblages but not in others. No specimens of lingulids were found perpendicular to the bedding.

Orthocones, eurypterid scales and appendages, small Pterinea tenuistriata, C. cornucopiae and C. longissimus fragments are minor elements of the LLB fauna here. Many of the shaly siltstone beds are unfossiliferous, or contain few fossils.

The graptolite evidence here, of ? S. incipiens with S. leintwardinensis, suggests that these beds are fairly low in the LLB succession (see p 172).

Leintwardine and Aymestrey: Synthesis

In the southern part of the Leintwardine area (eg. MQ, BB), and at Aymestrey, thinly flaggy, shelly LLB siltstones rest with sharp contacts on the uneven surface of the UBB Aymestry Limestone. In the main quarry at Aymestrey, there is evidence of erosion of the Limestone, indicating an unconformable junction. The conglomerate reported by Lawson ('73(a)) in the top of the Limestone on the Bengry Track occurs at this same level. At the UBB-LLB boundary in the northern part of Leintwardine (SH-), a basal LLB sandy I. orbicularis band (Newall '66) is followed by very calcareous siltstones and limestones packed with D. navicula virtually to the exclusion of other fossils. (These are the Dayia Shales of Elles and Slater (1906).)

Small scour channels at Aymestrey and NE of Wassell Barn, and assemblages of aligned shells, show the action of shelf-to-basin currents. Slumping at Lyepole Bridge, and channels cut at Leintwardine (Whitaker '62) and Aymestrey in the LLB reflect the instability of the shelf edge region. The hLLB channel-fill beds have a rather sparse, unusual fauna (eg. Fig 4.10 - C. longissimus). The base of the ULB at Shelderton (SR-) and Aymestrey is marked by phosphatised conglomerate horizons; N. lauensis enters the fauna at this level. Trilobites and ostracodes become important elements of the fauna in the topmost LLB and ULB.

C. KERRY

1. Normal sequence: Pant-y-llidiart Lane		SO.162.875	KY/1-, KY/2-, KY/3-
2. "	Dingle	SO.165.874	Pyl D -
3. Slumped " : Ring Hole		SO.125.836	RH1-, RH2-

Earp ('38) mapped and described the Ludlow rocks of the Kerry District. He recognised a number of assemblage zones, each of which, in addition, had a characteristic lithology. Faunal and facies changes from one sub-division to the next were transitional. The "Monograptus" leintwardinensis Shales, estimated here to be 150 m thick, correlate with the LLB. The A. gravi - N. lauensis fauna, equivalent to the ULB, formed the basal part of the overlying Dayia navicula Beds (whose total thickness = 370 m).

The Aymestry Limestone facies is not developed in this area, where the beds beneath the "M". leintwardinensis Shales are fine clastics with calcareous grit bands - the "Wilsonia" wilsoni Grits (760 m).

The lower part of the "M". leintwardinensis Shales were described as "soft ... smooth-fracturing shale with occasional thin bands of grit" (Earp '38 p 131). These shales were joined, and gradually largely replaced, by harder siltstones and laminated beds. There was no lithological change in the lower Dayia Beds. Laminated units were dominant, but bands of siltstone and shale were common. Earp commented upon some thick siltstones "traversed by numerous grey vermiform markings", within these beds.

In the SW part of the Kerry district, large scale slumping had affected many of the "M". leintwardinensis Shales. The direction of movement was to the SE.

Faunally, Earp found the lower sequences of the "M". leintwardinensis Shales to be poorly fossiliferous, with a fauna restricted mainly to infrequent graptolites and pteriniids. Graptolites became more common higher up, where assemblages of L. lata were typical. At the top, he recorded "frequent bands crowded with A. gravi, N. lauensis and D. navicula" (an assemblage equivalent to the ULB). The upper boundary was taken at the level where the graptolites disappeared. In the slumped series, fossils were scarce.

The normal sequences of the "M". leintwardinensis shales were examined in the Kerry Pole district, at Pant-y-llidiart, where the

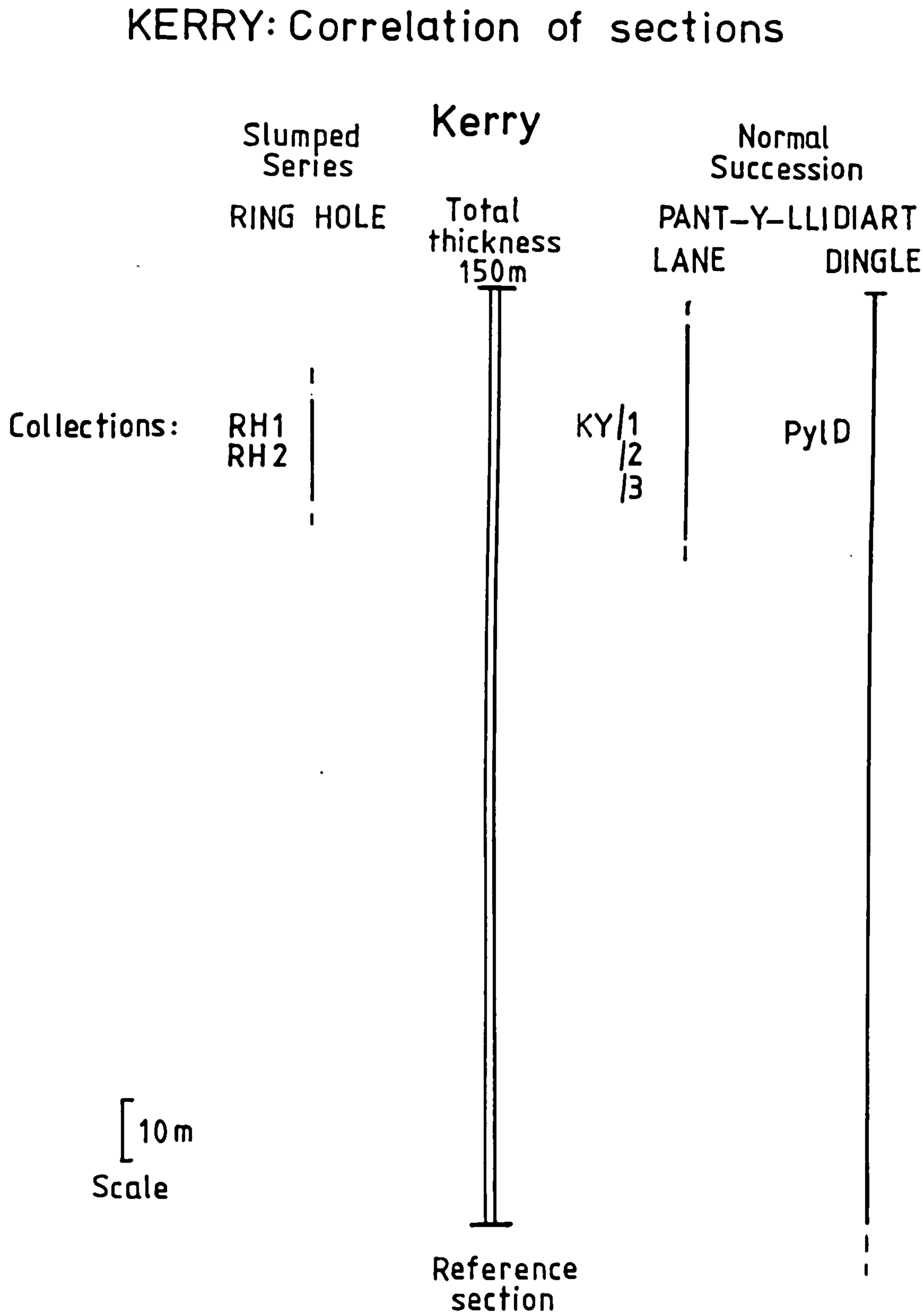


Fig. 4.14 : Kerry - Relative positions of sections in the succession.

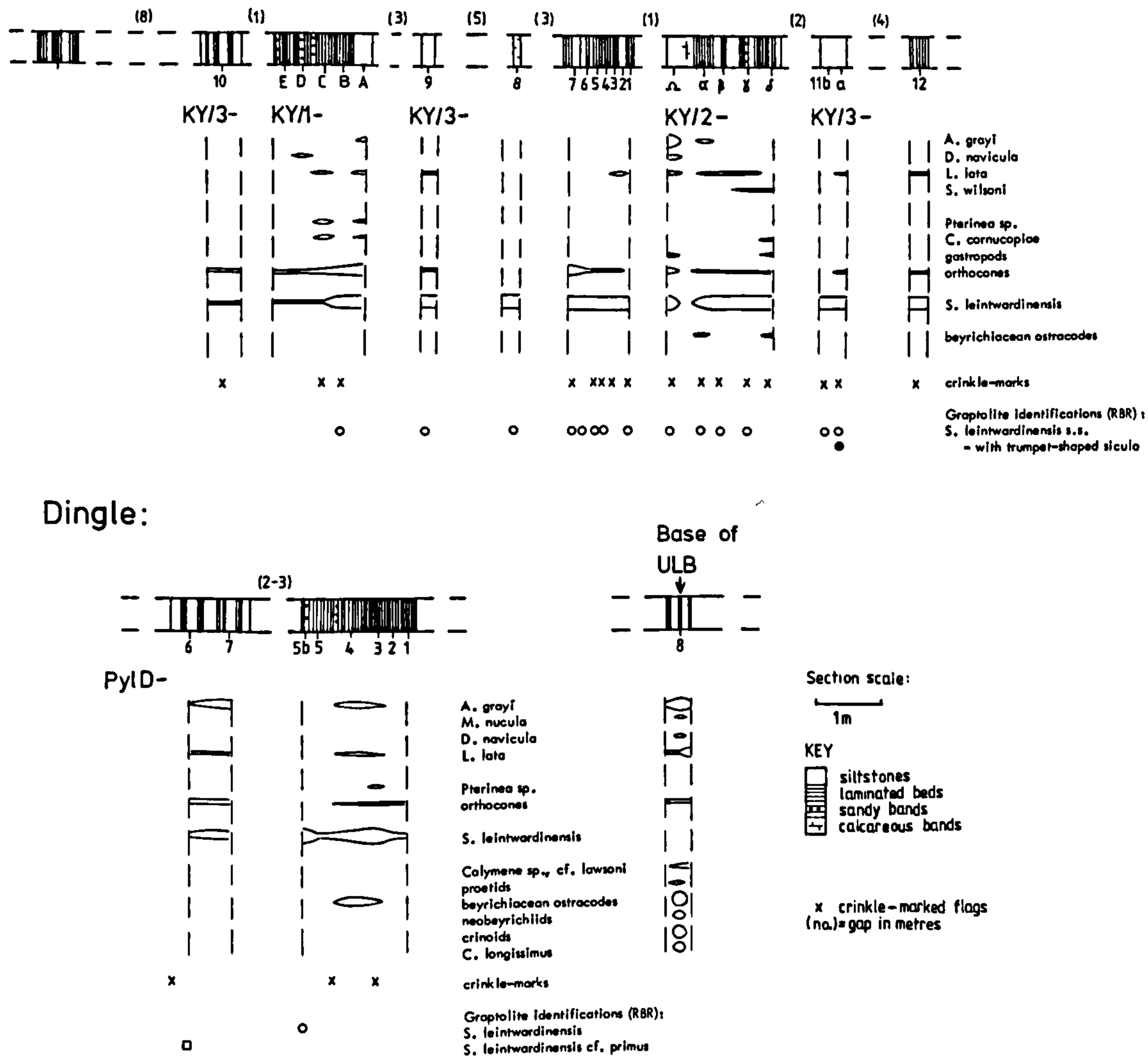


Fig. 4.15 : The succession of Pant-y-llidiart Lane and Dingle, Kerry.

middle to upper part of the succession was exposed. The equivalent level, in the slumped series was seen in the Ring Hole sections.

1. Pant-y-llidiart Lane KY/1-, KY/2-, KY/3- Fig. 4.15

The sequences examined were exposed in the banks of the lane leading to Cwm Quarry. They lie stratigraphically in the middle to upper part of the "M". leintwardinensis Shales. The relative positions of the collections are shown in Fig 4.14 p138. Approximately 30 m of the succession was covered.

The lowest 10 m of the series (including KY/3-10) comprise an alternation of closely laminated flags and thicker-bedded siltstones. The former units have micaceous and slightly coarser layers among the fine siltstone laminae. The flags are often crinkle-marked. Fossils are extremely sparse in this part of the sequence.

The beds of KY/1-E to A (75 cm) are dominantly thinly flaggy, laminated siltstones. The character varies from very finely (<1 mm) and evenly-bedded flags, to some with wider banding (up to 3-4 mm) in which minor discontinuities and small-scale current structures are seen. The lower 30 cm (D and E) have some coarser laminae, highly micaceous surfaces, and occasional planes of finely-disseminated organic material. Fossils, scarce in these bottom flags, become more frequent in the upper beds. S. leintwardinensis (RBR) and orthocones dominate the fauna, which includes rare L. lata valves, pteriniids and C. cornucopiae. A single valve each of A. gravi and D. navicula was found. The graptolites occur more commonly in silty laminae of the flags.

Collections KY/3- 9 to 1 were taken from beds over the next 12 m of sequence. 9 and 8 are from isolated bands of massive, calcareous siltstone. Both are rich in graptolites, which are distributed through the beds. In addition, collection 9 includes occasional drifted valves of L. lata. KY/3- 7 to 1 compose a 50 cm sequence of laminated and thicker-bedded flags. Some fairly massive bands are intercalated amongst thin, shaly flags. The lamination is often indistinct, and less even than in the lower beds. Layers which are commonly 1-2 mm or more thick, differ little in lithology. A few coarser bands and thin black "wispy" laminae also occur within these siltstones, however. Many of the flags are crinkle-marked. In the laminated units, fossils are generally on bedding surfaces. Patches of graptolites are found at

intervals, and orthocone internal moulds. In the unlaminated flags, graptolites are scattered through, often obliquely to the bedding.

Beds of KY/2 (Ω to δ) are about 1 m above KY/3-1. The lowest beds here are thickly bedded siltstones, with a few shelly fossils as well as graptolites and orthocones; A. gravi was quite common in one patch. A band of massive, unfossiliferous, slightly calcareous siltstone lies between Ω, and the overlying, well-laminated (thickness of layers from <1-3 mm) unit, α. Graptolites are common in planes of the latter unit, particularly in silty laminae. Mica-rich, decalcified layers also contain a number of graptolites. The higher beds have more unstriped flags interbedded with the laminated units. Graptolites remain the dominant fossils (including assemblages of parallel-aligned rhabdosomes in δ), but shells also occur rarely (L. lata valves and S. wilsoni). The strata of KY/2- are clearly crinkle-marked.

The top 6 m of the sequence include KY/3- 11 and 12. The former are thickly-bedded siltstones with planes of abundant graptolites, sometimes aligned. Rare valves of L. lata, and orthocones form the only associated fauna. By contrast, in collection 12, taken from laminated flags with layers ranging in thickness up to 3 mm, fossils are scarce. Only one L. lata valve and two orthocones were found in these flags. Again, the strata are crinkle-marked.

Overall, the abundance of the fauna, in which graptolites are prevalent, increases through the succession. In the upper strata, long and complete rhabdosomes were preserved on several planes, while other levels contain fragmented individuals. Lower in the sequence, occasional long specimens occur amongst shorter sections of rhabdosomes. The aligned assemblages (KY/2-δ, KY/3-11a) were orientated parallel to crinkle-marks, indicating that the orientations may have resulted from post-depositional movements. The graptolite identifications (RBR) are shown on the diagram. The individuals of S. leintwardinensis with a trumpet-shaped sicula from KY/3-11 are slightly unusual, and possibly indicative (RBR - pers. comm) of a high Leintwardinian level.

The rest of the fauna is numerically poor, with small, probably stunted, individuals. Orthocones (internal moulds) occur consistently, and occasionally quite frequently, through the succession; most specimens are short sections of the chambered portion of shells. Bivalves are represented by small pteriiids (P. tenuistriata) and

Cardiola spp. Rare gastropods (for example, Loxonema sp.), articulate brachiopods, and beyrichiacean ostracodes were found. A few L. lata valves occur at a number of levels through the succession.

No evidence of bioturbation was found.

2. Pant-y-Llidiart Dingle Pyl D- Fig. 4.15

The stream section extended through approximately the same part of the "M". leintwardinensis Shales as the Lane section - ie. the middle to upper portion - but also included the highest beds of the division. The sequences examined are shown diagrammatically in Fig

The lowest beds - Pyl D-6 and 7 - are fairly thickly-bedded siltstones, intercalated with thinner, laminated flags, and more calcareous bands. Crinkle-marked surfaces are common in the lower beds, while some flags from Pyl D-7 appear to have sole-marks. Fossils are sparse, and scattered through beds. Infrequent graptolites, valves of L. lata and A. gravi, and orthocones constitute the fauna.

The sequence Pyl D-5b to 1 lies 2-3 m above the first collections. These flags are dominantly laminated, except for the basal 3 cm band - 5b - of massive calcareous siltstone. The banding varies in its thickness and definition, being sometimes very fine, but in other parts, thicker and less even. Silty and muddy laminae alternate with more calcareous and coarser ones. Thin, black, wispy layers of organic material occur at intervals. Generally, the closely-laminated units are more thinly-flaggy than the rest. Some surfaces show small crinkle-marks.

Again, fossils are not common. Graptolites are relatively numerous in 5b and 3, although they are found in all the collections. Those in 3 are mainly concentrated in brown silty laminae of the flags. Collection 4 includes a plane of beyrichiacean ostracodes (identified as Amphitoxotidinae sp. nov. C (DJS)) associated with a few A. gravi, graptolites and L. lata.

The highest collection (Pyl D-8) was made from the top part of the section. The lithology here is an alternation of thin and thicker flags of laminated siltstone and more thickly-bedded units. The lamination is very even, compared with lower units, and flags have smooth bedding surfaces. Mostly, the strata are very poorly fossiliferous, with only occasional orthocones, A. gravi and L. lata valves. However, one

lenticular band (thickness 0-2 cm) is a decalcified horizon of shell moulds. A. gravi valves and beyrichiacean ostracodes are crowded together, with small crinoid columnals and calcium phosphate shell fragments. Minor constituents of the fauna include L. lata valves, and small calymenid and proetid skeletal elements. The ostracodes were identified (DJS) as N. scissa, N. cf. lauensis and Amphitoxotidinae sp. nov. C. From directly above this band (which thins out in one direction in less than 1 m), two quite large cranidia of Calymene sp. cf. lawsoni (DJS) were found. Higher beds have a similar, sparse fauna to those below the richly fossiliferous band. Graptolites were not found at this higher level.

The presence of N. cf. lauensis with A. gravi was taken to indicate the ULB in this area.

As in the Lane section, no evidence of bioturbation was found.

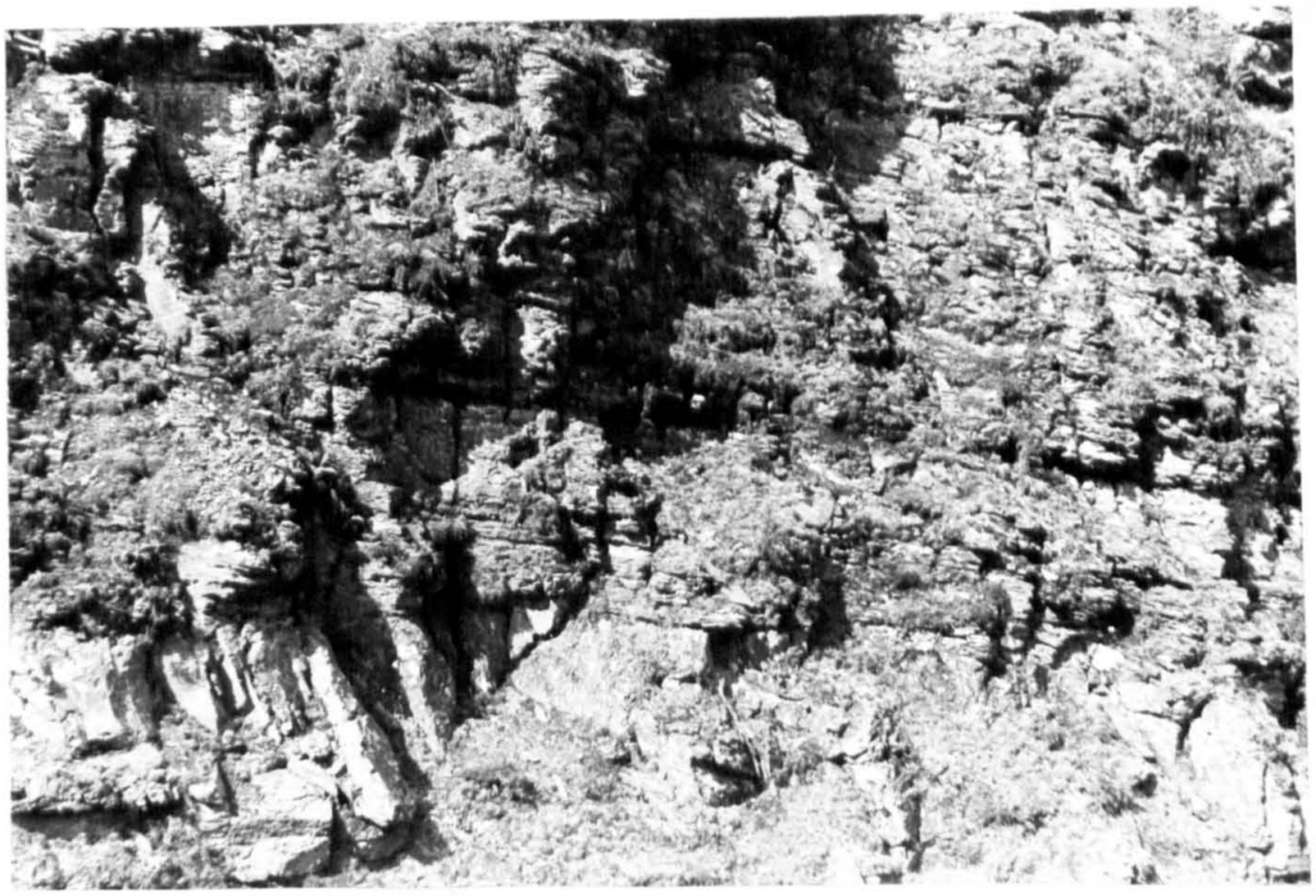
3. Ring Hole: RH1-, RH2-

Figs. 4.16 p144, 4.17 p145.

The rocks in the gorge sections comprise a series of well-bedded, siltstone and shale units alternating with slumped sequences. The period of slumping in this area extends from mid-Eltonian to late Leintwardinian times (through 800 m of succession); 70-100 m of the upper part of the succession are exposed in these sections (Bailey and Woodcock '76). The dip of the strata ranges between 10° and 20°, eastwards, so that the gorges provide both strike and dip sections.

The slump units are often 5 m or more thick, with variably-shaped, tight, recumbent and round-nosed folds, of generally small amplitude (commonly less than 2 m). Their hinge lines are dispersed fairly widely, but with a dominantly NE-SW trend. Vergence is to the SE, indicating a palaeoslope dip in that direction. There is no cleavage associated with the folds, but small microfolding lineations are strongly developed. Two intersecting sets of crinkle-marks are seen on many surfaces: the stronger one parallel to the fold hinges (NE-SW), and the weaker, approximately perpendicular to that. The sediments are thinly flaggy, tough, grey siltstones. In some slump units the contorted beds can be seen to pass laterally into more normally-bedded sequences.

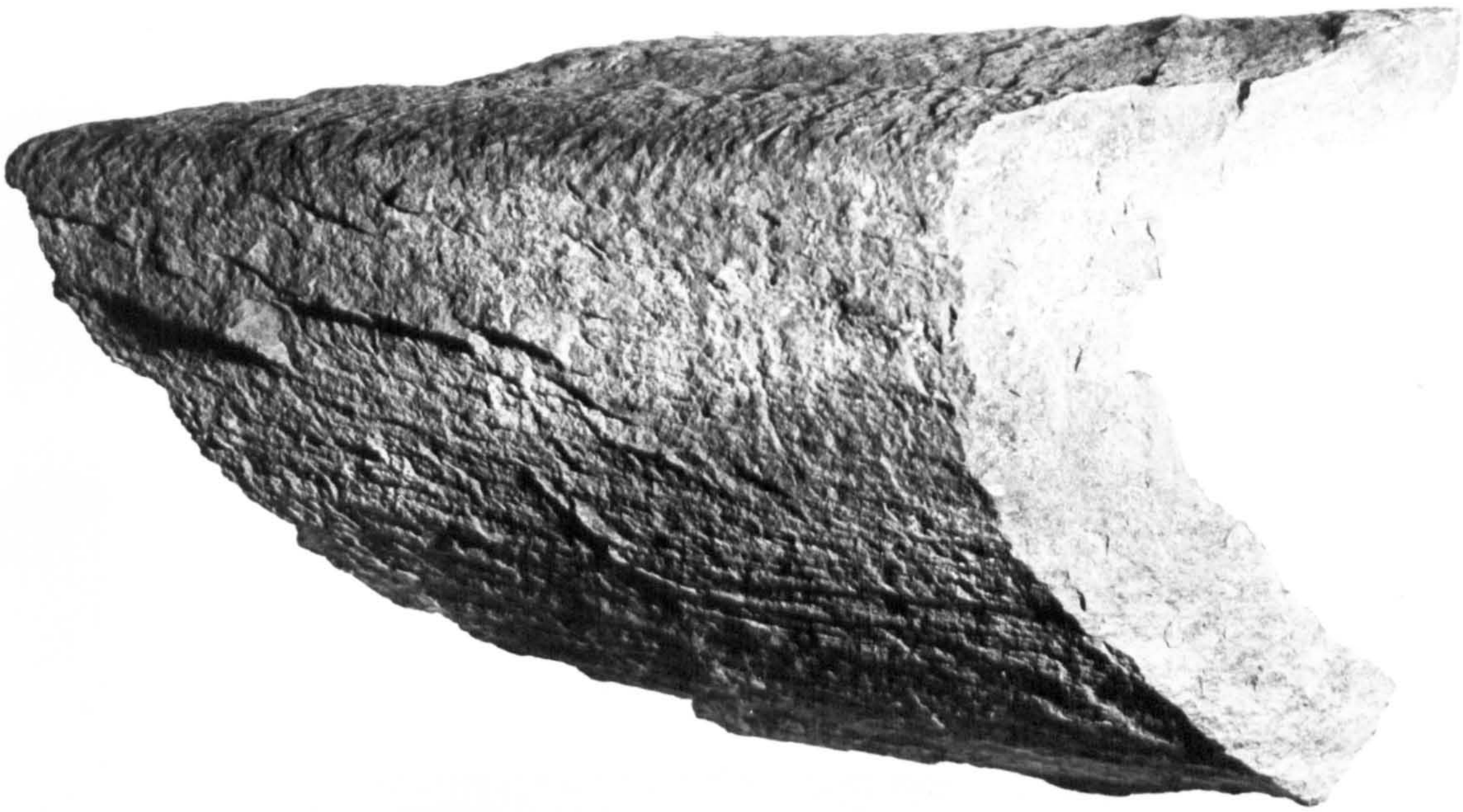
The undisturbed units are mainly thinner than the slumped sequences, commonly 1-2 m thick. They are well-bedded, thinly flaggy siltstones,



a : Slumped units alternating with normally-bedded siltstones. The former often have sharp upper contacts.

b : Folded, contorted strata of slumps above undisturbed siltstones. The boundary between the two is gradational.

Fig. 4·16 : Ring Hole - Slumped series. (upper Eltonia
Leintwardin



a : Nose of round-hinged slump fold. Crinkle-marks parallel to fold hinge. (x 1/2)

b : Folded beds showing lineations - crinkle-marks - parallel to fold hinge. (pen for scale)

Fig. 4·17 : Ring Hole slumps - Leintwardinian.

similar in lithology to the slumped beds. Coarser laminae alternate with finer beds, with only minor discontinuities in some very evenly-bedded units. Other parts are less thinly-bedded, with infrequent bands of coarser or muddier material. The undisturbed units are laterally extensive. A few beds show weakly-developed crinkle-marks.

The lower contacts of the slumped and normally-bedded units are typically gradual, but the upper contacts are sharp, sometimes erosional. The former condition probably reflects the high shear strains near the base of the moving sediment sheet and in the top of the underlying beds (Woodcock '76). The truncation of the top of the slump units indicates that the deformation took place prior to the deposition of overlying sediment.

Two collections were made from slumped beds in the upper part of the succession. Fossils are rare in these beds. RH2- included a few graptolites, identified as S. leintwardinensis (RBR), patches of scattered moulds of D. navicula, occasional S. wilsoni and orthocones among an infrequent fauna. RH1-, from slightly higher in the succession, yielded only rare orthocones.

From beds of undisturbed units, again the fauna is restricted; a few orthocones were the only fossils found.

Kerry: Synthesis

The thick succession (150 m) in the Kerry district is composed of poorly-fossiliferous, laminated and thinly-flaggy siltstones. In the SW, large scale slumping towards the SE extends through to the late Leintwardinian (Bailey and Woodcock '76). The sparse fauna is mainly graptolitic, with rare pelagic fossils (eg. small pteriniids and orthocones) and L. lata. The slumped beds include infrequent assemblages of scattered benthonic shelly fossils (eg. D. navicula).

At Pant-y-Llidiart Dingle (PylD-8), an ULB fauna with N. cf. lauensis and A. gravi was found in a thin fossiliferous seam at the top of the leintwardinensis beds.

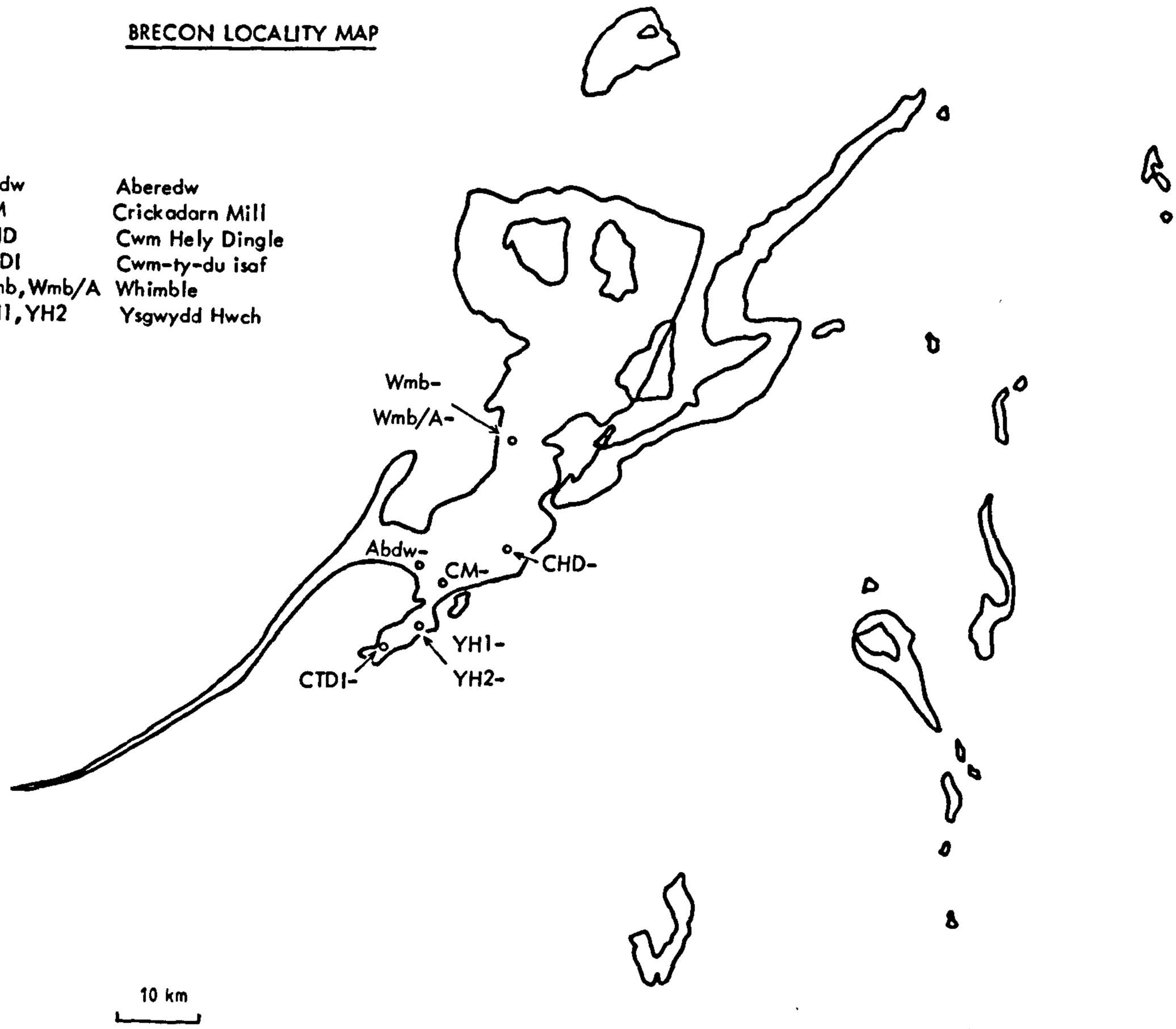


Fig.4.18 : Locality map showing the sections from the Brecon Anticlinal region.

D. BRECON ANTICLINAL REGION

The Silurian rocks of this area were mapped and described by Kirk ('49). She recognised a lithostratigraphical division - the Striped Flags - which included the zones of Pristiograptus tumescens and S. leintwardinensis. The top of the latter zone extended up into the overlying "Chonetoidea" gravi flags. The Striped Flags showed considerable thickness variations across the region. In the Lower Chapel district (ie. SW) a thickness of 335-360 m was recorded. Further NE, the succession of 105-160 m in the Brampton Scar-Wapley region thickened to the NW side of the anticline, and near New Radnor was 470 m.

Localities in the leintwardinensis zone of the Striped Flags were selected to examine briefly the faunal and facies variations across the area (see map in Fig 4.18 p 147). Detailed studies of the succession were not made in this region, which is not on the line of the main transect used for the project. However, its intermediate position between the shelf and basin areas is reflected by the mixed shelly and graptolitic fauna, which is useful for the correlation of the LLB fauna with the leintwardinensis zone.

1. Cwm-ty-du isaf CTDI- (SO.016.363)

The beds examined were from a fairly high level in the Striped Flags. The sequence comprises thinly-bedded, fine, laminated siltstones, with alternating muddy and silty bands, and more micaceous layers. The flags have smooth bedding surfaces. Numerous minor sedimentary discontinuities, and some small, cross-stratified ripples, can be seen in the lamination. Many of the siltstones are unfossiliferous, but thin horizons of shells and bioclastic debris occur at intervals. Several fragments of graptolites (? S. leintwardinensis (LC)) were found on otherwise barren planes. These, and rare pteriniids, are the only fossils from beds between the shell layers. In contrast, the fauna of the shell assemblages is dominated by brachiopods. D. navicula valves are crowded on these planes, along with some disarticulated M. nucula, I. orbicularis, S. lunata, P. ludloviensis, S. ornatella, and F. amygdalina. Orthocones (small, internal moulds) are fairly common. One D. navicula assemblage contained rare A. gravi valves, and a few small beyrichiacean ostracodes.

Siltstones of a similar lithology from a lower level in the Striped Flags contain very comparable faunas, except that the graptolite

here is M. tumescens (which occurs commonly on some planes). S. ludloviensis is an important element of the faunas in the lower zone.

Between the two series of Striped Flags is a sequence of massive, irregular, very calcareous siltstones. Thin horizons with rich faunas are separated by unfossiliferous beds. Abundant isorthids occur with M. nucula, A. reticularis and D. navicula. Pieces of branching bryozoa and P. lanceolata are common. Many Dalmanites sp. pygidia, some of which are large, are present in the assemblages. This fauna indicates a stratigraphic level below the LLB for these calcareous strata.

2. Ysgwydd Hwch YH2- SO.041.373

YH1- SO.042.372

The first of the two localities examined here - YH2 - includes rocks from the middle part of the Striped Flags, exposed along the stream. The strata are smooth, even, finely to more thickly laminated siltstones, in which minor current structures are commonly seen. Thicker beds of siltstone are intercalated among the laminated units.

Fossils are very sparse. Occasional valves of D. navicula are scattered on bedding planes. Rare M. nucula and I. orbicularis are present. Single specimens of L. lata (one valve), a beyrichiacean ostracode, and an orthocone (which was filled with fine bioclastic debris), complete the fauna.

The second locality - YH1 - was a small quarry of thickly-bedded, irregularly-splitting, hard calcareous siltstones, (approx. 4 m section) with some thinner, wispily-laminated bands. The fauna is mainly concentrated into fairly common shell horizons, although some fossils are distributed through beds. Assemblages are numerically rich.

The lower part of the quarry is characterised by almost monospecific bands of D. navicula, I. orbicularis, S. ludloviensis and M. nucula. Separate assemblages of F. amygdalina valves, sometimes with aligned individuals, occur at several levels. Less common elements of the fauna include small A. reticularis, S. wilsoni, S. lunata, A. grayi and S. ornatella. Fragments of graptolites of ? S. leintwardinensis (LC) were recorded from these beds.

Higher beds in the quarry show an increase in the abundance of S. ornatella, which becomes very common in bands and lenses. Valves are very variable in size in these assemblages. At other horizons, large

A. reticularis, and L. depressa with trails are numerous, together with D. navicula. Several valves of F. amygdalina and G. cymbaeformis lie in beds between the shell horizons. The faunas have become more diverse in this upper part. Skeletal elements of proetids (including warburgellids) are now common, while Calymene sp.(DJS) is present. Beyrichiacean ostracodes from these beds were identified as H. cf. loensis and Calcaribeyrichia sp.1 (DJS); they mostly occur in patches with A. gravi and fine fragmental material.

A number of the beds in the quarry show some narrow (2-3 mm) burrow traces running obliquely through the lamination. In patches of these flags, the layering had been almost destroyed, probably by more extensive biogenic reworking.

The beds in the quarry represent a stratigraphical level near the base of the "C" gravi flags. The typical lithology of the Striped Flags has been replaced by the thicker-bedded, more calcareous facies of the overlying division. Faunally, the assemblage appears to be high in the LLB. Slightly higher in the succession, fossils include A. gravi, neobeyrichiids, Calymene sp., Encrinurus sp. among a rich and diverse fauna (Lawson - pers. comm. '76). This assemblage is taken to indicate the ULB here.

3. Aberedw Abdw- SO.081.473

The crags by the river exposed some units of slumped beds alternating with undisturbed strata.

The slumped beds are finely-laminated siltstones and muddier bands, which have gentle folds and corrugations striking approximately NE-SW. Crinkle-marks across bedding surfaces have a similar trend. Two units are fully exposed here, and these are each less than 1 m thick. Fossils are rare in these beds, although many surfaces show aligned prod-marks and tool marks. These, and a plane of scattered, but orientated, shells (with S. wilsoni, M. nucula, D. navicula and an orthocone) indicate a direction of movement to the north-west.

The normally-bedded siltstones between the slumped units are very finely and evenly laminated, with interleaved muddy and silty laminae, and occasional micaceous and coarser bands. Minor sedimentary structures seen in the lamination include thin cross-bedded units and numerous

small discontinuities. Some planes are closely ripple-marked (Fig 4.19 p153). These flags appear to be unfossiliferous; one plane included some very worn, black fragments that were possibly graptolites or other organic material.

Wood (1900 - p 438) recorded one or two horizons of abundant S. leintwardinensis which occurred "associated with small specimens of L. lata", in the riverside crags at Aberedw, among a considerable thickness of unfossiliferous rocks. The sequence examined in the present study, although no diagnostic fossils were obtained, is thought to be from this stratigraphic level, ie. the upper Striped Flags of Kirk ('49).

4. Crickadarn Mill CM- SO.085.426

The escarpment on the north side of the river provided exposures through the top part of the Striped Flags and into the overlying "C". grayi flags.

The lowest strata are thinly-bedded, laminated, calcareous siltstones alternating with more irregular bands. Sandier and more micaceous laminae are interbedded with the calcareous and silty ones in finely-layered units. The unevenly-splitting siltstones have a more homogeneous lithology of calcareous siltstone. Fossils are scarce in these strata. Small prod-casts and groove-casts are commonly seen on under surfaces of flags with scattered Davia navicula shells. A few L. lata valves were found on one bedding surface.

Higher in the succession, the flags are irregularly, though thinly, bedded, calcareous siltstones. Small-scale, cross-bedded ripples and calcareous lenses, are common in these beds. Thin units show wispy lamination of siltier and more calcareous beds. Narrow burrow traces can be seen across the surfaces of some flags. Again, these beds are not very fossiliferous. D. navicula is the most widely distributed form, with small valves dispersed through beds as well as small lenticular accumulations at the bases of beds. Occasional valves of I. orbicularis and M. nucula are associated with these latter deposits.

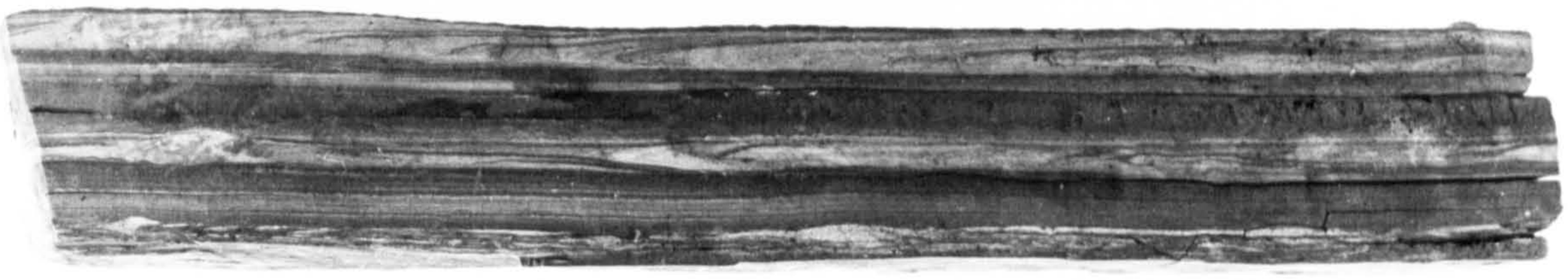
The next 6-7 m of the sequence, though similar in lithology, are much more fossiliferous. Burrow traces are fairly numerous on some surfaces. Shells are commonly crowded on bedding planes, and in thin lenses. Some are scattered through beds, and orthocones, pteriniids,

and tentaculitids most usually are separate from the shell horizons. Assemblages contain closely-packed, sometimes imbricated, valves of P. ludloviensis and D. navicula, often in monospecific faunas. At other levels disarticulated M. nucula, I. orbicularis, S. lunata, S. ludloviensis and S. wilsoni (flat specimens) are associated with these two prevalent species. Large amounts of bioclastic debris are included in some of the shell accumulations. Occasional planes have large, convex-up valves of P. ludloviensis which show some alignment of the hinge lines. The faunas are dominated by brachiopods, but F. amygdalina, G. cymbaeformis, bryozoa, crinoid columnals and Bucanopsis expansus are minor constituents of assemblages.

Towards the top of the sequence, the siltstones are less muddy and more thickly-bedded. At this level, beyrichiacean ostracodes and trilobites become more common. Among the former, N. confluens (DJS) was identified, while the latter includes C. puellaris (DJS) and proetids. Two specimens of articulated F. amygdalina were found perpendicular to the bedding, and apparently in situ (see p 257). Shells are concentrated less into bedding surface assemblages at this level, being found more evenly distributed, and randomly orientated, within beds. Small, decalcified "nests" of ostracodes, with A. gravi and fine shell debris, occur in some siltstones.

The next exposures up are the much more thickly-bedded, very calcareous siltstones corresponding to the "C". gravi flags of Kirk ('49). Massive, well-laminated beds with some cross-stratified units and ripple-marked surfaces, are interbedded with unlaminated, irregular, less calcareous, bands. The lower contacts of the laminated beds are sharp and sometimes erosive, but the upper boundaries are transitional. Numerous, narrow (mostly less than 1 mm across), silt-filled burrows run obliquely through, and parallel with, the lamination of these units (Fig 4.19 p 153). The bedding is often little disturbed by these traces, however. A few units show areas of more extensive reworking in the top layers, where the bedding has been destroyed. Fossils are uncommon within the laminated bands, and shells are largely restricted to thin lenses at their bases, or in the "unstriped" flags. Large orthocones (Michelinoceras bullatum, Kionoceras angulatum, and Lituites

a : Aberedw - Ripple-marked surface to flag. (x 1/2)



b : Aberedw - Side view of same flag showing small-scale current structures in finely-laminated muddy siltstones. (x 1/2)

c : Crickadarn Mill - Burrowed, very calcareous siltstones of the basal "C" grayi Flags. (x 4/3)

Fig. 4·19 : Brecon localities.

ibex) have a scattered distribution. M. nucula, S. ludloviensis and P. ludloviensis are prevalent in shell assemblages, but D. navicula has decreased greatly in abundance.

Strata 2-3 m higher in the succession have fewer, massive laminated units (mostly well-burrowed) within the sequence of thick, irregularly-bedded, calcareous siltstones. These beds are more fossiliferous, with frequent horizons packed with large valves of S. lunata, P. ludloviensis and M. nucula. Assemblages of bivalves (large individuals), including F. amygdalina, Pteronitella reticulata and Pterinea spp., occur commonly. Some planes have well-aligned individuals, but in others the valves are less uniformly arranged. A few articulated specimens of F. amygdalina were found. Large orthocones are very common (- K. angulatum, M. bullatum, L. ibex and unidentified species).

The appearance of the neobeyrichiid N. confluens, A. gravi and C. puellaris in faunas of the flags transitional between the thinly-bedded, irregular calcareous siltstones and the thicker "C". gravi flags was taken to indicate the base of the ULB here.

5. Cwm Hely Dingle CHD- SO.119.458

The lower exposures along the stream include some thin, even, closely-laminated siltstones, in which silty and muddy beds alternate with micaceous and coarser layers. A number of the smooth surfaces have prod-marks, and are finely crinkle-marked. The microfolds have a trend roughly NE-SW. Fossils are very sparse in these beds. Occasional monograptid fragments, and a few L. lata valves are distributed across planes. In addition, two specimens of L. lata were found apparently in situ, perpendicular to the bedding. The only other fossils recorded were rare small P. ludloviensis valves.

Higher beds in the succession are thinly and irregularly bedded, calcareous siltstones, with well-developed crinkle-marks on bedding surfaces. Shells are much more common at this level. P. ludloviensis valves, many still with spines, dominate many plane assemblages. M. nucula, I. orbicularis and S. lunata are minor elements of these faunas. Several orthocones are present on otherwise unfossiliferous planes.

A unit of clearly slumped, contorted, and crinkle-marked strata is composed of much more thickly-bedded, calcareous siltstones, lying directly upon thinly flaggy, wispily-laminated siltstones. One slumped

bed contains numerous articulated specimens of F. amygdalina, many of which are oblique to the bedding. Other shelly horizons have crowded valves of P. ludloviensis, alone, or with S. lunata, M. nucula, O. rugata, orthocones and F. amygdalina. A few valves of A. gravi are scattered in the slumped beds.

The crinkle-marked surfaces throughout the exposures suggest that these beds have all undergone some degree of post-depositional slumping. Movement in the lower, evenly-bedded, laminated units, must have been very slight. However, the bedding of the top, thick siltstones is highly disturbed, indicating more extensive transport. The direction of slumping, if perpendicular to the folding and crinkling, is from the SE or NW.

The fauna and lithology of the slump unit is typical of the "C". gravi flags. Underlying beds, by comparison with the Crickadarn Mill succession, correspond to a fairly high level in the upper Striped Flags.

6. The Whimble Wmb-, Wmb/A- SO.205.626

The exposures examined (at the hill summit) are of thinly flaggy siltstones, many finely-laminated, but others more thickly-bedded. The latter, especially, tend to split irregularly.

The shelly fauna is mainly concentrated into discrete horizons, with few individuals in the intervening beds. There are two types of these assemblages. The first is dominated by brachiopods, often in almost monospecific accumulations of crowded valves. D. navicula, M. nucula and I. orbicularis are prevalent species. Disarticulated S. ludloviensis, A. gravi, and P. ludloviensis, beyrichiacean ostracodes, orthocones and B. lloydii are minor constituents of the faunas. The second type of fossiliferous horizon is, typically, a thin, decalcified "biscuit" seam, in which abundant beyrichiacean ostracodes are associated with A. gravi valves, crinoid columnals, and fine bioclastic debris. One of these deposits also contained numerous, very small valves of D. navicula. The ostracode layers are much less laterally extensive than the brachiopod assemblages, mostly being confined to small "nests" and thin lenses.

In strata between the shelly horizons, some bands are rich in graptolites of S. leintwardinensis (RBR). In laminated units, the

rhabdosomes are distributed on planes, but some thicker-bedded siltstones have scattered, randomly-orientated specimens. There is little other fauna with the graptolites. One band contained a few L. lata valves with a patch of rhabdosomes. In others, rare A. gravi, orthocones and P. tenuistriata are present.

The presence of the bands of S. leintwardinensis among thinly-bedded flags with assemblages of A. gravi and beyrichiacean ostracodes, indicates a high level in the Striped Flags, and a position near the LLB-ULB boundary.

Strata (Wmb/A-) lower (200-300 m below) in the succession are thin, even, laminated, shaly siltstones, with smooth, and often micaceous, bedding surfaces. Two intersecting sets of crinkle-marks are developed on these planes, suggesting slight slump movements at this level in the Striped Flags. The beds appear to be unfossiliferous.

Brecon: Synthesis

The approximate geographical positions of the localities visited are shown in Fig 4.18 . Their faunas are plotted in Fig 4.20 .

The lower beds in the leintwardinensis zone of the Striped Flags were seen at Ysgwydd Hwch Dingle (YH2-), Aberedw, Crickadarn Mill, Cwm Hely Dingle, and the Whimble (Wmb/A-). The lithology is thinly and evenly-bedded, well-laminated, muddy and shaly siltstones, with smooth bedding surfaces. Indications of weak current activity are provided by the minor sedimentary discontinuities in the lamination, and small cross-bedded ripples. Fossils are sparse in these beds, with a restricted fauna of graptolites, L. lata, Pterinea spp., orthocones, and rare articulate brachiopods. Slump units alternate with normally-bedded sediments at Aberedw. Crinkle-marked surfaces are associated with these slumps, and were also seen in the well-laminated beds at Cwm Hely Dingle and on the Whimble (where two intersecting sets were developed). The main trend of crinkles and folds is NE-SW, with a direction of movement, suggested by prod-marks and aligned fossils, to the NW.

Higher in the succession of the Striped Flags, condensed shell bands occur within the siltstones. In the SW, at Cwm-ty-du isaf, and at the Whimble (Wmb-), the fossiliferous horizons are interbedded among mostly well-laminated units, and these intervening siltstones continue to have the limited faunas, with graptolites, described above.

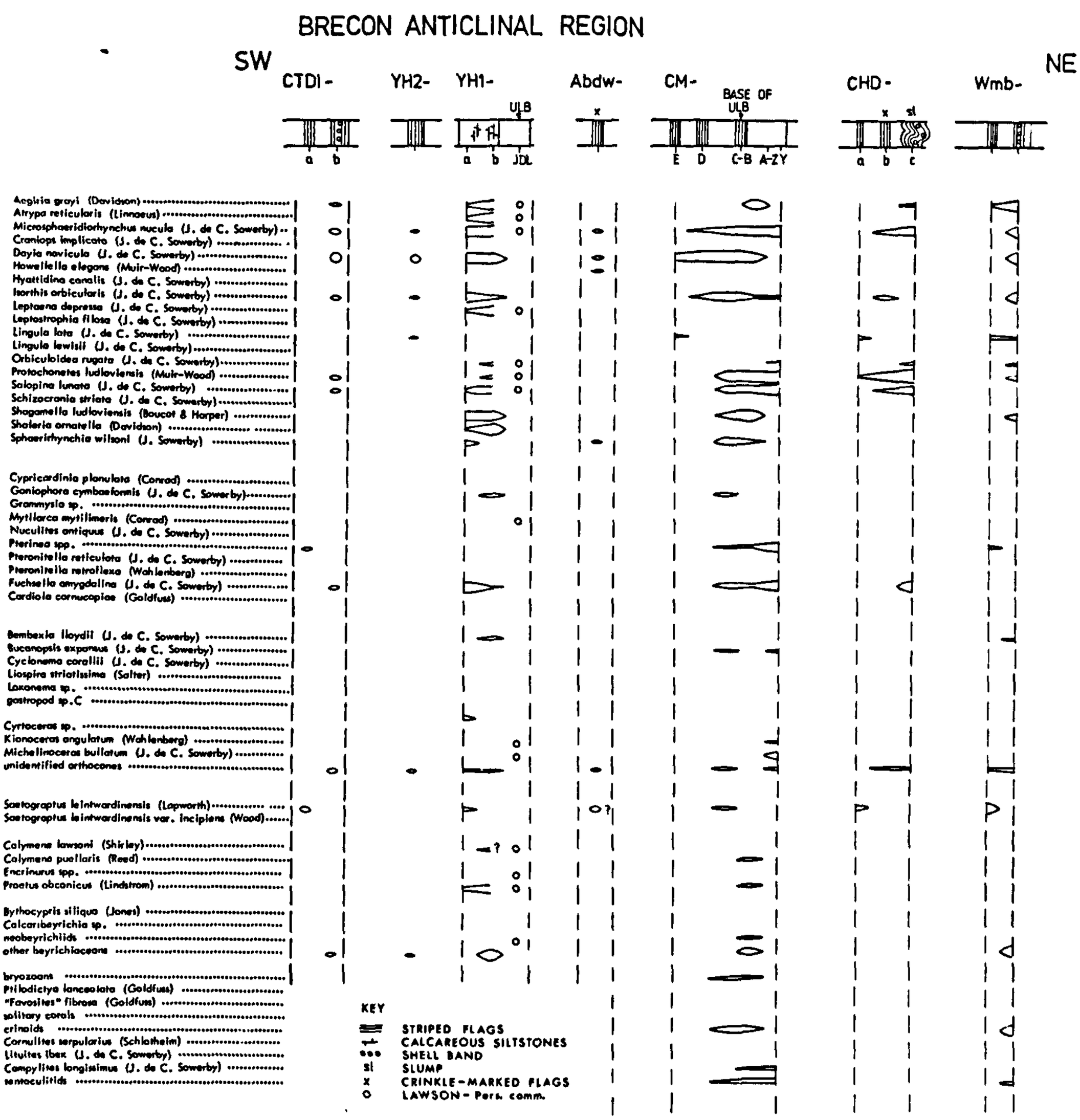


Fig. 4.20 : The succession in the Brecon sections.

However, at Ysgwydd Hwch (YH1-) and Crickadarn Mill, laminated beds become subordinate to irregularly and more thickly-bedded, calcareous siltstones, in which shell bands and lenses become common. In both localities, some of these higher beds are burrowed. At Ysgwydd Hwch, the siltstones are much more thickly flaggy and more calcareous than those at Crickadarn Mill. The latter are similar in facies and fauna to beds at Cwm Hely Dingle, which appear from their crinkle-marked surfaces to be slumped. Beds between the shell bands are poorly fossiliferous, but with scattered shells rather than graptolitic faunas.

The lithological transition to the "C". gravi flags, at Crickadarn Mill, is a fairly rapid change to thicker, irregular flags, in which very calcareous, thickly laminated units, cross-stratified in parts, alternate with 'unstriped' siltstones. The horizons with numerous, narrow, silt-filled burrows occur at this level. A faunal diversification, and appearance of ULB forms, takes place at the top of the thinner-bedded, muddier facies. At Ysgwydd Hwch (YH1-), the lithological passage is more gradational, and ULB fossils come in some way above the facies change. The top slumped beds at Cwm Hely Dingle, which are much more thickly-bedded than the underlying flags, contain a fauna resembling that of the "C". gravi flags at Crickadarn Mill.

E. KNIGHTON: Cwm Jenkin CJ- (SO.235.732)

The Ludlow rocks of the Knighton district were mapped and described by Holland ('59). The zone of S. leintwardinensis here corresponds to the uppermost part of the Bailey Hill Beds. Associated with the appearance of this graptolite is a change in the lithology, to thinner-bedded, shaly and flaggy siltstones, which takes place in the top 30-35 m of the group. The overlying Knucklas Castle Beds (460 m) are similarly-bedded, but more calcareous, flags, distinguished negatively by the rarity of their fossils. Graptolites have disappeared from the fauna at this level. No equivalent to the ULB can be recognised in the Knighton district.

The strata exposed in crags at Cwm Jenkin are thinly-bedded, shaly and flaggy calcareous siltstones. Laminated units are interbedded with more homogeneous flags. The former siltstones vary from being very finely and evenly-layered to having wider (2-3 mm), more sporadic or gently undulating, lamination. Small cross-bedded ripples and calcareous lenses are fairly common in some beds. The "striping" is due to an alternation of calcareous and siltier beds, with some micaceous layers. Many of the bedding surfaces of the siltstones are smooth, but a few show minor crinkling of the sediment.

Graptolites are the most common element of a relatively sparse, limited fauna. They occur both in the laminated and more thickly-bedded siltstones. In the latter beds, they are irregularly distributed, but are concentrated in silty laminae of the former. Specimens were identified as S. leintwardinensis and ? S. leintwardinensis primus (RBR). Shelly fossils are rare except for L. lata (complete, single valves), which occur with graptolites on several planes. In addition, a few L. lata specimens are found vertically through beds, possibly in situ. The rest of the fauna comprises orthocones, rare beyrichiacean ostracodes, and crinoid columnals.

F. LLANDOVERY: Clawdd British CB- SN.8745.3669

The strata in the quarry are thinly flaggy and shaly siltstones, with minor calcareous lenses. Some bands are closely laminated, with coarser-grained and more calcareous layers interleaved with fine, dark, muddy siltstones. The smooth bedding surfaces to flags are sometimes gently ripple-marked, and a number of small, cross-bedded lenses can be seen in section. Other flags are more thickly and unevenly bedded.

Shelly fossils are largely confined to bedding plane assemblages, and thin lenses. D. navicula and M. nucula dominate these faunas, with crinoid columnals, a few S. lunata, Glassia obovata, O. rugata and H. elegans. The shells are tightly-packed, sometimes imbricated, disarticulated valves, associated with much fragmental material. At separate horizons, graptolites, P. tenuistriata and C. cornucopiae are quite common. The graptolites (identified as S. leintwardinensis (RBR)) are mostly found in silty laminae. Pteriniids occur on the same planes as graptolites at several levels. A calymenid cranidium from these beds was identified as C. cf. puellaris (DJS).

From similar beds about 3 m above this collection, A. gravi, S. ornatella, N. lauensis and C. puellaris were recorded. (LRG. Bulletin 23 - '76). Their presence indicates a stratigraphic position for these higher beds in the ULB; the collection is therefore from very close to the LLB-ULB boundary.

CHAPTER FIVE

FACIES AND FAUNAL DISTRIBUTIONS

The stratigraphical data in Chapters 2, 3 and 4 has been used, together with the results obtained by other workers in areas not visited during the present study, to compile four facies maps for the Leintwardinian and a vertical range chart for areas on a basin-to-shelf transect. The distributions and abundances of selected fossils are plotted on these base maps, and are discussed in relation to the modes of life of the organisms to assess palaeoecological preferences and tolerances.

FACIES MAPS FOR THE LEINTWARDINIAN

The additional sources used to compile the facies and faunal maps are indicated on the locality map Fig 5.1 p 166. The key to the maps is shown in Fig 5.4 p 169 , and explained on p 165.

Map A - Basal LLB: Fig 5.2 p 167.

The base of the LLB in the shelf region is taken at the level of the disappearance of the diagnostic UBB fossils. In the northern part - at Ludlow, Wenlock Edge (including the IGS Dean borehole), Lye, Woodbury and Perton - the faunal changes take place in the upper beds of the Aymestry Limestone facies. Except at the type section (at Sunnyhill Quarry), this level is marked by a widespread development of conglomeratic limestone bands (discussed in Ch. 6 p309-29) in the basal LLB. At Chances Pitch, the gradual replacement of the Aymestry Limestone by siltier facies coincides with the UBB-LLB faunal changes, but the lower strata of the LLB include a number of conglomeratic bands.

The inliers further south (S. Woolhope, May Hill, Newnham and Purton, and in the Tites Point borehole (IGS)) have thicker, coarser and more numerous basal conglomerates. The Aymestry Limestone is not developed, or is missing, in these areas so that the lowest LLB deposits may rest unconformably on beds beneath. At Gorsley, 1.5 m of LLB siltstones lie on the eroded surface of the Gorsley limestone, which was correlated by Lawson ('54) with the Wenlock Limestone. This represents a considerable break in the succession. At Usk, Walmsley ('59) described a quartz conglomerate bed at the level of the base of the LLB, resting erosively on the underlying beds. The horizon appeared to thicken to the south, and thus may be derived from that direction.

In the SW part of the LLB outcrop, in the Llandovery-Llandeilo area, the facies were described by Potter and Price ('65 - p 396) as "a sandy variety of the shelf facies". The lithologies are largely non-calcareous. They overlie the red deltaic facies of the Trichrûg Beds in the Sawdde Gorge and Cennen Valley, which pass into more argillaceous lateral equivalents to the NE. West of Llandeilo, the Ludlow rocks are completely overstepped by younger rocks.

In the Leintwardine to Aymestrey area, the faunal changes at the UBB-LLB junction correspond with the facies change from the massive, nodular limestones to more thinly-bedded and silty strata. At Shelderton, the basal LLB are very shelly, calcareous siltstones and limestones of the Dayia beds, which lie directly upon the Aymestry Limestone with UBB fossils. The sharp contact at Aymestrey is unconformable, with fine LLB siltstones resting on the eroded top surface of the Limestone. Lawson ('73(a) - p 261) found a conglomeratic limestone bed at the top of the Limestone in the Bengry Track section at Aymestrey. This correlates with the similar deposits in other areas at this level.

West of Aymestrey, the shelly faunas of the type section are absent or rare, and correlation relies upon the occurrence of S. leintwardinensis. The succession consists of fine laminated siltstones over much of the outcrop, often poorly fossiliferous. Slumped beds at Lyepole Bridge (near Aymestrey) which contain shelly fossils are interbedded with undisturbed units of graptolitic siltstones. ? S. incipiens or S. leintwardinensis cf. primus together with S. leintwardinensis (RBR) from these latter beds indicate that the slumps are at a low level in the leintwardinensis zone. A major development of slumping in the SW Clun Forest district (Earp '40) extends through the zone.

Map B - "Middle" LLB: Fig 5.2 p 167

This facies map includes the main part of the LLB.

In the shelf inliers, the strata are thinly-bedded, calcareous siltstones and shelly limestones. Conglomeratic limestones are uncommon by this level in the succession. There is a rich benthonic fauna, which occurs, typically, in bedding-plane assemblages. Relatively few fossils are found in the sediments between the fossiliferous

horizons. The assemblages are commonly dominated by one or two species (usually brachiopods or bivalves), the prevalent types change repeatedly and frequently.

At Ludlow, the strata include parallel-laminated, calcareous siltstone units with basal shelly lenses and bands: the sheet-laminated siltstone facies (Ch. 6 p375). Fossils are again largely confined to discrete layers, with few in the intervening beds. It is in the middle LLB that D. navicula and I. orbicularis reach their acmes at Ludlow. The hLLB of Wenlock Edge (Shergold and Shirley - '68) are included in this map.

The Llandovery-Llandeilo region still has the non-calcareous shelly siltstone facies at this level.

Around Leintwardine, the instability of the shelf edge region is indicated by several submarine canyons cut in LLB times (Whitaker '62) which trend ENE-WSW from shelf to basin. Whitaker ('62 p 327) comments upon the less common benthonic fauna of the upper half of the LLB until towards the topmost beds. This applies both to the channels and to the sequences with conformable LLB successions (whose thickness of 30 m compares with up to 65 m in the erosive channel sequences). In the channels hLLB assemblages of exotic fauna, such as starfishes and eurypterids, are found at some levels. In the Main Quarry at Aymestrey, the strata above and below the conglomerate AY/A-Ca have markedly different faunas. The higher beds appear very comparable to the hLLB of Whitaker's channels, and the sequence is interpreted as consisting of channel-fill beds above the conglomerate (p 131).

In the areas of basinal facies, slumping is evident in many areas. In the Brecon Anticlinal, small-scale, local slump folds were found at Aberedw (Abdw-) and Cwm Hely Dingle (CHD-), while crinkle-marked beds were seen in the Striped Flags succession at the Whimble (Wmb/A-, in the lower beds). The main areas of slumping, where sediment movement continued periodically through the leintwardinensis beds, are Kerry and SW Clun Forest. The direction of slumping here is to the SE (Earp '38, '40), compared with the opposite trend of movement to the NW, for the contorted beds of the Brecon region. This indicates an axis for the Montgomery Trough between the two areas.

Map C - "top" LLB: Fig 5.2 p 167

This map shows the faunal distributions for a high level in the LLB. At the stratotype on the Whitcliffe, this includes beds with very common S. ornatella, together with A. reticularis and L. depressa, and with many S. leintwardinensis (LC), in very calcareous siltstones and shelly limestones. The ULB here were defined by Holland, Lawson and Walmsley ('63) on the addition of C. puellaris and E. stubblefieldi and A. grayi to the fauna. N. lauensis has not been found at the type section.

In the basinal areas, the extent of the laminated siltstone facies has diminished, to be replaced by more calcareous flags with rich, shelly faunas (eg. Ysgwydd Hwch: YH1-). Even within the Striped Flag sequences, incursions of shelly fossils are found in several sections (eg. Whimble Wmb-, and Crickadarn Mill) at this level. In the Kerry sequence, graptolites become more common in the upper strata.

Throughout the region, there is a diversification of the fauna in the top LLB. The changes are not accompanied by marked lithological transitions in the shelf sections, where the ULB are indicated chiefly by the acme of S. ornatella. At May Hill and Perton, the LLB-ULB boundary is taken at the level of conglomeratic limestone beds.

The Llandovery-Llandeilo region shows a more calcareous facies of fine siltstones and sandstones at this level in the succession.

Map D - grayi - lauensis beds: Fig 5.2 p 167

In the basinal areas and shelf edge region, N. lauensis comes into the fauna at a higher level than the beds with S. ornatella. Map D indicates the facies and fauna found at this horizon. It marks a further stage in the areal reduction of the Striped Flag lithologies, which are now limited to the N and NW of the outcrop. In addition, massive, thickly-bedded calcareous siltstones spread over a large area at this level - the "Chonetoidea" grayi Beds of Straw ('37) and Kirk ('49) - close to the appearance of N. lauensis - A. grayi fauna. The facies transition is rapid in some places, such as Crickadarn Mill (CM-), but more gradual in others (eg. Shelderton Road section, SR/2-, and Ysgwydd Hwch YH1-).

In the shelf edge region, phosphatised pebble-beds and conglomerates coincide with the appearance of N. lauensis at Aymestrey and Shelderton.

There are marked lithological changes at this horizon on Wenlock Edge, at the base of the high ULB (hULB) of Shergold and Shirley ('68). At Ludlow, the beds become more thickly flaggy close to the appearance of the diagnostic ostracode in the west, but the lithological transition appears to be higher in the succession in the eastern sections.

The shelf inliers show thinly-bedded calcareous siltstone facies through the thin ULB sequences. A. gravi and N. lauensis are rare, and the stratigraphical division is characterised by the abundance of S. ornatella. Phosphatised horizons and bone beds are found at a number of localities at the top of the ULB.

Vertical range chart: Fig 5.3 p 168

A vertical range chart for a transect from basin to shelf has been plotted. The facies defined for the distribution maps have been inserted on the diagram, and the parts of the succession studied in detail in each sequence are indicated by a solid line on the right of the stratigraphic column. Faunal abundances are shown for these sequences.

Key to the Facies Maps: Fig 5.4 p169

Aymestry Limestone facies:

The symbol is used to include the flaggy limestones of the southern part of Wenlock Edge and Ludlow, and the nodular, more silty, lateral equivalents in areas to the SE of this. (Woodbury, Perton, NE Wenlock Edge, and the Sedgley limestone of Lye).

Conglomeratic bands:

These indicate the areas with basal conglomerates, which are found within the Aymestry Limestone facies in some areas, but in sequences of calcareous siltstones in others.

Calcareous shelly siltstone facies:

This facies is found throughout the LLB and ULB in the southern shelf inliers. There is a gradual change from the irregularly-bedded limestone facies to more thinly flaggy, siltier beds, in the northern part of the shelf region, which takes place in the lower part of the LLB. The facies extends further west at the top of the LLB. There is a rich benthonic fauna.

Shelly siltstone facies:

The largely non-calcareous strata of the Llandovery-Llandeilo region, described by Potter and Price ('65) as a "sandy variety of the shelf facies". There is a benthonic fauna.

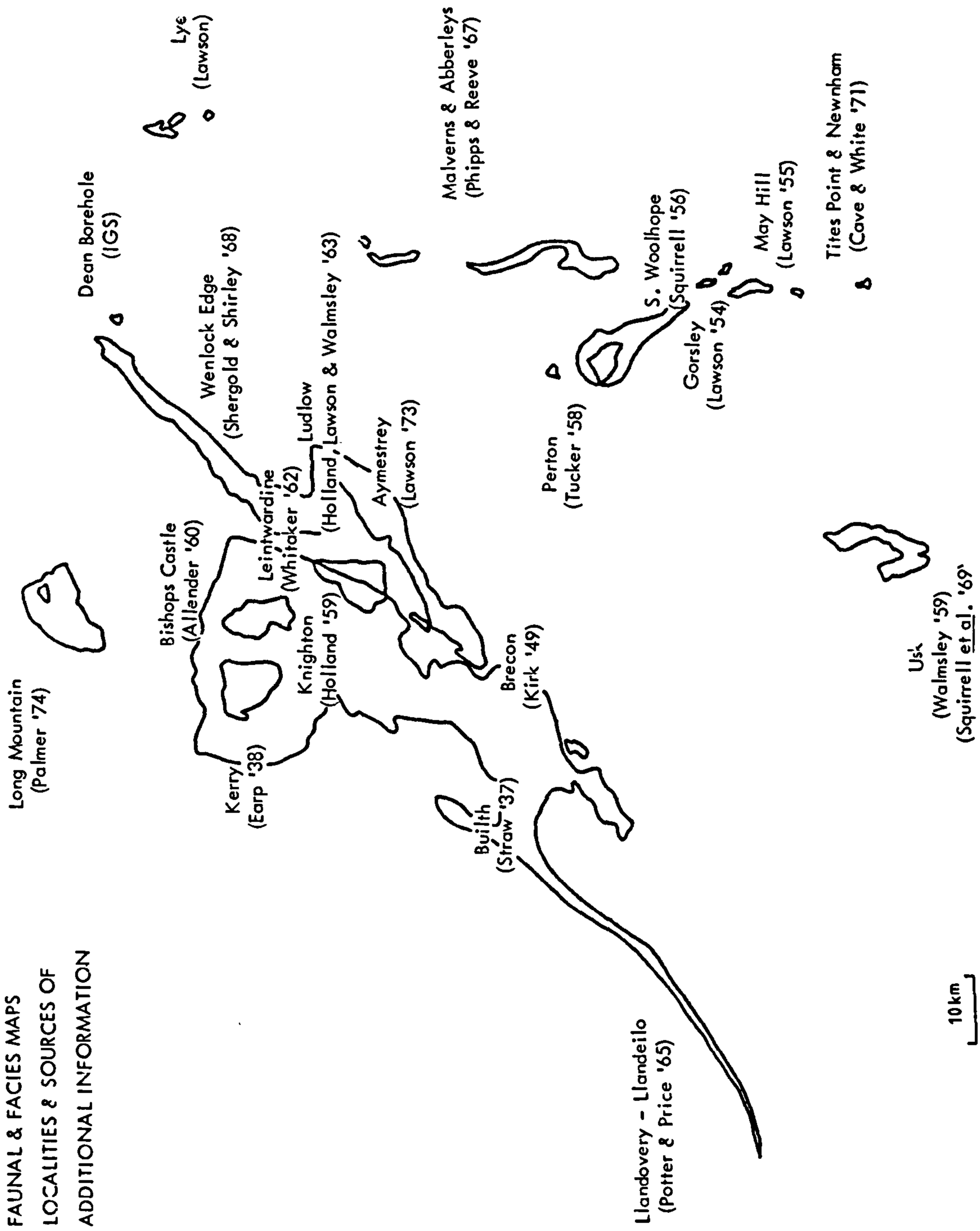


Fig. 5.1 : Localities and sources of additional information for the faunal and facies maps.

FACIES MAPS

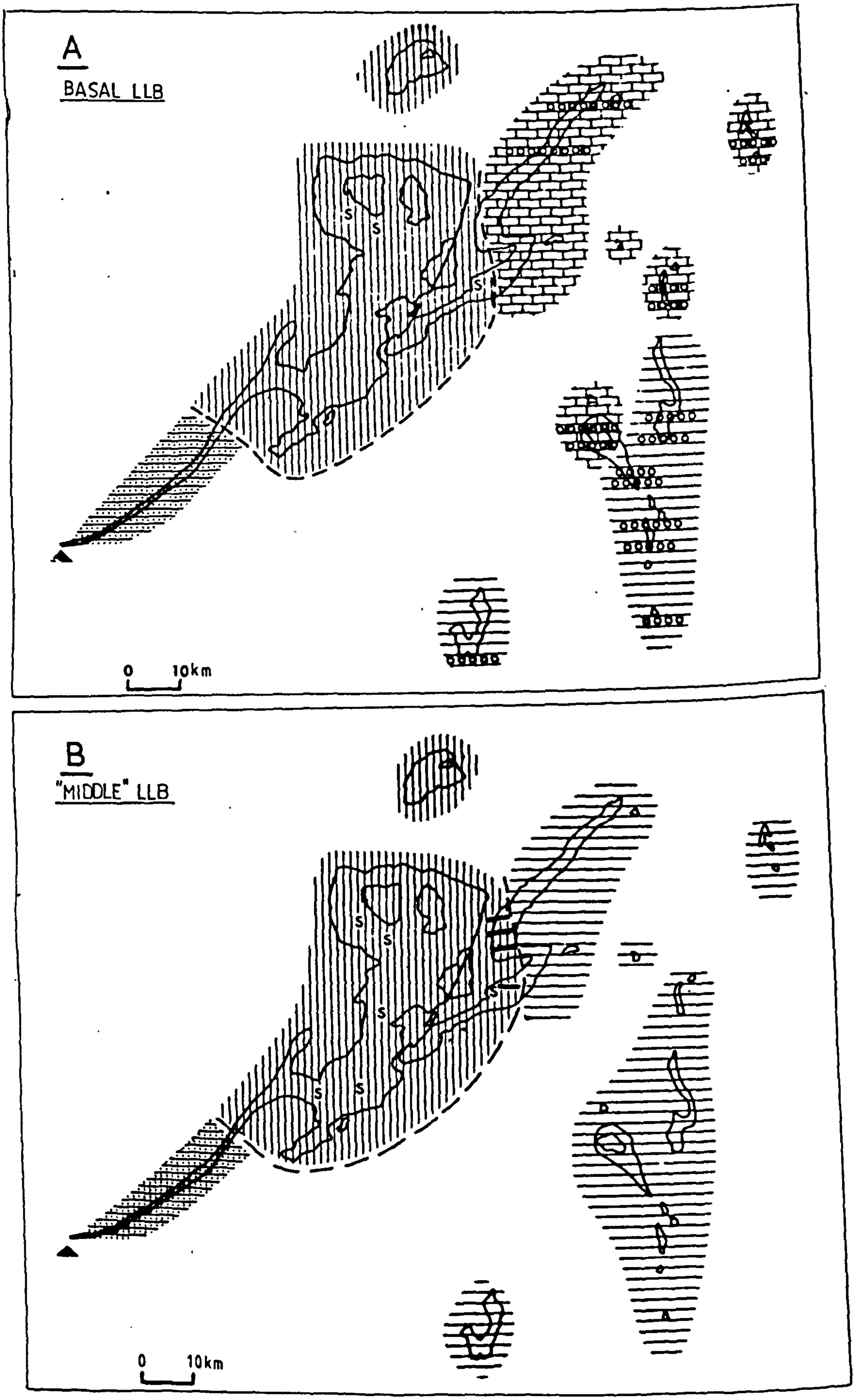
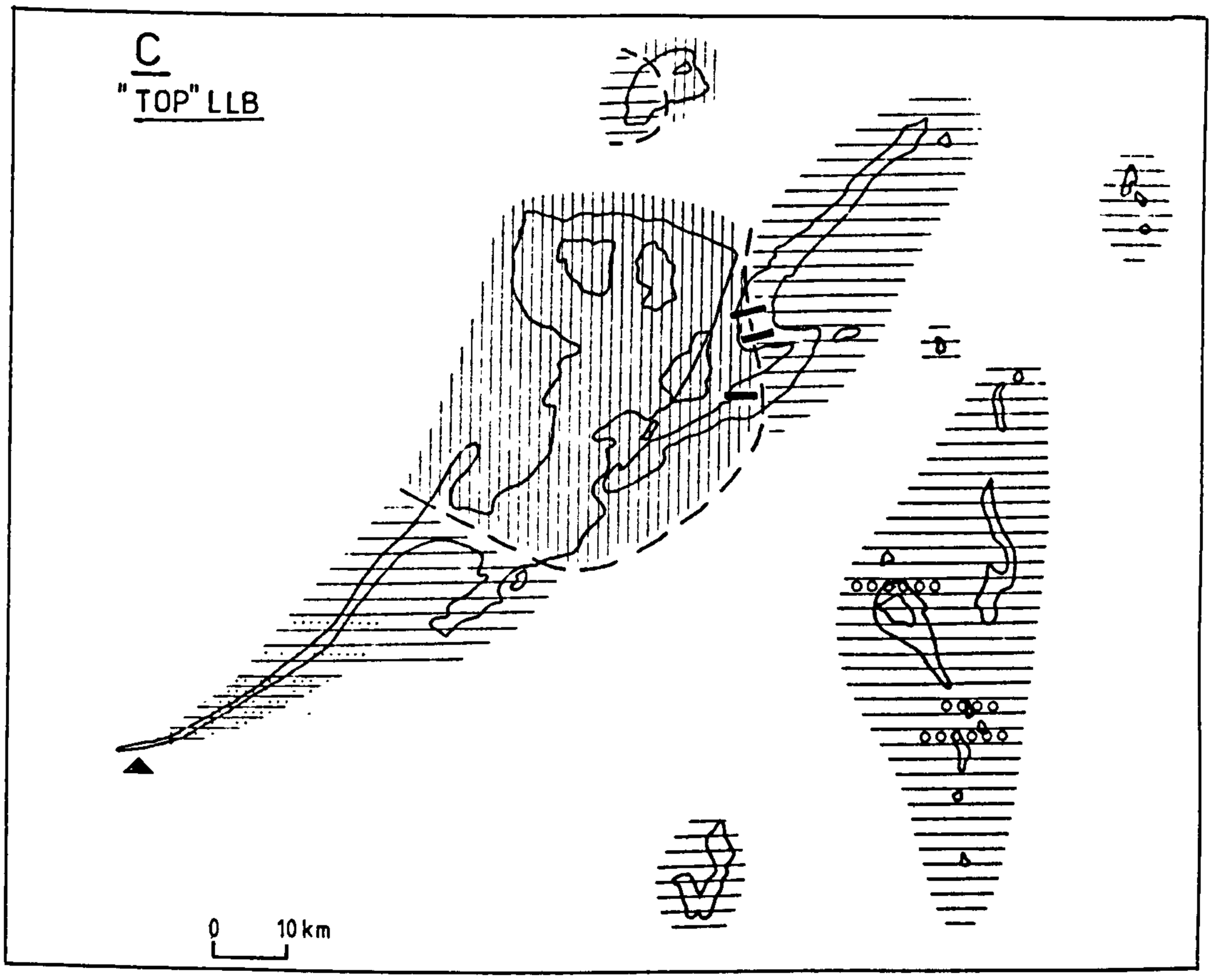


Fig. 5.2 : Facies maps for the Leintwardinian.



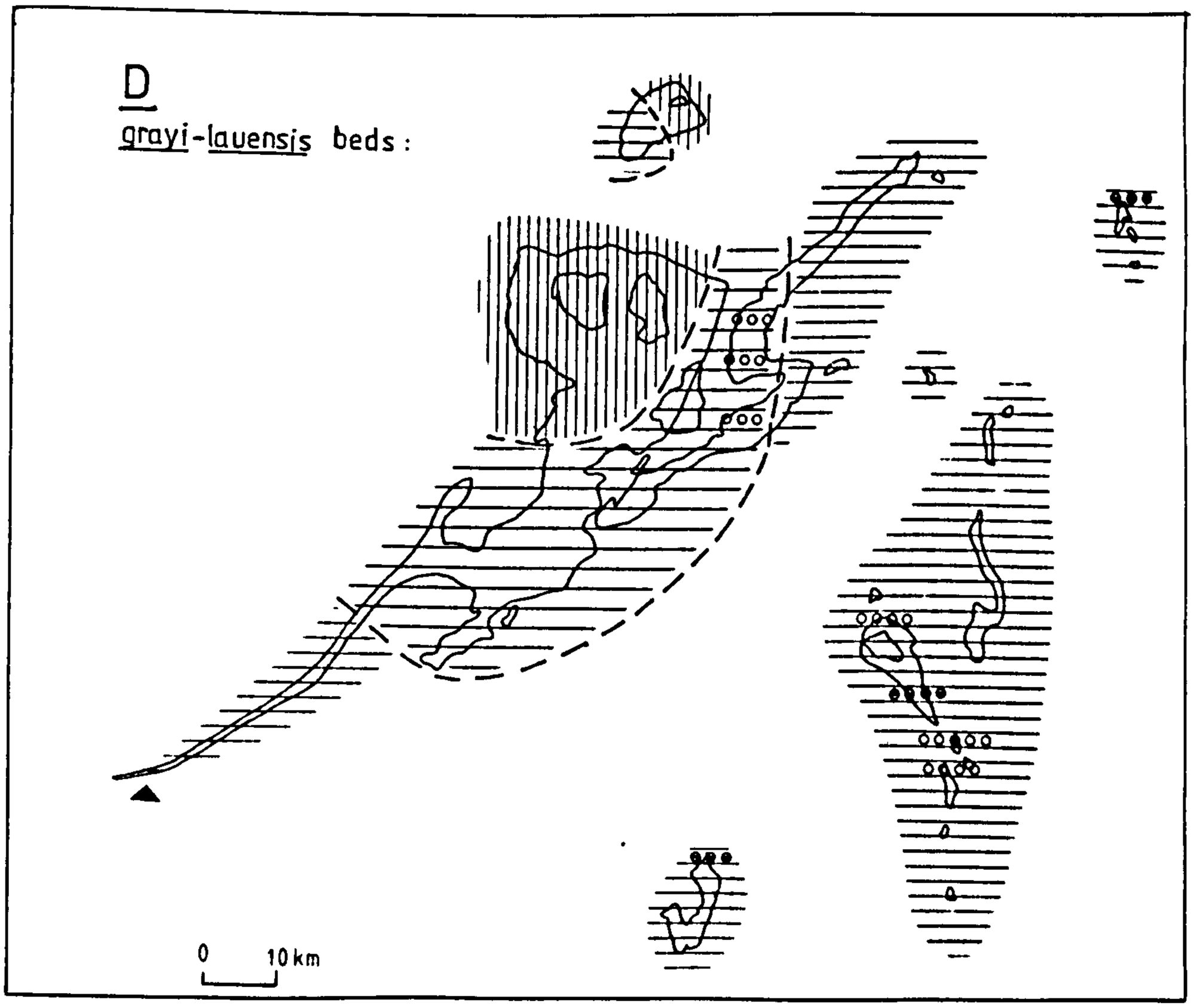


Fig. 5.2 : Facies maps for the Leintwardinian.

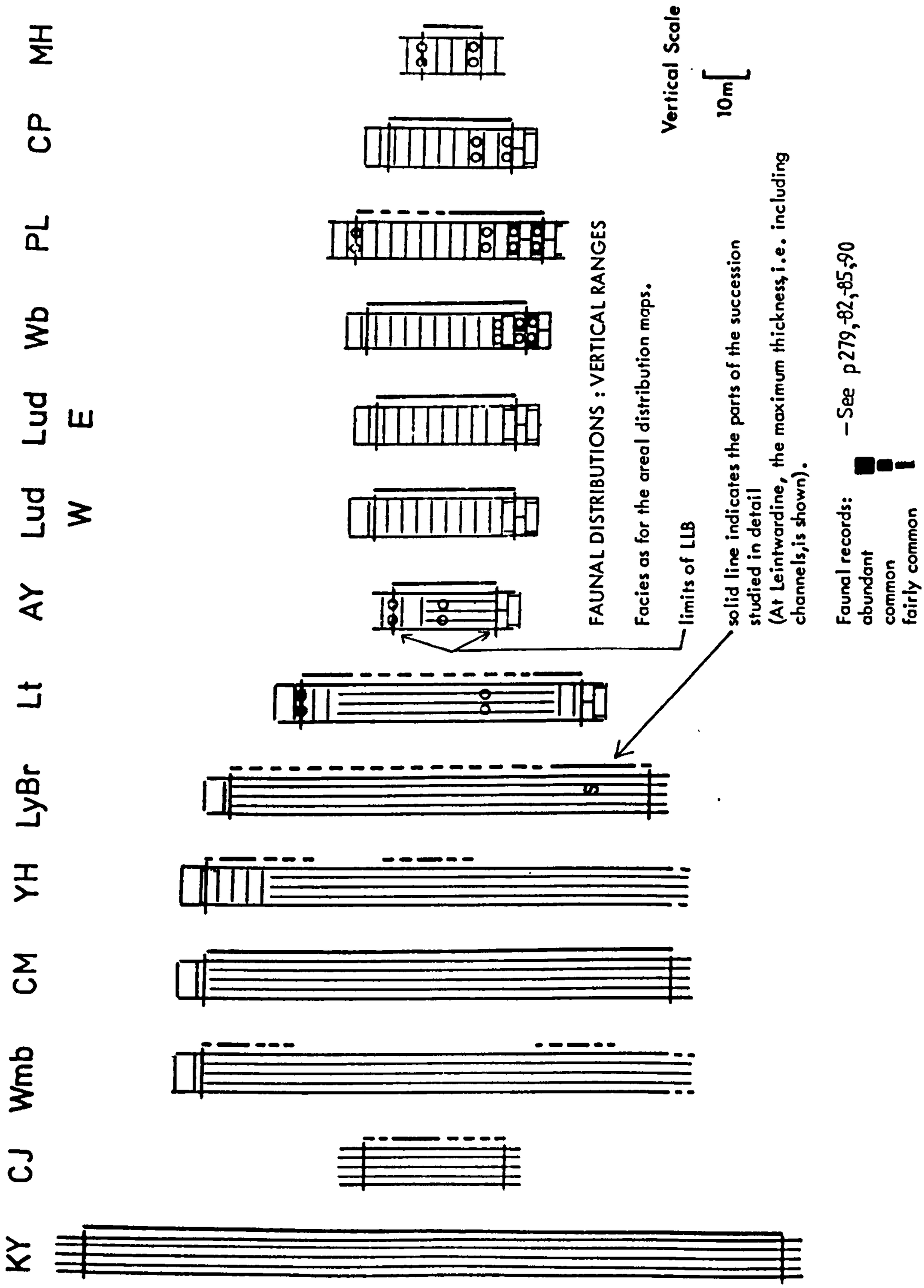


Fig. 5.3 : Vertical ranges for faunal distributions.

FACIES MAPS

KEY

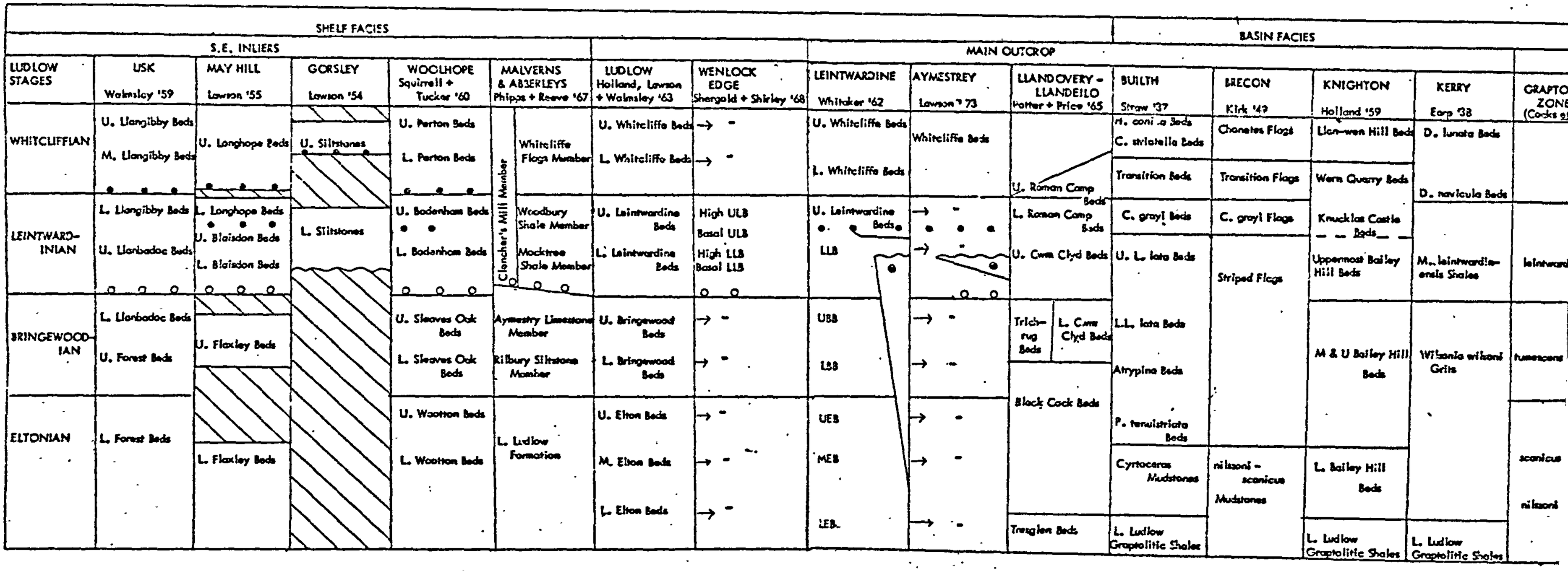
Aymestry Limestone facies
Conglomeratic beds
Calcareous shelly siltstone facies
Shelly siltstone facies
Laminated siltstone facies
Slumped beds
Submarine channels
Thickly-bedded, calc. siltstone facies
Bone-beds

FAUNAL DISTRIBUTIONS

KEY

● Common
◒ Fairly common
○ Present

Fig. 5.4 : Key to facies maps and faunal distribution maps.



KEY
- ● ● phosphatised pebble-bed or bone bed
- ○ ○ conglomerate
- erosion surface
- ⊖ channelling - Leintwardine : Whitaker '62
  Aymestrey : this study

Chart compiled from Holland, Lawson & Walmsley '63, and Cocks et al. '71.

CORRELATION CHART : THE LUDLOW SERIES OF THE WELSH BORDERLANDS AND WALES

Fig. 5.5

Laminated siltstone facies:

The thinly-bedded, fine siltstones of the basinal areas. These beds are generally non-calcareous. They are often poorly fossiliferous, with a mainly pelagic fauna. Slumped beds (S) occur at levels within this facies, and may have shelly faunas. The sequences at Aymestrey and Leintwardine have a mixture of shelly and graptolitic faunas in more calcareous, thin siltstones.

Bone-beds (thelodonts, etc):

These are found at the top of the ULB at Usk, S Woolhope and Gornal. Other areas have phosphatized pebbles and conglomeratic beds at this level.

Submarine canyons:

The Leintwardine channels of Whitaker ('62), and one at Aymestrey. These are mainly filled with hLLB (as defined by Whitaker '62).

FAUNAL DISTRIBUTION MAPS

The groups discussed are as follows:-

A Graptolites

B Brachiopods

C Trilobites

D Ostracodes

E Bivalves

F Gastropods

G Orthocones

H Bryozoa

Correlation of the local classifications for areas mentioned in the text are shown in Fig 5.5 p170.

A. GRAPTOLITES:

S. leintwardinensis (Lapworth) Fig 5.6 p 275

Identifications by RBR are shown on Fig 5.7 p172

Distribution:

The graptolite zone of S. leintwardinensis gives a fairly certain correlation of the basinal sequences with the Leintwardine Beds of the shelf. The graptolite assemblages are mostly monotypic, but S. leintwardinensis primus, Saetograptus n. sub - sp and occasional

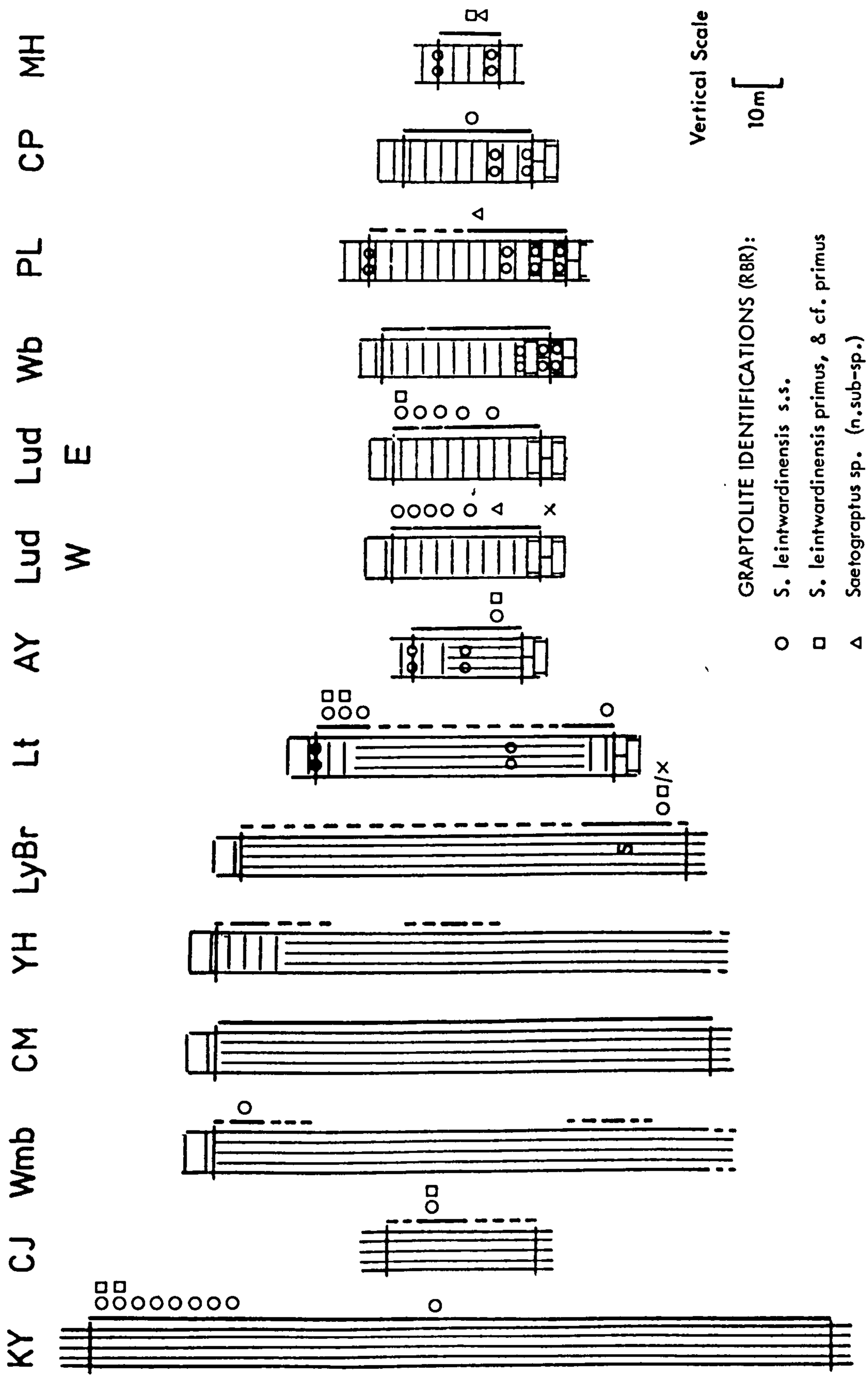


Fig. 5.7 : Graptolite identifications (RBR).

semi-spinose Saetograptus chimaera group forms also occur at this level. The saetograptid S. leintwardinensis incipiens was recorded in this study only from the topmost UBB at Ludlow (MF 33 - S.l. ? incipiens - RBR), and from a low level in the leintwardinensis zone at Lyepole Bridge where specimens identified (RBR) with S. leintwardinensis included ? S. leintwardinensis cf. primus or ? S. incipiens. This suggests the distinction of the S. incipiens and S. leintwardinensis zones in the Welsh Borderlands, as is recognised in Northern England (Rickards '67), the Long Mountain (Palmer '72), and N. Wales (Warren '71). The incipiens zone has not been distinguished in the European successions, but S. leintwardinensis has a cosmopolitan distribution throughout Europe.

The distribution pattern of the graptolites, and their relative abundance, are shown in Figs 5.6 and 5.7. Graptolites are comparatively scarce in the shelly shelf facies, and often fragmented. Their abundance increases towards the shelf edge, particularly in the finely laminated and more thickly-bedded, siltstone facies. Some graptolites are found in shelly assemblages, but more occur in other beds. Further west, at Lyepole Bridge, monospecific planes of crowded rhabdosomes, both aligned and randomly disposed, are fairly common at some levels. The concentration of individuals, and degree of breakage, varies greatly. The most common associated fossil is L. lata, which itself occurs in many monospecific assemblages in the same sequences. Other shells are rare in these faunas, but are concentrated in the interbedded slumped units. The shell accumulations represent allochthonous faunas transported downslope from shallower regions. In the basinal areas, fossils are uncommon compared with the shelf region. Shells are rare, even in slumped beds. The fauna is composed mainly of graptolites, with L. lata, orthocones and small pteriniids. Many of the graptolites are found as isolated specimens or in small patches on laminae, and oblique to the bedding of some unlaminated flags. They are fairly common in occasional bands, but many beds of the basinal sequences are unfossiliferous.

The stratotype for the base of the LLB lies in the top part of the Aymestry Limestone facies, which is overlain by calcareous shelly siltstones. Graptolites occur only rarely, and the lowest specifically identified (RBR) forms came from about 10 m above the basal bed (in

SY/A- va, xa, ya). These include S. leintwardinensis s.s. as well as S. leintwardinensis ? sub-sp. (RBR). At an approximately equivalent level in MF/E (bands T and X), Saetograptus sp., and S. chimaera group - ? Saetograptus fritschi (RBR) were found. In contrast, the fine muddy siltstones of the bLLB in the Leintwardine area, which lie with the sharp contact on the UBB limestone, contain fairly common graptolites. S. leintwardinensis (RBR) was identified from this level at Bow Bridge (BB-F).

Thus, the correlation of the graptolite zones with the shelly fauna at the type section is somewhat equivocal. However, S. leintwardinensis was identified in most areas of the shelf from beds above the basal conglomeratic facies (Map B). Towards the top of the LLB, graptolites become fairly consistently common in the shelly calcareous siltstones of the Ludlow and Leintwardine sections. A similar acme was recorded by Shergold and Shirley ('68) for their basal ULB (bULB) of Wenlock Edge, here correlated with the top LLB of the stratotype. At this level, there is a mixing of shelly and graptolitic faunas along the shelf edge region, with a reduction in extent of the laminated siltstone facies (Map C). Among the areas with Striped Flag lithology, at Kerry and at the Whimble (Wmb-) in the upper part of the leintwardinensis zone, graptolites become common, sometimes with L. lata, but rarely with other shells.

S. leintwardinensis extends up into the ULB at the type section (where N. lauensis is not recorded), and is reported rarely from shelf and basin areas in the ULB. It is uncommon at this level, and disappears from the fauna in the ULB. The distribution of the graptolite Bohemograptus bohemicus in higher beds appears to be confined to the Long Mountain and Clun Forest districts (Holland and Palmer '74). It is found in the thinly-flaggy siltstone facies which persists for longer in the N and NW. The strata have a restricted fauna in which benthonic forms are rare.

Ecology:

Graptolites are believed to have been colonial, lophophorate hemichordates, which lived planktonically. Their very wide distribution, preservation in a variety of lithologies, and rapid evolution as a

group make them very useful stratigraphical indices.

Lapworth (1897) proposed that graptolites were epiplanktonic, attached to floating algae of the Sargassum type. The absence of evidence of algal association, and doubts about such a wide areal extent for algal distribution, led to the alternative suggestion that graptolites might have had their own buoyancy mechanisms (eg. Bulman '55, '70; Kozlowski '71). Rickards ('75), from the nature and development of the nema, considered attachment by this organ to be unlikely, and supported the latter theory.

Modern zooplankton mostly exhibit diurnal depth changes and slight vertical zonation. Bulman ('64) argued, on structural and functional grounds, that graptolites were restricted to surface waters. Berry and Boucot ('72) attempted to relate graptolites to the Llandovery marine benthonic life zones - depth-controlled "communities" - of Ziegler ('65) and Ziegler et al. ('68). Some species, although not common, typify inshore environments, while the same species increase in abundance and occur with other species in offshore environments. They therefore proposed that the various species occupied different depth 'gyres' in the ocean. However, Rickards ('75) commented that the most common offshore species are those which are found infrequently in the inshore facies, and that the inshore types tend to have the more robust skeletons (for example, Monograptus priodon and retiolitids). The lateral distribution of graptolites can then be explained by selective preservation.

Pelagic organisms may occur in any environment to which they have sunk or drifted. The most distinctive graptolite association is with black shales which are devoid of other fossils. The euxinic sediments represent anaerobic conditions, without bottom circulation, and are often pyritic; depth of water is not in itself a controlling factor (Bulman '70). More widespread are thick sequences of fine clastic sediments with a graptolitic fauna; the Ludlow basinal successions are of this type. The presence of assemblages of aligned rhabdosomes in graptolitic strata indicates some current action, when an absence of benthos may reflect primarily an offshore position beyond the littoral zone. The associated fauna and sedimentological evidence are important for environmental assessments.

Conclusions:

The LLB distribution of graptolites shows them to be infrequent in the shelly sequences of the shelf areas, but increasing numerically towards the basinal areas of laminated siltstones. The relative scarcity in the former areas may result from selective destruction in the more agitated environments of the shelf. In the basinal strata, assemblages of aligned rhabdosomes at Lyepole Bridge show the presence of bottom currents. However, many graptolites in the Kerry sequence are haphazardly distributed in the sediments, indicating that bottom circulation here was restricted or lacking. Both areas have mainly pelagic faunas, but with L. lata as well. The intermediate shelf edge regions of Leintwardine and Aymestrey have mixed shelly and graptolitic faunas. In the upper half of the LLB, graptolites become more common elements of the fauna also at Ludlow.

In the ULB, the decline in abundance of graptolites corresponds with the westward extension of the shelly benthonic faunas and calcareous siltstone facies. The younger graptolite zone of B. bohemicus is recognisable only in the areas of laminated siltstones to the N and NW (eg. Long Mountain - Holland and Palmer '74), where shelly faunas and facies are not developed until Whitcliffe times.

The basinal graptolitic sequences in the LLB contain only rare benthonic fossils. Gentle reworking of the sediment must have taken place to produce the fine lamination of the beds. The occurrence of a few L. lata individuals perpendicular to the bedding in these areas indicates that conditions were adverse but not inimical to all benthos. The evidence suggests that the basin had a restricted circulation, but that even in areas where current action is more apparent (eg. Lyepole Bridge), conditions were still unfavourable for most benthos.

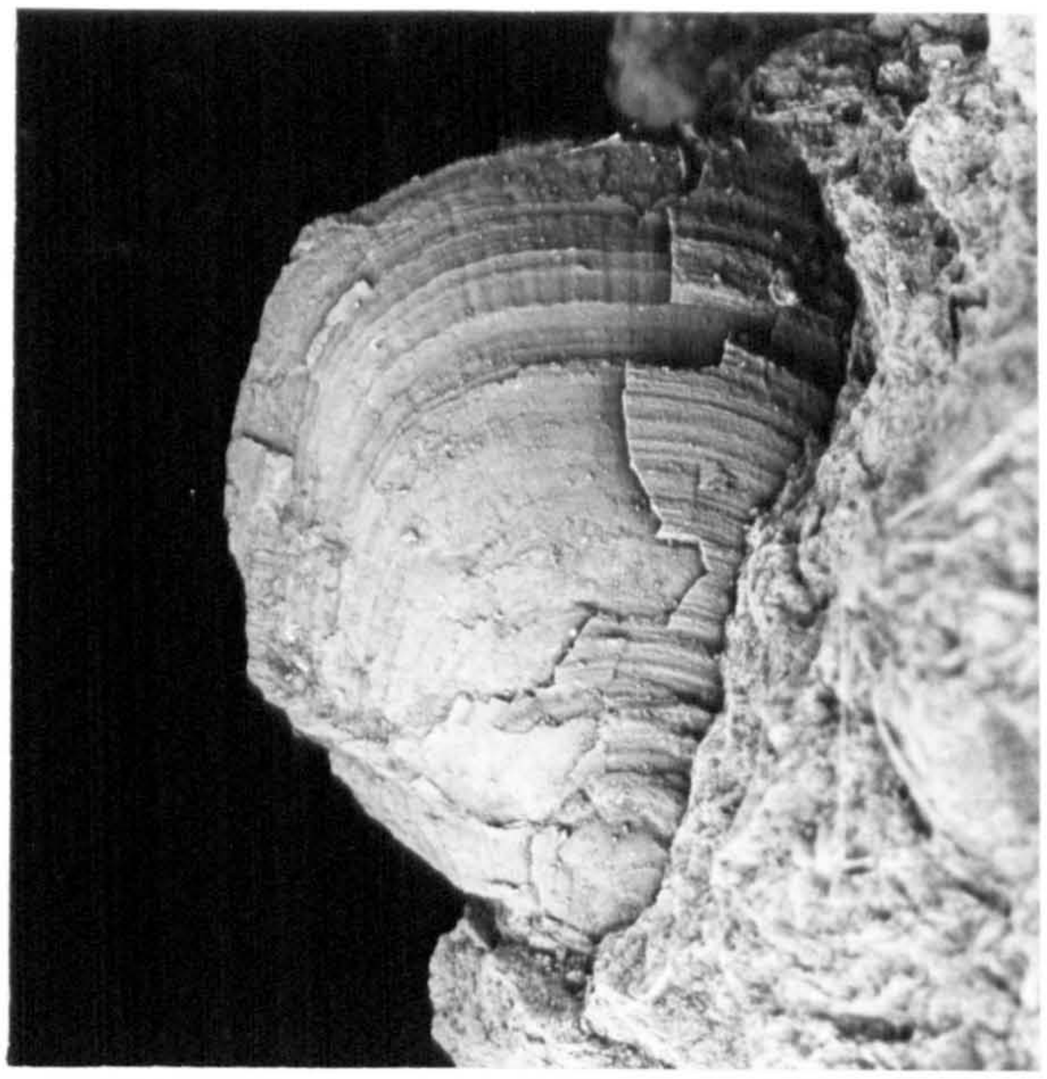
B. BRACHIOPODS - Inarticulate

1. L. lewisii (J. de C. Sowerby) and L. lata (J. de C. Sowerby)

Figs 5.8 p 276 5.9 p 177

Leintwardine Beds Distribution:

The two common species of lingulid in the Leintwardinian are L. lewisii and L. lata. The former has a distribution centred in the shelf region, while the latter is largely restricted to the basinal areas of thinly-bedded laminated siltstones. The two distributions overlap in the shelf edge areas.



a : L. lewisii, perpendicular to the bedding. Large squared form with pronounced growth lines. (x 4; MF/C)

b : L. lata, perpendicular to the bedding. Small, ovoid, thin-shelled form. (x 7; AY/1)

Fig. 5.9 : LLB Lingula spp.

L. lewisii:

L. lewisii occurs very commonly in the UBB Aymestry Limestone. Large individuals are frequently found perpendicular to the bedding, often in nodules. The species occurs similarly in the LLB Aymestry Limestone facies (Map A). The greatest abundance found was in the Ludlow anticline, where numerous articulated individuals were orientated vertically through the strata. Rare, separate valves of L. lewisii were found in the Chances Pitch sequence. At May Hill, the basal limestone conglomerates have many fragments of calcium phosphate shell, but no identifiable lingulids. The species has been recorded from the Llandovery-Llandeilo region by Potter and Price ('65); the attitude of the shells to the bedding was not commented upon, however.

In the main part of the LLB (Map B), L. lewisii has a widespread distribution throughout the areas of calcareous shelly siltstone facies. It was not found in the thinly-bedded flags of the Leintwardine and Aymestrey areas at this level. In the SE shelf inliers, uncommon drifted valves occur among the shell assemblages, but at Woodbury and Ludlow, specimens perpendicular to the bedding are fairly common as well.

Map C, for the topmost LLB, shows the re-appearance of L. lewisii in the shelf edge region. Although individuals are uncommon, the Shelderton Road section SR/2- fauna included specimens at right angles to the bedding. The Woodbury and Ludlow sequences had individuals orientated vertically in beds. Map D shows the records of L. lewisii in the ULB.

In the SW of the outcrop, Potter and Price ('65) noted the very common occurrence of L. lewisii in the condensed sequence of the Cennen valley (high LLB and ULB). It was less abundant in the Llandovery area, though still fairly common. In the ULB ("C", gravi flags), L. lewisii was recorded from Builth (Straw '37); it was not noted there in the LLB.

L. lata:

L. lata occurs in the leintwardinensis beds of the basinal sequences. Its lateral range overlaps that of L. lewisii in the shelf edge sections of Leintwardine and Aymestrey. It is very rare in the shelf inliers.

The highest abundance found was in the laminated siltstones of Lyepole Bridge Quarry (Ly Br). Planes of the undisturbed units between slumps have limited faunas of L. lata, graptolites, and pteriniids. Other benthonic fossils are uncommon in these beds. Many surfaces have monospecific assemblages of lingulids or graptolites, but others have the two associated together. The density, and degrees of alignment and breakage, of the fossils vary. No specimens of L. lata here were found perpendicular to the bedding, but because of the high proportion of complete valves in some assemblages, the lingulids are inferred to be locally derived (Fig. 4.13). (Similar, occasional plane faunas of L. lata and graptolites were described by Wood (1900) from Aberedw).

Infrequent specimens inclined through the bedding were found in the lower part of the LLB at Aymestrey and at Leintwardine, and in the Brecon Anticlinal region (Map A).

L. lata occurs infrequently through the laminated siltstone successions, associated with a sparse, mainly pelagic fauna. Valves are generally small, and single. However, rare complete, perpendicular specimens were found among those at Cwm Jenkin (CJ), in the Knighton district. The topmost LLB at Ludlow and Leintwardine included vertically-orientated individuals as well as single, drifted valves. (Map C).

L. lata is rare in the ULB (Map D); it is recorded only from Builth (Straw '37) and Ludlow (Holland, Lawson and Walmsley '63). In this study, L. lata was not found at the gravi - lauensis level, but died out shortly below (for example, at Shelderton SR/2-, and Ludlow MF/A-).

Vertical Distribution in Ludlow Series:

L. lewisii is reported to be present in many shelly faunas of the shelf lower in the Ludlow Series, but is only common in the UBB Aymestry Limestone of Woolhope (Squirrell and Tucker '60) and the Elton Beds of the Malverns (Phipps and Reeve '67). In shelf sequences above the Leintwardine Beds, the species is recorded from the UWB of several areas, and up to the basal Downtonian at Woolhope. L. lewisii is not recorded west of Aymestrey in the Ludlow except for Straw's ('37) "rare" occurrence at Builth in the "C". gravi Beds (ULB).

L. lata, in contrast, occurs consistently in the basinal successions (eg. at Kerry (Earp '38)) below the leintwardinensis zone,

although not commonly, but is recorded only from Woolhope (Squirrell and Tucker '60: in UBB-UWB) and Usk (Walmsley '59 - in Elton Beds) in the shelf inliers. At Ludlow (Holland, Lawson and Walmsley '63) it is found only in the graptolitic MEB and UEB faunas.

Ecology:

Lingulids are inarticulate brachiopods with an elongate, phosphatic shell. The valves are similar, spatulate in outline, and gently convex. The beaks are terminal, with the pedicle emerging posteriorly between valves. Recent species have a long, flexible pedicle, and are spirolophous, with the apices of spires medianly directed.

All Recent lingulids are infaunal, living in burrows. The conservative shell morphology, from Ordovician times to the present, suggests that the mode of life has not changed. Fossil specimens preserved perpendicular to the bedding are apparently in situ.

The pedicle, which is structurally different and not homologous with that of articulates (Rudwick '65), has been considered to be the principal burrowing instrument, with the animal entering the sediment pedicle-first (eg. Craig '52, Newall '70). Trueman and Ansell ('69) drew analogies with the muscular foot of bivalves, the burrow being excavated by progressive extensions of the fleshy pedicle coordinated with shovelling and lateral movements by the valves to increase the width. They questioned (quoting Chuang,, and Purchon - pers comms.) whether adult individuals of Lingula could actively burrow, because of reportedly weak musculature of the pedicle.

Thayer and Steele-Petrovic ('75) observed the burrowing of a living lingulid Glottidia pyramidata. They noted that the animal enters the sediment anterior-end first, using the pedicle to lift the valves into the burrowing position. (Paine ('63) had also observed entry of G. pyramidata in this orientation, and not pedicle first). Penetration of the sediment is by circular and scissors motions of the valves, the setae passing particles back over the shell where they become enmeshed by mucus issuing from between the valves. The burrow is U-shaped, with the individual coming to rest with its anterior end near the sediment-water interface, and pedicle in the ascending limb of the U.

Thayer and Steele-Petrovic ('75) commented upon the unique burrowing mechanism, which contrasts with the hydrostatic coelom that

most non-arthropod invertebrates use for burrowing. The setae are large and closely-spaced compared with those of articulates, but are not characteristic of all inarticulates (the epifaunal Craniacea lack setae - Rudwick '70). In addition, the shell musculature is greatly enlarged in lingulids, compared with sessile epifaunal inarticulates such as Crania and Discinisca (Thayer and Steele-Petrovic '75). These are interpreted as adaptations for the infaunal habit. It is probable that all lingulids burrowed in the same manner as G. pyramidata.

For fossil lingulids, this allows the observed variable orientations of specimens oblique to the bedding, and even anterior-end down, to be explained, since the animal may be preserved in any part of the U. The scarcity of trace fossils of such burrows is partly accounted for by the rapid collapse of the descending limb, after removal of the pedicle, seen in G. pyramidata (Thayer and Steele-Petrovic '75). However, Szmuc et al. ('76) have recently named a new trace fossil genus for lingulid burrows, Lingulichnites, arguing that such structures are overlooked in the literature unless specifically defined. In this study, burrows were not seen associated with specimens perpendicular to the bedding.

For an infaunal existence, it is essential that the animals should be able to exhume themselves after burial, particularly in the turbulent littoral environments. Escape burrowing was observed in experiments on G. pyramidata by Paine ('63) and Thayer and Steele-Petrovic ('75).

The geographical distribution of Recent lingulids is centred in tropical and sub-tropical seas, at depths of less than 40 m (Craig '52, Paine '70). Living lingulids are found in sediments of predominantly sand-sized particles (Paine '70). Their absence from gravel-size sediments (Paine '70) may reflect an inability of the valves to move such large particles during burrowing (Thayer and Steele-Petrovic '75). Paine ('70) found Lingula inhabited finer sediment than Glottidia, but neither exhibited a preference for muddy environments. He proposed, therefore, that the preponderance of fossil lingulids found in fine shales reflects a preservational bias, unless the habitat preference has changed. The scarcity of in situ individuals in carbonates was related by Paine ('70) to an intolerance of "suspended inorganic materials" - presumably sediment particles held in suspension in the carbonate matrix - but to high shear strengths opposing penetration by the shell by Thayer and Steele-Petrovic ('75).

Newall ('70) reported Lingula in 'borings' in Heliolites colonies. He considered that the lingulids could not have created the tubes, but had occupied them after their vacation. However, divergence of the corallites around some shells, and the increasing width of the 'boring' upwards both suggest that the lingulid settled in an area of the living coral, modifying its growth, and moving upward as the coral grew. Similar responses of coral growth to the presence of a foreign object are frequently found in Recent corals (Patton '73). The improbability that Lingula bored into the skeleton is discussed by Thayer and Steele-Petrovic ('75), based upon several lines of evidence.

The euryhaline character of modern lingulids is reflected by their distribution in near-shore and brackish-water environments (Craig '52). Cloud ('48) remarked also upon their high tolerance to conditions of low oxygen content. Similar responses to these factors are interpreted from occurrences in the fossil record, for instance in the Downtonian strata, and in 'brackish water' shale bands of the Coal Measure cyclothems. The Lingula community of Ziegler et al. ('68) is their shallowest assemblage, composed of lingulids, mollusca, worms and a few articulate brachiopod species.

Paine ('70) noted that G. albida has its maximum abundance, in the Gulf of California, at depths of greater than 10 m - which he considered 'deep' for lingulids. Comparable observations for this species and area were made by Mattox ('55), who found "unattached" individuals (up to a density of 43 per 2 sq. ft area) down to 82 m depth, and reported G. albida from depths between the intertidal zone and 147 m. This species, therefore, displays a wide tolerance to, or preference for, deeper environments, compared with many other lingulid species.

Fossil lingulids are found commonly in some fine-grained dark shales which are interpreted to represent deeper water conditions. Ziegler et al. ('68) mentioned the presence of small (2-3 mm) lingulids in Silurian graptolitic shales. These specimens, Bulman ('64) had suggested, might be giant larvae resulting from delayed settling in adverse conditions. Other similar records of lingulids with pelagic faunas (in the Devonian) are provided by Noble and Ferguson ('71), and Bowen et al. ('74). Pyrite in the shales, and the absence of bioturbation, indicate anoxic conditions. Bowen et al. ('74) also found some linear aggregates of lingulids larger (4-5 mm) than the

others (2-3 mm), and with styliolinids. There was no topographical feature to produce the distribution of the assemblages which, it was proposed, might have been transported in attached to plant material.

The pelagic larval phase of some inarticulates, including lingulids, lasts considerably longer than that of articulates (several weeks compared to hours) and unlike the passive, pelagic forms of the latter, the larvae can actively swim and feed (Rudwick '70). The periodic drifting of lingulid larvae with currents into bathyal and abyssal depth zones was reported by Mileikovsky ('71), while Rudwick ('65) noted the frequent presence of inarticulate larvae among mid-oceanic plankton. A prolonged pelagic phase will clearly extend the limits of dispersal of a species. The duration of the pelagic phase appears to be partly related to latitude, with invertebrates in tropical seas having longer larval stages than those in temperate and cold regions (Scheltema '71).

An Ordovician assemblage of L. tenuigranulata found perpendicular to the bedding in strata interpreted to represent an offshore shelf environment were regarded by Pickerill ('73) as resulting from a successful spat-fall in an atypical site. This was from an interpretation of Lingula as primarily an intertidal genus, which evidently cannot be assumed. The individuals were all very large (>3.9 cm long), suggesting that conditions here were favourable for their colonisation.

Summary of ecology:

Lingulids are infaunal brachiopods, which burrow anterior-end first. Modern forms are most common in very shallow, warm seas. They show a high tolerance to a range of salinities and oxygen-levels. Some species have their maximum abundance in deeper conditions (eg. G. albida). The pelagic phase of the life cycle is prolonged, with the larvae adapted for feeding and swimming. The possible extent of dispersal achieved by this stage is shown by the presence of larvae in mid-oceanic areas.

Fossil lingulids have a similar morphology to Recent forms. Individuals positioned perpendicular to the bedding are apparently in situ, and indicate that the mode of life has not changed either. Fossil forms are usually found in strata interpreted as very shallow to brackish water environments, but some occur in deeper water deposits.

Conclusions:

L. lewisii is distributed in areas of Aymestry Limestone facies and calcareous siltstone facies, but is rare in the laminated siltstone sequences. It is frequently found perpendicular to the bedding, apparently in situ. Specimens within nodules of limestone in the Aymestry Limestone suggest, in view of the rarity of modern lingulids in carbonate deposits, a secondary origin for the nodules. The diversity of the associated fauna and the sedimentary evidence indicate that conditions were fully marine, not intertidal or brackish, throughout the Leintwardinian.

L. lata is found widely in the laminated siltstones, where the associated fauna is dominantly pelagic. Its lateral range overlaps with L. lewisii only in the shelf edge region. Rare individuals inclined vertically through the bedding show that some were indigenous to the basinal areas. Similarly, at Lyepole Bridge Quarry, L. lata and graptolites are found in abundance only in the normally-bedded units, while benthonic forms are confined to slump beds; the high proportion of undamaged valves in some L. lata assemblages argues against much transport having taken place.

At other levels in the Ludlow Series, the distributions of the two species are equivalent to their LLB pattern. L. lata disappeared from the fauna below the gravi-lauensis horizon in the areas studied, but is recorded from the ULB of a few areas. L. lewisii occurs above the Leintwardine Beds in several areas.

L. lata was evidently adapted to deeper water environments. The scarcity or absence of epifaunal benthos in these areas indicates that conditions were adverse to such forms. The motile nature of lingulids will allow greater tolerance than sessile forms to the high rate of basinal sedimentation. Other explanations may include a high tolerance to turbidity and to low oxygen-levels. The action of gentle bottom currents is shown by the Lyepole Bridge fauna (because the L. lata valves here have been exhumed by reworking of the top sediments), and by the laminated structure of the siltstones. Thus, the bottom water must have constantly held much sediment in suspension.

The suggestions that lingulids in deeper habitats are atypical and the result of single spat-falls (Pickerill '73), or are giant larvae

(Bulman '64), are feasible because of the prolonged larval phase. However, the distribution pattern of L. lata shows that the species is extremely rare in the shelf inliers, and only common westwards from Ludlow - ie. the shelf edge and basinal distribution appears to be an original feature. L. lata is a small-sized species, but is separable from small individuals of L. lewisii (see photographs). Therefore, the basinal lingulids are not larval forms of L. lewisii that have been transported into unfavourable environments.

The LLB lingulid species overlap a little in their areal distributions. Where they do occur in the same sequences, both have been found perpendicular to the bedding (eg. top LLB at Ludlow and Leintwardine, in Map C), and are inferred to have had similar modes of life. Ager ('65) expected that individuals would grow to a larger adult size in optimal conditions. For L. lewisii, the mean length in the SE inliers was 16.9 mm (10 individuals) compared with 10.2 mm (55 individuals) at Ludlow. The largest L. lata valves were at Lyepole Bridge; those found further west were typically small. The spatial separation of the "optimal" areas suggests that the region of overlap was peripheral to the species' ranges, so that the distributions reflect ecological preferences, not "refuge" sites.

B. BRACHIOPODS - Articulate

1. S. ludloviensis (Boucot and Harper) Fig 5.10 p 277

Leintwardine Beds Distribution:

S. ludloviensis is found most abundantly in the Leintwardine-Ludlow region, but occurs less commonly throughout the inliers. In the basinal sequences, it has a very limited distribution.

The species is characteristically abundant with D. navicula, in the silty facies of the bLLB at Aymestrey and in the Leintwardine area. Close-packed accumulations of disarticulated valves occur at many levels in these beds. The small scour channels at Aymestrey are commonly filled with S. ludloviensis valves, while planes of scattered, convex-surface upwards, shells are also numerous. Newall ('66) examined populations from the Aymestrey sequence and concluded that the assemblages represented residual life communities, and had not travelled far. He based this on several lines of evidence: such as the stability of shells once in the convex-up position, the preservation of complete

valves with spines among the populations, and the presence of interbedded planes of small, possibly immature, valves. However, deposits of largely comminuted and broken shells were also found (LC) at many levels in AY/A-, alternating with assemblages with undamaged valves. The alignment of the hinge-lines of shells, umbone orientations, and the trend of the scour channels, indicate currents flowing ENE-WNW (see p 126).

Further evidence of shelf-to-basin currents is provided by the slumped beds at this level at Lyepole Bridge Quarry, whose shelly debris-rich bands include abundant valves of S. ludloviensis. The species does not occur in the normally bedded units here, which suggests that it has been transported in from the shelf edge area with the mass sediment flow.

The higher part of the LLB in AY/A-, where only 9 m of thin siltstones are found (cf. 24 m in Mere Hill Wood: Lawson '73(a)), are cut out by a channel above AY/A-Ca. In the channel-fill beds, which correspond to a high level in the succession (- the ostracode N. nutans (DJS) was identified from the basal conglomerate (AY/A-Ca) of these beds), no S. ludloviensis was found. At Shelderton (SR/2-), S. ludloviensis is very common in the upper part of the hLLB (though less so than at the base of the LLB), but disappears shortly below the N. nutans level. Shells are mostly concentrated into thin, impersistent plane assemblages of scattered valves. Whitaker ('62) recorded the species as 'present' in the ULB of the Leintwardine area, but it has clearly diminished greatly in abundance by this time.

In the Ludlow area S. ludloviensis occurs fairly frequently in the basal LLB of the western facies, but does not become really common in any sections until the siltier lithologies have replaced the Aymestry Limestone facies. The species then remains very common throughout the LLB, with its local acme in the middle part of the succession (eg. in MF/F-). D. navicula also achieves its maximum abundance at Ludlow at a similar level. Close-packed, plane assemblages (many monospecific) of convex-up valves of S. ludloviensis alternate, in the sheet-laminated siltstone facies, with bands dominated by other species. In the western section MF/A-, S. ludloviensis dies out rapidly in the top 5 m of the LLB (at the level where A. gravi appears), but the species

persists in the eastern sequence SY/B- up into the ULB before dwindling in abundance.

In the shelf inliers, S. ludloviensis in much less common, but increases in abundance above the Aymestry Limestone facies. At Chances Pitch and Perton ~~Lane~~, it becomes very common in the shelly, calcareous siltstone facies, in species-dominated assemblages, often comprising thin shell limestones. The species has another, minor acme in the top LLB at Chances Pitch, but was not found at this level (LC) in the other inliers. Its presence has been recorded in the ULB of these areas however (Lawson '55, Tucker '60, Phipps and Reeve '67).

In the Brecon Anticlinal area, Ysgwydd Hwch (YH1-), in the shelly calcareous siltstone facies of the top LLB, is the only locality where S. ludloviensis was found commonly. Here, it occurs in thin, monospecific bands of disarticulated valves, alternating with similar accumulations of other species. It had disappeared from the fauna at the grayi-lauensis level (Lawson - pers. comm. '76). The species was found rarely in shelly assemblages at similar levels in the flaggy laminated siltstone facies at Crickadarn Hill and The Whimble; in the former, it did not extend up to the grayi-lauensis level.

S. ludloviensis was not recorded in the Llandovery-Llandeilo region by Potter and Price ('65), and was not found (LC) in the basinal regions of Knighton and Kerry.

Vertical distribution:

Sp: Lower Elton Beds (LEB) (Lawson '73(a)) - Whitcliffe Beds.

S. ludloviensis is found in many basinal sequences in the lower part of the Ludlow Series, as well as in areas of shelly shelf facies. This contrasts with the LLB distribution where the species is concentrated in the shelf edge and shelf regions.

For example, the species is the index fossil for the "Chonetes laevigata" (= S. ludloviensis) beds of Builth (Straw '37), which contain scanicus zone graptolites and correlate with the Middle Elton Beds (MEB) of Ludlow (see correlation chart in Fig 5.5 p 170). The sediments are shales and rubbly mudstones, which are largely slumped (Straw '37, '53). Fossils are confined mainly to thin sandy laminae, and consist of the small brachiopods S. ludloviensis and D. navicula, with beyrichiacean ostracodes and crinoid columnals. Graptolites and cyrtocones form the associated fauna. This is the lowest stratigraphical level at which

S. ludloviensis is important in basinal sequences. At a comparable horizon on the shelf, S. ludloviensis is characteristic of the L. Forest Beds (= Elton Beds) of Usk (Walmsley '59).

This brachiopod species occurs commonly in beds of the tumescens zone. At this level in the Striped Flags of the Brecon Anticlinal region (Kirk '49), it is found in slumped beds, and in shelly silty laminae, in sequences where many of the intervening fine siltstones are unfossiliferous or have pelagic faunas. The equivalent beds at Kerry (Earp '38) are the lower part of the "W" wilsoni Grits. These are turbiditic sediments in which shelly fossils are concentrated in the soles of beds, and fossils are sparse in the interbedded dark mudstones; S. ludloviensis is very common in the shell accumulations. At Aymestrey, the tumescens zone comprises the fine, poorly fossiliferous siltstones of the Upper Elton Beds (UEB) in which thin shell bands of S. ludloviensis occur at intervals, and the irregularly flaggy Lower Bringewood Beds (LBB) in which the species forms part of the richer shelly fauna (Lawson '73(a)). Slumps here in the UEB have lenses in which S. ludloviensis is common, while the normally-bedded units have sparse, graptolitic faunas (Lawson '73(a) - p 253: SO.418.660). At Leintwardine (Whitaker '62) and Ludlow (Holland, Lawson and Walmsley '63), the species is a frequent element of shelly assemblages in the graptolitic UEB. It becomes very common in the LBB among the diverse faunas in which large brachiopods are prominent. The correlation of the tumescens zone in the shelf sequences relies upon the shelly faunas of the UEB and LBB, because graptolites diminish in abundance eastwards. S. ludloviensis is fairly common to common in the shelf inliers at this level - for instance, in the Rilbury Siltstone (= LLB) of the Malverns (Phipps and Reeve '67).

The distribution of S. ludloviensis thus extends throughout the Ludlow outcrop, and is not restricted to, or centred in, the basinal areas. The occurrence of shells in the latter areas - in the soles of turbidites, in thin seams in sequences with mainly pelagic faunas, and relatively abundantly in slumped beds - suggests that they have been transported in. Mass sediment movement in the lower part of the Ludlow involved downslope slumping, and turbidity current transport along the axis of the trough (Bailey '64, '69, Bailey and Woodcock '76). Shells have presumably travelled in from shallower areas where benthonic faunas

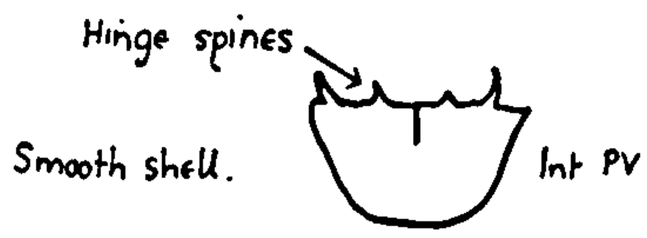
are indigenous. The rarity of shelly fossils through large thicknesses of sediment in basinal areas, except in clearly transported assemblages, argues against benthos living locally.

For shelf sequences, the degree of articulation and breakage of shells is not known. However, the usual association of S. ludloviensis with benthonic faunas suggests that this species is itself benthonic.

The species' geographical distribution is therefore comparable in the lower part of the Ludlow with the LLB. The wider occurrence and abundance in basinal areas, in the earlier period, of S. ludloviensis is considered to result from extensive transport, rather than from the species inhabiting these areas.

A facies preference for siltier lithologies, as found in the LLB, may be discerned lower in the Ludlow Series. Lawson ('73(a) - p 263) commented upon the more common occurrence of S. ludloviensis in the silty LBB of Aymestrey than at Ludlow, where the lithology is more calcareous. In the Malverns, the Rilbury Siltstone Member and Aymestry Limestone Member show complementary thickness changes, and were considered by Phipps and Reeve ('67 - p 348) to be partly stratigraphically equivalent. Faunal differences between the two can be related to the environment therefore. S. ludloviensis is very common in the siltstone, but not in the nodular limestone facies. In the Aymestry Limestone facies of the shelf and shelf edge, S. ludloviensis is only a minor constituent of faunas, although numerous both below and above the Limestone where the lithologies are siltier. (For example, at Leintwardine (Whitaker '62), and Ludlow (Holland, Lawson and Walmsley '63)). The distribution relates closely to the facies changes. Potter and Price ('65 - p 397) considered that the absence of S. ludloviensis from the Llandovery-Llandeilo region in the Ludlow was due to the sandy non-calcareous facies there. Thus the species appears to prefer fine clastic sediments.

Ecology:



Shagamella ludloviensis

S. ludloviensis is a small smooth anoplid chonetid. The shell

is semi-circular, widest along the hinge-line, with a strongly concavo-convex profile. Hollow internal spines project posteriorly at high angles from the margin of the pedicle valve interarea. There is a pedicle opening only in the early growth stages. The lophophore is inferred to be schizolophous or spirolophous (Muir-Wood '65).

Muir-Wood ('65) proposed that adult chonetids rested free on the sediment with the smaller, brachial valve uppermost. The hinge spines might function as "balancers", or for entanglement or attachment of the shell. In small forms which have light shells, it was noted that a floating habit might have been adopted.

Bergstrom ('68) considered this mode of life for S. ludloviensis, from a study of ? LLB (- stated as Bringewood Beds in his paper) siltstones of Aymestrey. He argued, from the association of some S. ludloviensis valves found with a patch of dark material which he interpreted as an algal film, that the species lived biocoenotically, attached by its spines to algae. However, he noted the relative thickness of the shell of S. ludloviensis compared with Sericoidea, and considered an epiplanktonic mode of life to be less probable for the former species.

Rudwick ('70) suggested that the small concavo-convex shell of some chonetids would have been adapted for swimming. Vigorous snapping shut of the shell might propel it over short distances, near the bottom, although a nektonic ecology was unlikely. He considered that the tubular spines served a sensory function, by projecting the sensitive mantle edges outwards from the shell.

Brunton ('72) concentrated upon possible water circulation systems through the lophophore in the chonetacean shell. He invoked very wide opening of the shell, as in Recent Megathiris. The spines of benthonic species acted to stabilise the individual, by preventing the shell being overturned by the currents into which it faced.

Conclusions:

The distribution of S. ludloviensis in the LLB shows its greatest abundance in the Ludlow to Leintwardine and Aymestrey regions. It is most common in silty lithologies. The retention of the delicate spines on disarticulated shells in some assemblages in these areas argues against considerable transport having occurred. However, other assemblages of disarticulated, broken shells in the same sequences show

the effects of current deposition and turbulence. The light, thin shell and lack of pedicle attachment suggest a requirement for quiet water conditions.

The concentration of the species in areas, and in assemblages, with benthonic faunas suggests that it is itself benthonic. The shells may have rested free on the substrate using the spines for stabilisation. A biocoenotic ecology (Bergstrom '68), attached to algal vegetation, is also possible, but the uncommon occurrence of S. ludloviensis in basinal areas in the leintwardinensis beds makes an epiplanktonic habit improbable. The more widespread basinal distribution lower in the Ludlow Series is concluded to result from shell transport in slumps and turbidites, rather than from a floating ecology or from the species inhabiting these areas. The preference for fine clastic sediments is shown at other levels in the Ludlow as well as in the LLB. It is unlikely that the mode of life of S. ludloviensis changed through the Ludlow period.

S. ludloviensis is less common in the SE inliers, and it declines at the top of the LLB and above. This indicates an intolerance to the coarser sediments and agitated conditions which characterise more proximal shelf environments. The absence of the species from the Llandovery region (Potter and Price '65) in the Ludlow supports this conclusion.

2. P. ludloviensis (Muir-Wood) Fig 5.11 p 278 , 5.12 p 279

Leintwardine Beds Distribution:

This species, which is largely confined to the shelf area, becomes common earlier in the SE in the LLB (Map A). It does not increase in abundance until the higher part of the LLB in areas further north (Map B, and vertical range chart Fig 5.12). The spread of the species' distribution into the basinal areas occurs mainly in the "C" gravi Beds (Map D) and above. However, the higher beds of the Striped Flags (Map C) show the initial incursion of shelly faunas with P. ludloviensis into sequences of poorly fossiliferous, laminated siltstones (for example, at Crickadarn Mill, CM-). Shelly faunas are not found in the Kerry and Knighton areas until Whitcliffe times, the sequences remaining sparsely fossiliferous up to that level. The facies change to more thickly-bedded siltstones corresponds to the main influx of shelly

faunas across the basinal region.

P. ludloviensis is nowhere common in the Aymestry Limestone facies (Map A), but occurs more numerously in the SE inliers in the basal LLB. Squirrell ('56) recorded an acme of the species at S. Woolhope in the basal conglomeratic facies. It becomes increasingly abundant above the conglomeratic beds in the other inliers, forming a prevalent fossil in many assemblages. Commonly, these bands comprise shell limestones, containing dense accumulations of large valves. In all the shelf inlier sections, the species continues in abundance into the ULB. Many plane assemblages include specimens with spines, although the valves are characteristically disarticulated.

At Ludlow, P. ludloviensis is far less common in the LLB, and does not appear abundantly until the ULB. It occurs in small numbers throughout the LLB however. The decrease in abundance continues westwards, and the species is absent in the LLB of the shelf edge region. Here it enters the fauna in the ULB, but does not become common until the Whitcliffe Beds.

P. ludloviensis does not occur in the northern basinal sequences (eg. Kerry - Earp '38) of the leintwardinensis beds until the upper part of the zone, when rare small valves are present. In the SW areas, small P. ludloviensis (many with spines) are found in monospecific assemblages in the shelly, upper Striped Flags at Crickadarn Mill (CM-). Size and abundance of valves increase in the overlying "C" gravi flags here. P. ludloviensis came into the fauna at a similar level in other sections in this region (eg. CTDI-, YH1-). The species occurs fairly commonly in the ULB, but the greatest abundance of P. ludloviensis in the basinal areas is in the Whitcliffe Beds.

Vertical Distribution:

(G.: Wenlock - U. Ludlow (Brunton '72))

P. ludloviensis is present from the LBB upwards but does not reach its acme until the Whitcliffe Beds. It is not usually common below the LLB (- except in the Llandeilo region: Potter and Price ('65)), although occurring widely through the areas of shelf facies. It occurs rarely in a few basinal sequences below the leintwardinensis zone; for example, in slumped horizons of the tumescens beds at Cwm Craig Ddu (Straw '53).

This distribution is typically that of a benthonic species, restricted largely to shelf areas. Its occurrence in fossiliferous beds of slumps, yet absence from normally-bedded units of basinal areas, indicates that the shelly faunas have been transported in with the sediment from shallower areas, and are not indigenous.

The main westward spread of the species' distribution at the top of the Leintwardinian is accompanied by the facies change to coarser, more thickly-bedded, calcareous siltstones over much of the basin region. In the N and NW of the outcrop (eg. Kerry), where the thinly-bedded, poorly fossiliferous strata persist to higher in the succession, P. ludloviensis does not become common until calcareous siltstones with shelly faunas are developed (eg. in the "Dalmanella" lunata Beds (= Upper Whitcliffe Beds (UWB) Fig 5.5 p 170) of Kerry (Earp '38)). The cosmopolitan nature of the Whitcliffe Beds facies and fauna indicates the diminution of the distinction between "shelf" and "basin".

P. ludloviensis, with S. lunata and M. nucula, is characteristic of the Whitcliffe Beds fauna throughout the Ludlow outcrop, and reaches its acme at this level. The diversity of articulate brachiopod species is low, and molluscs and annelids become important faunal elements in these beds (Holland, Lawson and Walmsley '63 - p 120). In the type area, P. ludloviensis remains common up to the Ludlow bone-bed (ie. base of Downtonian Stage) above which a Lingula-mollusc assemblage is found (Holland, Lawson and Walmsley '63 - p 146).

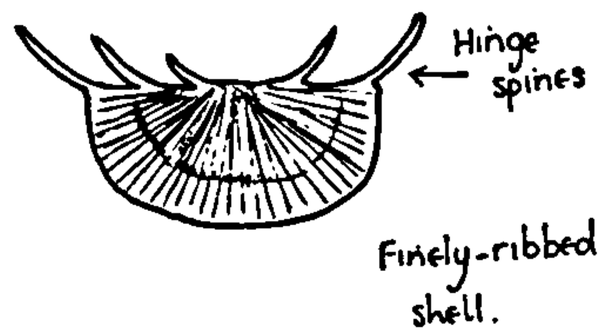
A comparable association to the Whitcliffe assemblage was recorded by Potter and Price ('65) from the Carn Powell facies immediately below the red, deltaic Trichrûg Beds (Bringewoodian) of the Llandeilo region. Molluscs were dominant in the fauna of these purple sandstones, together with P. ludloviensis, M. nucula and orthocones. Potter and Price related this faunal composition to the environment of shallow, sandy conditions and transition from marine to non-marine facies.

Assemblages from the Whitcliffe Beds of Ludlow, Woodbury Quarry and Perton have been noted (LC) to contain valves of P. ludloviensis with spines still attached. Such delicate structures are unlikely to be preserved during extensive transport, and hence these shells are thought to have been locally derived. The typical occurrence is of disarticulated valves in a convex-up attitude; Newall ('66) performed

flume experiments which illustrated the stability of valves once in this orientation, so that if easily "flipped" to this position the shells may not have travelled far. (See Ch 6 p 335).

Ecology:

Protochonetes ludloviensis



P. ludloviensis is a chonetid with a medium-sized capillate shell which has low-angled oblique hinge spines. Its profile is plano - to concavo-convex. Only early growth stages have a pedicle opening. The lophophore is inferred to be schizolophous or spirolophous (Muir-Wood '65).

(P. ludloviensis was considered by Böger ('68) to be conspecific with P. striatellus (Dalman). However, Bassett and Cocks ('74) consider this doubtful and retain them as separate species).

For a discussion of the ecology of chonetids see p 190.

Conclusions:

P. ludloviensis has a benthonic distribution. It shows a high tolerance of shallow, silty conditions. It decreases in abundance towards the shelf edge in the LLB, and most individuals in the fine laminated siltstone facies (eg. Crickadarn Mill CM-) are small. The presence of spines on valves at Crickadarn Mill indicates that these shells have not travelled extensively; the size may reflect unfavourable conditions (Ager '65).

P. ludloviensis occurs commonly from lower in the succession in the SE shelf inliers. The subsequent westward extension with time seen in the LLB continues in higher beds across the basinal areas, and corresponds to the lithological change to thicker, calcareous siltstones.

The preservation of spines in LLB and Whitcliffe Beds assemblages suggests that these valves have not travelled far. Shell limestones in the LLB, which commonly are composed of numerous, disarticulated and broken valves, represent current accumulations. Calcareous siltstones interbedded with these bands include horizons of complete valves with spines. Such assemblages indicate an ecological preference for less turbulent environments, since the delicate spines will not survive

agitated conditions. P. ludloviensis probably rested unattached on the substrate so that maintenance of stability is very important and the spines may well have functioned for this (Muir-Wood '62).

The species distribution shows an intolerance to the environments of the shelf edge and basin during the LLB. This indicates a facies control on the distribution; the persistence of P. ludloviensis during transitions from marine to non-marine facies relates to a high tolerance for shallow, silty and sandy conditions in more proximal shelf environments.

3. A. gravi (Davidson) Fig 5.14 p 280, Fig 5.13 p 279

Leintwardine Beds Distribution:

A. gravi occurs commonly in the ULB. It forms one of the faunal indices for this division (Holland, Lawson and Walmsley '63 - p 117). Its distribution is centred on the basinal areas. In the shelf sequences, it is found rarely and in only a few localities. It occurs sporadically in the lower leintwardinensis beds of the basin. (Map B)

The species enters the sequence and becomes common in the upper part of the LLB (Map C) in the type area, appearing lower in the succession and being more common in the western section MF/A- than in the eastern sequences (see Fig 5.13 p 279). At Leintwardine, the top 6 m at Shelderton (SR/2-) have abundant A. gravi. The poorly fossiliferous, channel-fill hLLB at Aymestrey (AY/A-) (and on the Bengry Track above the disappearance of typical LLB shelly fossils) have occasional 'nests' of A. gravi with shell debris and ostracodes. The highest beds of the Striped Flags in the Brecon Anticlinal sections show the fairly common occurrence of A. gravi at this level. (eg. YH1-, Wmb-). The typical distribution of the species is in assemblages with beyrichiacean ostracodes and fine bioclastic debris, separate from other horizons of shelly fossils. Single valves of A. gravi are randomly scattered through other beds.

The main concentration of A. gravi is found in the ULB (Map D), at the appearance of N. lauensis. There is a rapid increase in the abundance of the brachiopod at this level. Over much of the basinal region, this coincides with the facies change to the more thickly-bedded calcareous siltstones of the "C" gravi flags. However, the horizon is also present in the thinly flaggy lithologies of the Kerry area;

"biscuit" seams of crowded A. gravi and beyrichiacean ostracodes (that included N. cf. lauensis and N. scissa (DJS)) were found in Pant-y-Llidiart Dingle (PylD-8).

As in the highest LLB, A. gravi and ostracodes characteristically occur together in the ULB, in thin fossiliferous seams, or "nests" that may be inclined slightly to the bedding. Such horizons are developed at frequent intervals in the ULB of Leintwardine and Aymestrey. Further east at Ludlow, the western silty facies include abundant A. gravi in basal ULB assemblages, but in the eastern, more calcareous facies, the species is much less common. A. gravi occurs in some thin fossiliferous seams in the ULB at the stratotype on the Whitcliffe (Holland, Lawson and Walmsley '63).

In the shelf inliers, A. gravi is very rare. Lawson and Whitaker ('69) reported it to be present at a fairly high level in the L. Longhope Beds (ULB) at May Hill, and also in the U. Bodenham Beds (ULB) at Perton.

The distribution maps show the spread of the geographical range of A. gravi, and its increasing abundance, through the Leintwardinian. It is initially restricted to the basinal sequences (Map B), but extends progressively to the S and E (Maps C and D). In the ULB, it has its greatest areal coverage, but is very rare east of Ludlow in the shelly calcareous siltstone facies.

Vertical Distribution:

G. : L. Llandovery - U. Ludlow (Brunton '72)

Cocks ('70) commented upon the common, but "patchy", distribution of A. gravi in the Llandovery and Ludlow successions, but its rarity in the Wenlock. In the latter it is present in the Wenlock Shale of several areas (for instance, Ludlow (Holland, Lawson and Walmsley '63), Woolhope (Squirrell and Tucker '60), and Wenlock Edge (Shergold and Shirley '68)), but not in the Limestone. In the Ludlow, a similar concentration in fine clastic sediments is observed. The species is not found in the Aymestry Limestone facies, although occurring at a stratigraphically equivalent level in the "Wilsonia" wilsoni Grits of Kerry (Earp '38).

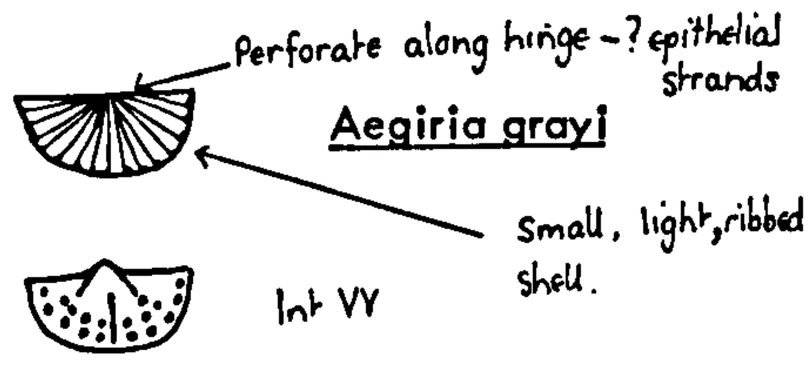
Below the LLB, A. gravi is common in many areas at various levels in the Elton Beds, and in the LBB. In the type area (Holland, Lawson and Walmsley '63 - p 107), A. gravi is associated with graptolites,

orthocones and beyrichiacean ostracodes in the MEB. These are thinly flaggy and shaly siltstones, in which benthonic forms are rare, in contrast with the shelly LEB fauna of small brachiopods and trilobites. (A. grayi is a fairly common constituent of the LEB fauna as well). The transitional lithological change to the calcareous, coarse siltstone flags of the UEB is accompanied by a change in the graptolite species, and addition of S. ludloviensis to the fauna. A. grayi is less numerous, but the qualitative faunal composition remains similar. At Woolhope (Squirrell and Tucker '60), A. grayi was recorded very commonly in the shelly mudstones and siltstones of the L. Wootton Beds (= LEB and MEB; Fig 5.5). It continues, but with diminished abundance, in the overlying, more calcareous, U. Wootton Beds (UEB), which have a fauna dominated by graptolites and Chonetes cf. minima, with molluscs. A grayi is infrequent at Leintwardine (Whitaker '62) until the LBB calcareous siltstones, which have a diverse shelly fauna associated with graptolites.

At Knighton (Holland '59), in the basinal sequences, an abundance of A. grayi was noted in the turbiditic siltstones of the L. Bailey Hill Beds (= MEB). It was recorded at an equivalent level at Builth (Straw '37, '53) in the slumped series. Kirk ('49) recorded the species commonly in both slumped and normal developments of some nilssoni-scanicus beds (= MEB) of the SW Brecon Anticlinal region, in mudstones with a fauna of graptolites and small shells.

The species distribution below the leintwardinensis zone is in fine clastic sediments, and often in mixed shelly and graptolitic faunas. The upper limit of its range corresponds closely to the top of the ULB. At the type area (Holland, Lawson and Walmsley '63 - p 145), A. grayi remains common in bands up to the base of the Lower Whitcliffe Beds (LWB), where it disappears. Many elements of the Leintwardine Beds fauna die out at this level. Similar faunal changes take place in other areas, often without marked lithological change (eg. Builth - Straw '37, Kerry - Earp '38).

Ecology:



A. gravi is a small, slightly concavo-convex plectambonitacean, with a finely costellate shell. There is a narrow pedicle foramen. The brachial valve has a well-developed lophophore platform and dorsal median septum. The lophophore is inferred to have been schizolophous or ptycholophous (Muir-Wood and Williams '65).

The ecology of A. gravi was considered by Cocks ('70) in relation to its Llandovery distribution. In clastic rocks, the species occurs rarely in the Stricklandia community, and commonly in the Clorinda community (Ziegler, Cocks and Bambach '68). It is also found in some assemblages in Llandovery beds which have a restricted benthonic fauna, where conditions are deduced to have been inimical to brachiopods.

Bergstrom ('68) described assemblages of a closely-related genus, Sericoidea, from graptolitic shales in the Ordovician of Scania. A few articulated individuals were found in one horizon (although, mostly, valves were separate). He argued that the species lived biocoenotically, attached to plants perhaps by epithelial strands as in Eochonetes (Muir-Wood '65 - p 175). The plants might have grown in the shale environment, but it appeared to have been adverse to other life. Alternatively, the shells could have been transported, still attached to uprooted algae, by currents, before being deposited. However, Bergstrom commented that the light thin shell of these plectambonitaceans was well-adapted for an epiplanktonic existence attached to floating algae, rather than on anchored vegetation.

Cocks ('70) favoured pedicle attachment to rooted algae to explain the occurrence of scattered valves of Aegiria among his benthonic communities as well as the assemblages in sequences with restricted faunas. He considered that the Clorinda community specimens were locally derived. The basis for this conclusion is questionable, relying upon the random dispersal of shells in sequences which have restricted faunas compared with aggregrated distributions in the Clorinda

community. Cocks noted no morphological difference between the specimens among benthonic faunas and the others, and concluded the modes of life were similar.

The small light shell of A. gravi would derive stability from attachment, for example, to plant material (whereas it would be very susceptible to transport if it lay free on the surface). The shell is well-adapted for an epiplanktonic existence attached to floating weed, but this does not preclude attachment to anchored vegetation.

Conclusions:

In the Leintwardine Beds, A. gravi is restricted in its vertical range to the upper part of the LLB and the ULB, and laterally is only common in the areas west of Ludlow. It is characteristically found in thin, decalcified seams or impersistent lenses of fossils, together with beyrichiacean ostracodes. Single valves of A. gravi are dispersed through some beds. Assemblages of shelly benthonic fossils are found at separate levels in sequences. In the ULB, the wide areal distribution of A. gravi - ostracode horizons extends into different lithologies, including the thick "C" gravi beds siltstones, the thinly flaggy siltstones of Kerry and the Long Mountain, and the calcareous siltstone flags of Ludlow.

At other stratigraphic levels, A. gravi is reported from fine clastic sequences with restricted, and often pelagic, faunas; but also with shelly faunas. It is not found in carbonate facies. A.gravi disappears from the fauna at the top of the ULB.

Closely related genera, eg. Sericoidea, appear to have comparable distributions. The light thin shell has been interpreted as an adaptation to an epiplanktonic mode of life (Bergstrom '68). The distribution may also be explained by attachment to anchored vegetation (Bergstrom '68 Cocks '70), with the shells being transported extensively still entangled in uprooted algae. The scarcity of benthonic forms in some sequences where A. gravi occurs, the distinction of A. gravi horizons from interbedded assemblages of benthos, and the independence of facies in the ULB all suggest that a mode of life on the sediment surface is less probable. Its rarity in the shelf inlier sequences could result from selective destruction of the light thin shell in the conditions of greater turbulence which are associated with more proximal shelf environments. However, it seems likely to reflect an original

feature of the distribution, with the species being concentrated in fairly quiet environments.

4. S. ornatella (Davidson) Fig 5.15 p 281 , 5.16 p 282

Leintwardine Beds Distribution

The species exhibits a complementary distribution to S. wilsoni in the high LLB of the shelf facies, becoming dominant as the rhynchonellid dies out (Fig 5.16 cf. 5.17). It is present, less commonly, throughout the LLB of the shelf, however.

S. ornatella becomes rapidly very abundant in the shelf inliers, at approximately the level of disappearance of S. wilsoni. Bands of closely-packed valves, in monospecific assemblages, characterise this faunal acme. The species occurs sporadically through the LLB, and minor acmes were recorded in the succession at Perton, Chances Pitch and Woodbury. However, the top expansion in the shelf inliers forms a distinctive horizon, which has been correlated with the ULB of Ludlow (eg. Holland et al. '59).

In the type area, this acme is not so distinctive, with the species found consistently through the upper half of the LLB becoming abundant in the E in the top 10 m of succession below the ULB, often in monospecific assemblages. It does not become abundant in western sections at Ludlow until higher in the sequence, in the top 5 m of LLB. The ULB show a continuing abundance of S. ornatella in assemblages through the division.

West of Ludlow, there is a very marked decrease in the abundance of the species. It is not common in the Leintwardine region: it occurs in small numbers towards the top of the LLB at Shelderton (SR/2-). Whitaker ('62) recorded it as "present" in his ULB. At Wenlock Edge, Shergold and Shirley ('68) noted the abundances shown in the maps, which are comparable to the Leintwardine succession.

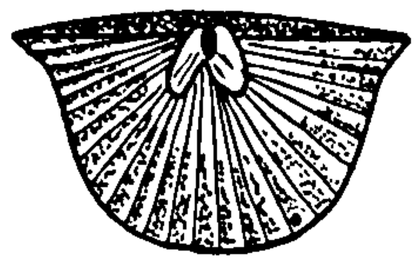
S. ornatella was found commonly in the top LLB at Ysgwydd Hwch (YH1-) in shelly calcareous facies, at a level below the gravi-lauensis fauna. In the shelly laminated siltstone facies of the top part of the Striped Flags in other Brecon sections, the species was not found. No shelly development was present at the top of the "M" leintwardinensis Shales of Kerry (where A. gravi and N. lauensis were found).

Thus, the "ornatella" beds are very much restricted to the shelly calcareous siltstones of the shelf inliers. At Ludlow and further west, the strophomenid is less common, and the acme occurs at a lower level than the gravi-lauensis horizon (Maps C and D).

Vertical Distribution:

S. ornatella sl. is confined to the top part of the UBB and Leintwardine Beds, although the closely related types Shaleria sp. nov and Brachyprion sp. are fairly common in the Bringewood Beds. The top of the range corresponds to the ULB-LWBboundary at the stratotype (Holland, Lawson and Walmsley '63), where the species disappears with the faunal change at this level.

Ecology:



Shaleria ornatella

S. ornatella has a broad, semi-circular, flattened shell, slightly concavo-convex in profile. There is unequally parvicostellate ornamentation on the shell, which is densely pseudopunctate. The hinge has simple teeth and hinge denticles. The apical foramen is closed. The lophophore type is thought to be schizolophous or spirolophous.

Stropheodontids lacked a functional pedicle. The shell is well-adapted for an unattached mode of life, resting freely on the sediment. The surface area is large compared with the volume of the shell, so that a "snow-shoe" effect is produced (eg. Williams '53, Bowen et al. '74).

Bowen et al. ('74) suggested that stropheodontids may have been able to "swim" in a pectenid manner for short distances, in order to clear the shell of sediment (as proposed by Rudwick ('61)).

Williams ('53) commented upon some accumulations of "stacked" valves of stropheodontids, oblique to the bedding with the umbones downwards. There was no distortion of the growth lines on shells that might be expected if the crowded association represented a life assemblage. He noted the common occurrence of conjoined shells with

the convex surface upwards and shell margin buried in the sediment; this was assumed to be a death orientation, because the commissure must lie above the surface to allow feeding and respiration. The life attitude must then be resting upon the convex valve.

The characteristic distribution of stropheodontids in fine-grained sediment has been recorded by several workers (eg. McGhee '76, Bowen et al. '74).

Conclusions:

The distribution shows a restriction of the species to shelf areas, with the greatest abundance in the ULB of the SE inliers when "banks" composed monospecifically of S. ornatella are developed. S. ornatella is much less numerous west of Ludlow, and many individuals are small. The acme here occurs below the grayi-lauensis level, and the species is not common in the thickly-bedded siltstones of the "C" grayi beds.

The shell shape shows adaptation for a free-living existence, perhaps on soft sediment. The lithology in which S. ornatella generally occurs is a calcareous siltstone; "stacked" assemblages in shelly limestones represent current accumulations. Disarticulated valves in bedding-plane assemblages are mainly convex-surface up, which is the stable orientation - they may not have travelled far (see population surveys p 354).

The distribution pattern indicates that S. ornatella may be intolerant to sedimentation and turbidity. Its high concentration in the shelf sequences, and decrease in size and abundance westwards could be explained thus. In the ULB of the shelf inliers, phosphatised horizons, conglomerates, and bone-beds (Map D) suggest periods of stand-still in deposition.

5. L. depressa (J. de C. Sowerby) Fig 5.18 p283

Leintwardine Beds distribution:

L. depressa is common over much of the shelf and shelf edge region in the Aymestry Limestone facies of the top UBB. It declines in abundance at, or shortly below, the base of the LLB (Map A). In the main part of the LLB, its presence is confined to the northern shelf sections (except for infrequent occurrences in the SE inliers) - Map B. At the top of the LLB, or in the ULB, there is an acme of L. depressa, together with A. reticularis, over a large part of the outcrop (Maps C and D). The species does not occur in the laminated siltstone facies of the basinal region.

L. depressa is consistently present through the upper half of the LLB at Ludlow. In the sheet-laminated siltstone facies, it is frequently a minor constituent in plane assemblages of S. ludloviensis, D. navicula, small beyrichiacean ostracodes and proetids. Many of the L. depressa valves still retained the trails. The shells were usually convex-surface up, and occasional planes had individuals aligned with the hinge-lines parallel. Although the L. depressa shells were clearly current-orientated, the preservation of the trails may indicate that transport had not been extensive.

The acme of L. depressa and A. reticularis is widespread. The areal extent of the former increases markedly at this level, as well as its abundance. The two species of large brachiopods are commonly associated with S. ornatella in the calcareous shelly siltstone facies. In the Brecon Anticlinal area at Ysgwydd Hwch (YH1-), the acme (with S. ornatella) occurs in calcareous siltstones that are transitional between the thin laminated siltstones of the Striped Flags and the overlying massive "C" grayi Flags of the grayi-lauensis horizon.

Vertical Distribution:

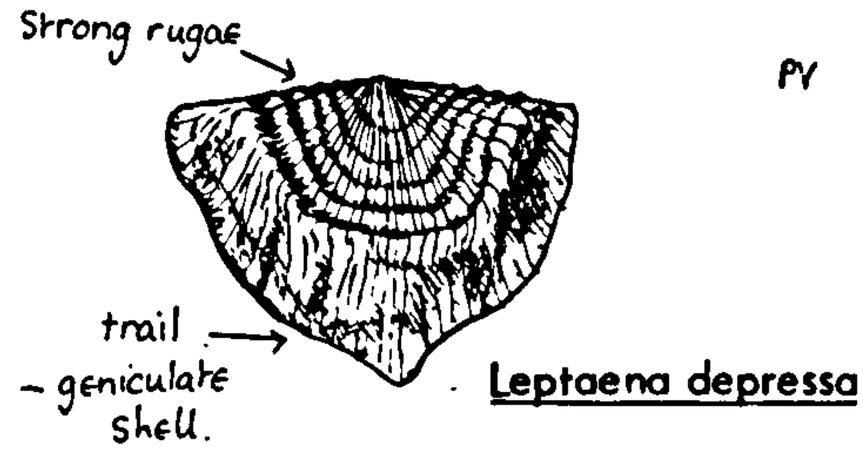
Sp.: Late Wenlock and Ludlow (Bassett and Cocks '74)

L. depressa occurs commonly in the shelf areas in the Bringewood Beds. The "strophomenid siltstones" of the LLB have L. depressa together with S. euglypha, L. filosa, Mesopholidostrophia, and A. funiculata as prevalent fossils in many assemblages. The species also remains common in the less fossiliferous, nodular Aymestry Limestone facies of the UBB. It is most frequent in units with S. euglypha and A. reticularis, rather than the coral-rich and Kirkidium units in the main outcrop (Newall '66). The former units were interpreted by Newall as the lowest energy environment of the Limestone.

At Ludlow, L. depressa disappears from the fauna in the ULB-LWB faunal change. It is reported from a few areas above this level, for example at Builth (Straw '37), but has died out in most areas along with many Leintwardine Beds forms.

The Much Wenlock Limestone fauna commonly includes L. depressa (or a closely related form L. rhomboidalis).

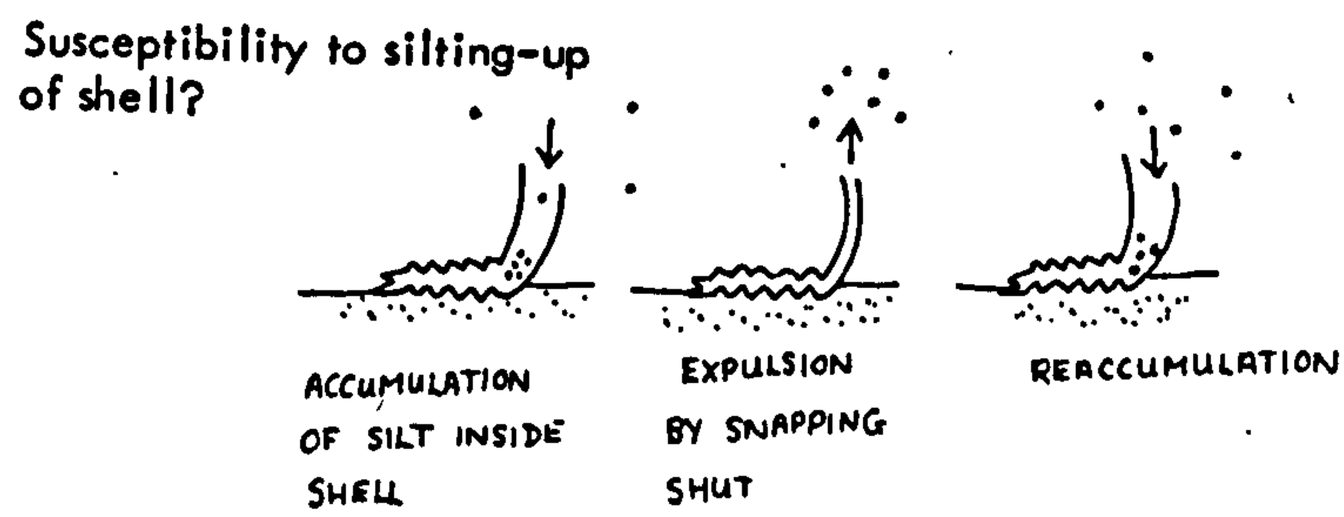
Ecology:



L. depressa is a large, concavo-convex strophomenacean, with a sharply geniculated shell (dorsally directed). The disc and trail are separated by a narrow, projecting ridge. The shell is finely-ribbed, and strong concentric rugae are developed on the disc. The apical foramen persists throughout ontogeny. The lophophore is considered to be schizolophous or spirolophous (Muir-Wood and Williams '65).

In the treatise, Muir-Wood ('65) proposed that Leptaena retained a functional pedicle throughout life. Rudwick ('65) suggested that the geniculation of the shell was adapted for a life position resting on the convex value. This could sink quite deeply in the sediment, providing stability, while the commissure would still be slightly above the surface to allow feeding and respiration. Sediment on the concave valve would camouflage the shell against predators. The broad shell, and very large surface area to volume, are usually considered as adaptations for resting on a soft substrate.

Shiells ('68) interpreted the functional morphology of Kochiproductus, a large productoid with a flange on the trail margin. He pointed out the difficulty of clearinga geniculated shell of sediment accumulating inside if the shell margin is steeply inclined - as it will be in Leptaena if it rests on the convex valve.



Conclusions:

L. depressa only becomes common in the higher part of the LLB, in areas of calcareous siltstone facies. The areal distribution is closely

similar to that of S. ornatella. There is a widespread acme in the topmost LLB to ULB, of L. depressa and A. reticularis. The two species are often abundant with S. ornatella in assemblages.

At other stratigraphic levels, L. depressa is associated with other strophomenids, in calcareous siltstones and limestones. It disappears widely from the fauna above the ULB.

The shell appears adapted for resting on the convex valve on the substrate, either freely or pedically anchored. The trail permits the commissure to project above the substrate even if the shell is partly buried.

The vertical and lateral distributions of L. depressa suggests that it is intolerant of sedimentation and turbidity: it is commonly found in more calcareous beds, and is rare in basinal areas. The difficulty of eliminating sediment from the shell, together with its susceptibility to sediment entering it (Shiells '68), may be controlling factors. The acme at the top of the LLB may therefore result from a slowing of sedimentation over the shelf at this level.

6. I. orbicularis (J. de C. Sowerby) Fig 5.18 p283 , Fig 5.20 p285

Leintwardine Beds Distribution:

I. orbicularis has a wide distribution through the LLB of the shelf and shelf edge regions, but is rare in the basinal areas.

The species is fairly common in the top Aymestry Limestone facies of the UBB, and extends up into the LLB, where it becomes increasingly numerous. At the base of the LLB in the Leintwardine region, abundant I. orbicularis valves are concentrated monospecifically into a band - corresponding to the "Orthis" orbicularis horizon of Alexander ('36) - which caps the Limestone. D. navicula dominates the fauna of many other beds in the shelf edge sequences at this level. I. orbicularis characteristically occurs monospecifically, or as the prevalent fossil, in plane assemblages of disarticulated valves. It becomes increasingly common as D. navicula declines relatively in abundance (eg. above LD-K at Lawnwell Dingle Fig. 4.3 p110). Some shelly limestone bands at Lawnwell Dingle contained a greater proportion of articulated specimens, but most assemblages were of single valves.

I. orbicularis is common in the slump fauna at Lyepole Bridge Quarry, but rare in the undisturbed beds. Its occurrence here supports a derivation from the shelf area for the contorted sediments.

In the hLLB in the Leintwardine area, when fossils become generally less numerous (Whitaker '62), I. orbicularis remains common in some bedding plane assemblages. In the top part of the hLLB, in the Shelderton Road section, though, I. orbicularis declines in abundance, and disappears from the shell assemblages in the highest beds. Whitaker ('62) did not record the species in the ULB. At Aymestrey, the hLLB channel-fill beds do not include I. orbicularis. These beds correspond to a level above the disappearance of the species in the Shelderton Road section. I. orbicularis was not reported by Lawson ('73(a)) from the ULB at Aymestrey.

In the Aymestry Limestone facies of the basal LLB at Ludlow, I. orbicularis increases in abundance fairly rapidly after the disappearance of the characteristic UBB forms. It dominates many assemblages in these lower beds, particularly in the western sections, occurring mostly as disarticulated valves, but with some bands containing a greater proportion of complete specimens. The acme at Ludlow, however, is in the beds above the Limestone facies, and develops earlier in the west than in the east. I. orbicularis forms a prevalent fossil in many of the shell bands in the sheet-laminated siltstone facies, alternating in dominance with D. navicula, S. ludloviensis, M. nucula and S. wilsoni. It disappears from the fauna, along with the former two species, in the upper 5 m of the LLB in the western section MF/A-, but continues to be very common up into the ULB in the east at SY/B-. A similar distribution is found at Wenlock Edge, where Shergold and Shirley ('68) recorded the species' greatest abundance to be in their high LLB, which follow transitionally from the Aymestry Limestone facies. I. orbicularis became very abundant in bands which they equated with Alexander's basal LLB marker horizon. Lawson and Whitaker ('69) questioned the validity of such a correlation based upon this widespread and common species.

In the shelf inliers, I. orbicularis becomes very abundant above the Aymestry Limestone, and conglomeratic facies of the lowermost LLB (Map B), to dominate the fauna in numerous assemblages. Frequently the concentration of shells is high, so that the accumulations comprise shell limestones. At May Hill, the shells in many assemblages are large and a similar observation was made by Walmsley at Usk ('59 - p 493).

The acme for this species in the inliers occurs in the middle to upper part of the LLB, although it is very common throughout. It declines in importance in the faunas of the ULB, particularly in the southern sections.

The maps show the concentration of the distribution in the shelf facies. At the top of the LLB, when the abundance of I. orbicularis has declined in the SE shell inliers (Map C), the areal extent westwards has increased. Assemblages of I. orbicularis valves are found in shelly horizons of the top Striped Flags in several "basinal" sequences (eg. Whimble Wmb-, and Crickadarn Mill CM-). The decrease in abundance continues, and in the ULB the species is only common in the Malverns and Abberley Hills (Phipps and Reeve '67; and Map D).

Vertical distribution

G.: U. Llandovery - Eifel (Boucot '75)

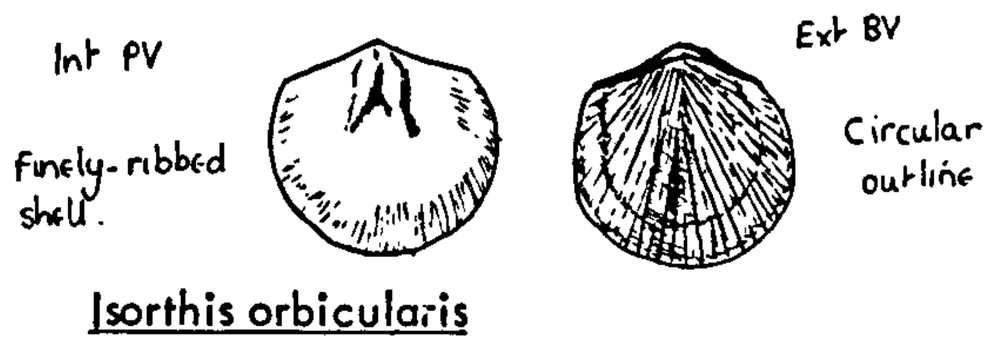
In the LLB, I. orbicularis is the dominant species of isorthid, although Isorthis clivosa, a closely-related species, also occurs rarely. The relative proportions of the two species outside the LLB are not known, but I. clivosa is the species prevalent in Wenlock rocks (Hurst '75). Hurst ('75) stated that, while I. clivosa was characteristic of the Isorthis community of Calef and Hancock ('74), I. orbicularis was more common in their shallower Sphaerirhynchia community. He considered the two species to display different environmental preferences, therefore. The occurrence of the genus in other parts of the Ludlow series will be considered only briefly.

In the shelf areas, isorthids are found in shelly faunas of the Elton and Bringewood Beds, but are absent or uncommon in the sequences with graptolitic, restricted assemblages; for example, the MEB and UEB of Ludlow (Holland, Lawson and Walmsley '63), and U. Wootton Beds (UEB) of Woolhope (Squirrell and Tucker '60). Isorthis is a common element of the shelly fauna from the soles of turbidite units in the basinal successions. The "W" wilsoni Grits of Kerry (Earp '38), and Bailey Hill Beds of Knighton (Holland '59), in the nilssoni-scanicus and tumescens zones, are sequences of this type. At Cwm Craig Ddu (Straw '53), the equivalent strata are largely slumped. Here, shelly horizons (which include Isorthis very commonly) are confined to slumps, and benthonic forms are rare in the interbedded, undisturbed shales. Thus, the

basinal occurrences of Isorthis indicate that the shells have been transported in, and were not indigenous in these areas.

The decline of Isorthis in the ULB (Map D) is followed by its disappearance from the fauna in the LWB.

Ecology:



Isorthis orbicularis

I. orbicularis is an endopunctate enteletacean, with a biconvex strophic shell which is finely costellate. The shell has a shallow sulcus in the brachial valve. There is a strongly bilobate ventral muscle field. The apical foramen remains throughout ontogeny. Orthids are inferred to have been schizolophous or spirolophous (Williams and Wright '65).

Orthids are thought, because of the persistence of the apical foramen, to have had a functional pedicle for support and anchorage. They, therefore, probably required a hard site for attachment (Rudwick '65).

Conclusions:

I. orbicularis has a distribution in the LLB centred in the shelf and shelf edge areas. It becomes very common above the Aymestry Limestone facies (see vertical range chart Fig 5.20 p 285) and remains so through the LLB. The acme of abundance is found in the middle part of the LLB. The areal distribution extends westwards at the top of the LLB (Map C). However, the species declines in abundance in the upper part of the Leintwardinian and soon disappears from the fauna.

Isorthids lower in the Ludlow succession are common constituents of shelly faunas in the shelf areas. Their basinal occurrences are in turbidites and slumps, and are considered to be transported assemblages from areas with benthonic faunas - ie. from shelf environments.

The enteletaceans are interpreted as pedically-attached forms, and probably required a hard site for attachment to the substrate. They are most common in the LLB in the calcareous siltstone facies, often in densely-packed current accumulations of disarticulated valves which

comprise shell limestones. Assemblages are frequently monospecific, with valves dominantly orientated convex surface up. However, some horizons with more articulated specimens are found in many sequences; these assemblages show that I. orbicularis did live locally. Therefore, the clearly transported LLB assemblages may not have moved far. However, the species clearly occupied a wide area of the LLB shelf, and extensive transport may have occurred without causing mixing of different faunas. The LLB distribution shows that the areas of laminated siltstone facies were not favourable for colonisation by I. orbicularis.

7. S. lunata (J. de C. Sowerby) Figs 5.22 p 286 , and 5.21 p 285

S. lunata has a similar distribution pattern to P. ludloviensis (eg. Fig 5.11 p 278). Together with the latter, it reaches its maximum abundance in the Whitcliffe Beds, where it is a characteristic species of shell assemblages. S. lunata enters the fauna and rapidly becomes very common in the LLB of the shelf region. It has a broadly complementary vertical distribution to I. orbicularis (Figs 5.20 and 5.21 p 285).

In the basal LLB (Map A) the only sections in which S. lunata is present are at Ludlow, Aymestrey, and Leintwardine, where it occurs commonly in some plane assemblages of the siltier lithologies. It is rare in the Aymestry Limestone facies. At this level, I. orbicularis dominates many faunas throughout the outcrop.

The first appearance of S. lunata in the shelf inliers comes in beds above the conglomeratic facies (see Fig 5.21 p 285). It does not become a prominent constituent of the fauna until the upper part of the LLB (Map C). Then it dominates many assemblages, often virtually exclusively. In all the successions, its acme for the LLB comes above that of I. orbicularis (Figs 5.20 and 5.21 p 285).

West of Ludlow, the abundance decreases considerably, and S. lunata is not found in the Brecon Anticlinal region until the top of the Striped Flags (Map C). In the shelly horizons of the upper part of the laminated siltstone facies, S. lunata was found to be a minor faunal constituent at several localities (CTD1-, YH1-, CHD-, CM-). It becomes more common in shelly assemblages of the overlying "C" gravi beds. (Map D)

In the northern areas of thinly flaggy siltstones, S. lunata does not occur in the leintwardinensis beds.

Vertical Distribution:

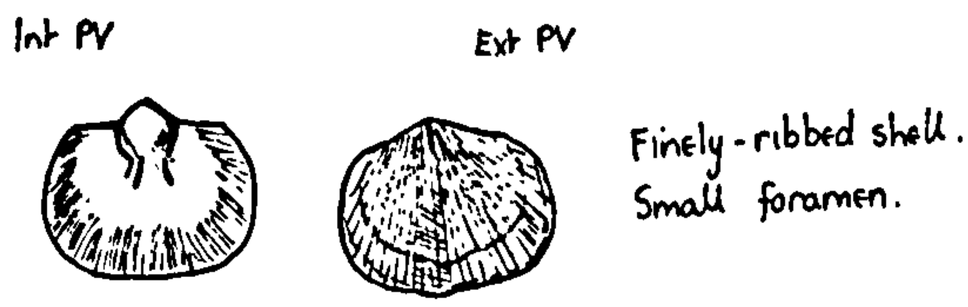
G: U. Llandovery - Eifel (Boucot '75)

In the type area, S. lunata becomes particularly numerous in the UWB (Holland, Lawson and Walmsley '63 p 121). These are more regularly-bedded calcareous siltstones, in which fossils are generally commoner. The species is also abundant in the LWB however.

In the Kerry (Earp '38), Knighton (Holland '59) and Long Mountain (Palmer '72) areas, the full shelly development of the Whitcliffe Beds is not found until the UWB, when S. lunata appears and rapidly becomes very common (for example, in the "D." lunata beds of Kerry: Earp '38). It is at this level that the whole outcrop is characterised by cosmopolitan shelly faunas. The lithology is typically calcareous siltstones, in which plane assemblages of crowded valves of P. ludloviensis, S. lunata and M. nucula occur commonly, and molluscs form important faunal constituents.

The three brachiopods extend rarely into the basal beds of the overlying Downtonian in some areas, for example, at Perton (Squirrell and Tucker '60). The decline of the UWB fauna is sudden, and leaves a restricted fauna of lingulids and molluscs; the Ludlow Bone-Bed and phosphatised pebble-beds are at the horizon of faunal change in many shelf areas.

Ecology:



Salopina lunata

S. lunata is an enteletacean species similar in form to I. orbicularis. It has a cordate ventral muscle field.

Like I. orbicularis, this species is adapted for a pedically-attached mode of life. It probably required a hard site for anchorage on the substrate.

Conclusions:

The LLB distribution of S. lunata is centred in the areas of calcareous siltstone facies. The species becomes common earlier in the SE shelf inliers. This level is progressively higher westwards, and

parallels the extension of the species' areal distribution over the basinal region. The trend continues above the Leintwardine Beds, until in the UWB the species is abundant throughout the outcrop. Like I. orbicularis, assemblages of S. lunata are frequently monospecific, and mostly composed of disarticulated valves. However, a few interbedded assemblages with many articulated specimens suggest that the species was indigenous in the shelf region. The absence of S. lunata in the sequences of thinly laminated siltstones indicates that these conditions were unfavourable.

S. lunata is very common, in the ULB (Map D) and above, in the thickly-bedded siltstone facies. It is still not found in the thin flags of the N and NW (eg. Kerry). The persistence of the species in abundance up to the Downtonian must indicate its tolerance of shallow, silty environments.

S. lunata is inferred to have been pedically-attached. Its vertical and lateral distribution shows a preference for conditions in more proximal parts of the shelf. I. orbicularis is often found in the same sequences in the LLB, but in separate assemblages. The two species have similar, wide distributions in the areas of calcareous siltstone facies. I. orbicularis declines at the top of the LLB, when S. lunata becomes increasingly common. The two species have very similar forms, and by inference, have comparable modes of life. The vertical replacement of Isorthis by S. lunata supports this conclusion.

8. S. wilsoni (J. Sowerby) Fig 5.23 p 287, Fig 5.17 p 282

Leintwardine Beds distribution:

The distribution maps show the concentration of the species in the shelf and shelf edge regions. The greatest abundance is found in the SE inliers, where it also persists longer (Map C, and Fig 5.17 p 282). The decline and disappearance of S. wilsoni in the topmost LLB is rapid. The species is not found above the Leintwardine Beds.

S. wilsoni occurs abundantly throughout the shelf region in the basal LLB (Map A). It is a prevalent species in numerous assemblages, and very common in the conglomeratic limestone beds of the lower part of the division in the inliers. There are considerable numbers of S. wilsoni in the basal shelly calcareous facies at Shelderton (eg. Lawnwell Dingle), but the species diminishes in importance in the

overlying thin siltstones. Similarly at Aymestrey, the species becomes less common above the basal beds, although still occurring in monospecific assemblages at levels.

The slumped units in the lower part of the leintwardinensis beds at Lyepole Bridge Quarry, W. of Aymestrey, have bands of shelly fossils in which S. wilsoni is abundant. The interbedded undisturbed sequences here have a very different fauna, dominated by graptolites and L. lata; S. wilsoni is rare in these beds. The slump fauna, which is largely benthonic, appears to be derived from shelf areas to the east. Indeed, further west, a few S. wilsoni occur sporadically in the laminated siltstone facies, but benthonic fossils are rare.

The acme of S. wilsoni is reached in the middle to upper part of the LLB in the shelf. Monospecific accumulations of articulated specimens are characteristic of this part of the succession. The thinly flaggy siltstones of the Leintwardine region are less fossiliferous at this level, however. S. wilsoni occurs in assemblages of scattered, aligned shells in these beds - for example, in the LLB in the quarry NE of Wassell Barn (TL5-), and in the channel-infilling hLLB of Martin's Shell (SO.4109.7543). Mostly, these S. wilsoni individuals are of a large, flat variety. The basinal sequences at Aberedw (Abdw-) and the Ring Hole (RH2-) include rare specimens of S. wilsoni in slumped sequences in the middle to upper part of the leintwardinensis beds.

In the higher part of the LLB, S. wilsoni declines and disappears from the fauna in the northern and western areas of the shelly siltstone facies (Map C), and S. ornatella becomes rapidly more common in these areas. In the shelf inliers, the rhynchonellid persists and is abundant at this level. It dies out suddenly in the shelf inliers, at the level where S. ornatella becomes prevalent (Map D). It is not found in the thickly-bedded siltstones of the "C" gravi Flags.

Vertical distribution:

G.: Wenlock - mid-Ems (Boucot '75)

The common occurrence of S. wilsoni through great thicknesses of sediment, in basinal areas below the leintwardinensis zone, is reflected in its selection as an index fossil; for example, the "Wilsonia" Shales of Builth (Straw '37) and "Wilsonia" wilsoni Grits of Kerry (Earp '38). These divisions are not stratigraphically equivalent. The former includes the tumescens zone and part of the leintwardinensis zone, while

the latter covers nilssoni-scanicus and tumescens beds.

In the northern part of the basin (eg. Kerry and Knighton), the beds with S. wilsoni in abundance are turbiditic siltstones (Holland and Lawson '63). Shells are concentrated in the soles of turbidite units, while the interbedded shaly siltstones have restricted, graptolitic faunas. S. wilsoni and other benthonic fossils have been introduced into the basinal areas with the turbidity currents. Their absence in the intercalated, less calcareous shales indicates that the environment was inimical to benthonic forms.

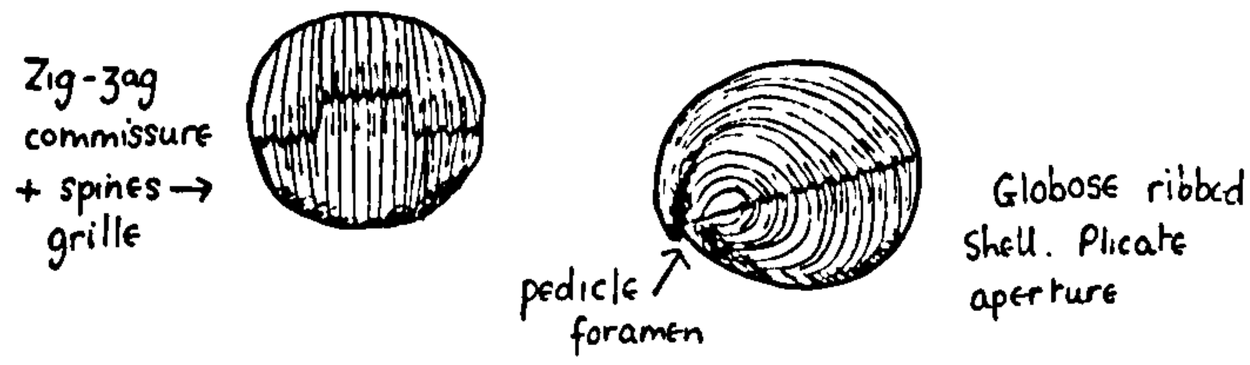
In the Builth region (Straw '37, '53), the "Wilsonia" Shales are a sequence of shales with thin slumped beds, followed by coarsely laminated shales. At Cwm Craig Ddu, Straw ('53 p 215) commented on the concentration of shelly fossils in the slumped beds, in contrast with the graptolitic fauna of the interbedded shales. This again suggests that S. wilsoni has been transported into the region and was not indigenous here. Similarly, Kirk ('49) commented upon the shelly fauna (S. ludloviensis, M. nucula and S. wilsoni) of slumps in the tumescens beds of the Striped Flags in the Brecon Anticlinal region, compared with the sparse, mainly pelagic fauna of the interbedded undisturbed units. Within normally bedded, graptolitic, sequences of laminated siltstones, shells are found in infrequent, lenticular and thin, horizons, and only rarely dispersed through beds. The shell assemblages are commonly monospecific (eg. Straw '37 p 433).

In the shelf areas, S. wilsoni is a common constituent of shelly faunas in the Bringewood Beds - for example at Perton (Squirrell and Tucker '60), and Ludlow (Holland, Lawson and Walmsley '63).

S. wilsoni is a long-ranging species. It is a common fossil in the Much Wenlock Limestone of shelf areas (eg. Hurst '75).

Ecology:

Sphaerirhynchia wilsoni



S. wilsoni is an uncinulinid rhynchonellid. The shell is usually globose, but flat forms are also found, the species displays growth

dimorphism (Westbroek et al. '75). Marginal spines are developed along the valve margins of the spherical form. There is a strong, dorsal median deflection of the commissure. The costae are mostly much flattened and longitudinally grooved. There is a very small pedicle opening. Recent rhynchonellids are spirolophous.

Rhynchonellid ecology:

The life orientation of the LLB rhynchonellids (S. wilsoni and M. nucula) is deduced by comparison with living species. There is an open foramen in both the LLB species, presumed to have housed a functional pedicle. The size of the pedicle opening appears not to be directly related to its strength in modern forms (Thayer '75(a)), so that the smaller foramen of S. wilsoni may not be significant.

The New Zealand genus Notosaria is widespread, gregarious, and typically occurs in clusters with the beaks crowded around a hard site of attachment (Bowen '68, reported in Bowen et al. '74). Specimens were found attached to the holdfast of Macrocystis, a marine alga. Groups of shells were common on beaches where detached algal strands had been washed by waves, and could clearly be dispersed widely in this manner.

Ager ('62) suggested that some Mesozoic rhynchonelloids found scattered in argillaceous sediments, associated with mainly pelagic fauna or forms adapted for soft substrates, may have been deposited from Sargassum-type seaweed to which they were attached. He noted that these individuals were thin-shelled and small compared with those associated with benthonic faunas.

Bowen et al. ('74) noted a widespread distribution in their U. Devonian marine communities for Leiorhynchus, which occurred in thin coquinites composed almost exclusively of its articulated shells, but also in dark shales interpreted to represent an abiotic environment. "Camarotoechia" was found to have a comparable distribution, although it was noted that the two species were rarely common together. The species were thought to have lived like Notosaria, with the occurrences in soft sediment explained by transport attached to uprooted plants before deposition.

Bowen et al. ('74) also commented upon specimens of Leiorhynchus which apparently lacked an open foramen, but had a posteriorly thickened shell to maintain their orientation. Clusters of shells orientated umbo-down were common. The living terebratellid Neothyris has a similar habit, and appears to survive rolling about by currents

without ill-effect.

Westbroek et al. ('75) interpreted the ecology of S. wilsoni to be pedically attached, resting on the brachial valve on the sediment. In this position, the lateral inhalent currents are higher above the surface than the median exhalent current (by analogy with Notosaria). The geniculation of a brephic shell to produce a globose individual was considered to correspond to the development of marginal spines, which form a grille to exclude silt from the shell. The spines project from the valve margins and lie inside the mantle cavity of the opposite valve; this is only possible in the geniculated shell form.

Ziegler et al. ('68) commented on the abundance of "Camarotoechia" in their most nearshore, Lingula community, and considered that the rhynchonellid genus might be unusually euryhaline. Ager ('65) had concluded that some Mesozoic rhynchonellids might be tolerant of reduced salinities, because of their presence beyond other species in transitions from marine to non-marine deposits.

Ager ('65) also related shell form to ecology. He considered strongly ribbed, thick shells with large pedicle openings to be adapted for shallow , rough environments. Both LLB rhynchonellids have such shell forms capable of withstanding agitated, turbid conditions. M. nucula, with its large pedicle opening, and coarser ribbing and plication, may be better adapted for the turbulent, sandy environments associated with a proximal shelf region.

Conclusions:

The LLB distribution shows S. wilsoni to be extremely common in the calcareous siltstone facies of the shelf, but rare in the areas of laminated siltstones apart from in slumps. Shells are very frequently articulated. Monospecific assemblages comprising shell limestones (coquinites) are found at numerous levels in the shelf inliers, and are considered to be current accumulations (see p 353). The extent of transport of these spherical shells cannot be estimated; they appear very resistant to disarticulation and breakage. The decline and disappearance of the species occurs earlier in the northern shelf areas (eg. at Ludlow - see Fig 5.17 p 282).

S. wilsoni is widespread in both shelf and basin areas lower in the Ludlow Series. Its distribution in basinal areas is mainly in slumped sequences and turbidites, or concentrated in thin, lenticular

horizons in laminated siltstones. These occurrences are considered to represent transported assemblages brought in from other areas. The sparse, graptolitic and pelagic faunas of interbedded shales indicate that these conditions were adverse to benthonic forms. The common presence of S. wilsoni in shelly shelf sequences is comparable to its LLB distribution.

S. wilsoni is adapted for pedicle attachment, resting on the brachial valve. It probably required a hard site for anchorage. Globose forms had marginal spines, interpreted to be a device for exclusion of silt from the shell (Westbroek et al. '75), like the zig-zag plications of the commissure (Rudwick '64). The dorsal median deflection of the commissure serves to separate inhalent and exhalent currents, as in Notosaria.

Bowen et al. ('74) considered that the occurrence of assemblages of rhynchonellids in unfossiliferous dark shales could be explained by epiplanktonic "rafting", attached to plants. Comparable assemblages in the Ludlow basinal sequences could result from such transport (eg. in the laminated shales of Builth), rather than from the species inhabiting these areas.

The shell morphology is well-adapted to withstand disarticulation and breakage (- the LLB coquinites illustrate this), with its globose, ribbed form and zig-zag commissure. Pedicle attachment and modifications for exclusion of particles from the shell are other features suited to withstand turbulent conditions. The lesser abundance of S. wilsoni in the shelf edge areas indicates a preference for less muddy environments. This may reflect the need for a hard substrate for attachment, or be due to an inability to prevent fine sediment particles entering the shell.

The decline and disappearance of S. wilsoni is relatively rapid. It is not accompained by marked lithological change.

9. M. nucula (J. de C. Sowerby) Fig 5.24 p 288

Leintwardine Beds Distribution:

This rhynchonellid has a very wide distribution centred on the shelf and shelf edge regions. It is found very infrequently in sequences of the laminated siltstone facies west of Aymestrey, except in slumped beds (eg. Ring Hole (RHl-): Kerry, Aberedw (Abdw), Lyepole Bridge (LyBr)).

It is not until the top of the Striped Flag lithology, that M. nucula becomes more common in basinal sequences; for example, in the shelly assemblages at several localities in the Brecon Anticlinal region (Map C). The abundance of M. nucula in these areas increases in the "C" gravi Flags (Map D). M. nucula is a prevalent species of the Whitcliffe faunas together with P. ludloviensis and S. lunata.

In the shelf facies, M. nucula rapidly becomes abundant in the basal LLB, along with the facies change to more thinly-bedded, calcareous siltstones (Maps A and B). It is a prevalent species in the basal limestone conglomerates in the SE inliers. The acme occurs in the main part of the LLB, where numerous bedding-plane assemblages are dominated by M. nucula. The shells are commonly articulated. At Ludlow (MF/F-), small clusters of specimens were found at levels in the siltstones. S. wilsoni is often abundant in the same sequences, but the two rhynchonellids are usually found in separate assemblages.

The species remains abundant in the ULB, when its areal distribution has increased westwards across the basinal region in the thick calcareous siltstone facies.

The distribution pattern in the LLB is closely similar to that of the other rhynchonellid, S. wilsoni. Both are largely confined to the shelf facies. However, S. wilsoni is found in greater abundance in sequences of Aymestry Limestone facies (see Map A). The decline of S. wilsoni near the LL-UL boundary is not reflected by M. nucula, which is abundant in assemblages through the ULB and Whitcliffe Beds.

Vertical Distribution:

M. nucula has a similar distribution to S. wilsoni in the lower part of the Ludlow Series, occurring widely in both shelf and basin areas. Shells are frequently articulated and unbroken.

The species is common in the shelly soles of turbidites, for example in the Bailey Hill Beds of Knighton (Holland '59), and in the fossiliferous horizons of slumped beds at Builth, such as the Cyrtoceras Mudstones (= MEB: Fig 5.5 p 170) Straw '37. It is rare in the interbedded graptolitic shales in the latter region. Similarly, higher in the succession at Builth (Straw '37), in the coarsely laminated shales of the Lower L. lata beds (in tumescens zone), M. nucula is concentrated in thin lenticular beds of shells (which are often

monospecific), that occur at levels in the poorly-fossiliferous sequence. The species is largely confined to assemblages which have clearly been transported into the basinal areas. The absence of benthonic fossils in intervening strata argues against M. nucula being locally derived. In shelf areas, M. nucula is present in the fauna, though not a prevalent species, with other benthonic forms. It is uncommon in the small shell fauna of the LEB throughout the shelf, however.

M. nucula is a dominant brachiopod species in the Whitcliffe Beds, together with P. ludloviensis and S. lunata. It is most abundant in the LWB at Ludlow; these beds correspond to the "Rhynchonella" Flags of Elles and Slater (1906). Like the other characteristic Whitcliffe brachiopods, M. nucula is only a minor element of the fauna of the Kerry, Knighton and Long Mountain regions until the UWB, when it is very common throughout the whole outcrop. It extends, although rarely, into the basal Downtonian beds in some areas, for instance at Kerry (Earp '38) and Perton (Squirrell and Tucker '60).

Ecology:

Microsphaeridiorhynchus nucula

(This genus is poorly known and probably represents a heterogeneous grouping).

The shell is variably globose to flat, with rounded, unequal costae. There is a well-defined ventral sulcus and dorsal fold, and undulating plicated commissure. The shell is only slightly inflated in the umbonal region, where there is an apical foramen.

For the discussion of rhynchonellid ecology see p 214 ff.

Conclusions:

The LLB distribution shows the highest abundance of M. nucula in the shelf areas, in the calcareous siltstone facies. Assemblages of shells are commonly articulated, and monospecific. Many are clearly transported accumulations, but small clusters of articulated shells in siltstones at Ludlow may represent an original distribution feature.

West of Aymestrey, M. nucula occurs only sporadically in the laminated siltstones, except in slumped beds, until the top of the LLB, when shell assemblages become more frequent. A marked increase in abundance accompanies the facies change to thickly-bedded siltstones in the basinal areas.

The distribution of M. nucula is closely similar to S. wilsoni in the lower part of the Ludlow, though it is less common. The two rhynchonellids are usually found in separate assemblages. After the disappearance of S. wilsoni in the top LLB, M. nucula becomes increasingly prevalent in faunas. It extends, in some areas, up into the basal Downtonian beds.

M. nucula is inferred to have lived gregariously, pedically attached to hard sites. Living rhynchonellids (Notosaria) have been also found attached in clusters to algal holdfasts, and transported with uprooted algal strands (Bowen '68, in Bowen et al. '74). This mechanism may be invoked to explain thin shell horizons of M. nucula in some basinal sequences, particularly in the lower part of the Ludlow (Bowen et al. '74, Ager '62). The absence of benthonic forms in the interbedded sediments make it unlikely that M. nucula lived in these areas. Other successions in the basin where M. nucula is common include slumps and turbidites, whose faunas have been transported in from shallower regions.

The widespread persistence of M. nucula to the top of the Ludlow Series indicates a high tolerance or preference for very shallow, silty environments. The pedically-attached shell is strongly-ribbed, with a plicated commissure which is interpreted as a device for exclusion of particles from the shell (Rudwick '64). These morphological features suggest a resistance to turbulent, turbid environments.

The LLB distribution of M. nucula suggests that it was indigenous to shelf areas. The diversity of the associated fauna shows that conditions were not approaching the limits of its tolerance to shallow, proximal shelf environments.

10. A. reticularis (Linnaeus) Figs. 5.25 p289 . 5.26 p 290

Leintwardine Beds Distribution:

A. reticularis has a widespread distribution over the shelf and shelf edge region in the LLB, but does not occur in the basinal sequences west of Aymestrey.

The greatest abundance is in the basal LLB (Map A). The species continues up from the UBB; A. reticularis is characteristically very common in the high UBB strata of the Aymestry Limestone facies. In the Ludlow anticline, the lithological transition to more thinly-bedded, calcareous siltstones is accompanied by a decrease in numbers of A. reticularis. A similar relationship between the facies and this species' abundance is seen in the other shelf sections (Fig 5.26 p290).

In the uppermost Aymestry Limestone strata at Ludlow, in the Bringewood Chase sections MF/E and MF/C, bands with some articulated specimens alternated with horizons of disarticulated and broken valves. The latter assemblages were mostly dominated by one type of valve:-

	PV	BV	PV/BV
MF/E- Ua	22	14	1.6
Wa	10	11	0.9
Xa	13	23	0.6
MF/C- t	17	3	5.7
u	12	19	0.6
v	11	16	0.7

This bias, and the large amounts of bioclastic debris in the shell bands, indicate that the disarticulated shells are current accumulations. However, the complete individuals are unlikely to have moved far. A few metres higher in the succession at MF/E-, in beds M-R, an increase in the proportion of nodular and limestone bands in the flaggy siltstones was accompanied by a minor acme of A. reticularis. Here, clusters of large articulated specimens, mostly BV down, were found at several levels. Single valves of some smaller individuals were interspersed among the shells. These assemblages may represent in situ populations (cf. Worsley and Broadhurst '75).

The Aymestry Limestone of the LLB at Perton and Woodbury has some bands with many articulated individuals (variably orientated), but others have mainly separate valves. In the basal LLB at Chances Pitch, which are dominantly flaggy calcareous siltstones, a few assemblages include complete specimens. Single valves are usually prevalent in assemblages here though. Further south, at S. Woolhope and May Hill, the basal limestone conglomerates include broken and disarticulated, thick valves of A. reticularis.

The concentration in calcareous facies is also indicated in the shelf edge sections by the common occurrence of A. reticularis in the calcareous flags of the basal LLB at Shelderton (eg. Lawnwell Dingle), Mocktree Quarries (MQ/6-, MQ/7-) and Bow Bridge (BB-), and its rapid decline in abundance in the higher, siltier beds. In all these sequences, A. reticularis is typically disarticulated, and many valves are broken. At Aymestrey, the bottom layers of the thinly flaggy LLB are crowded with worn, single valves, but the species is uncommon in the siltstones above.

In the main part of the LLB (Map B), A. reticularis persists in the shelly calcareous siltstone facies of the shelf sequences. The abundance is greatly diminished compared with its lower prevalence. It often occurs in bands of shelly and detrital limestone, and generally is disarticulated.

There is a widespread later acme of A. reticularis, commonly along with L. depressa, in the high LLB or basal ULB (Maps C and D). The horizon corresponds closely to the level where S. wilsoni declines rapidly in abundance and S. ornatella becomes more common. Frequently, large individuals of A. reticularis and L. depressa are found together, in nodular and calcareous siltstones. The westward extension of shelly facies in the high LLB is marked by the appearance of this faunal acme at Leintwardine (SR/2-), and at Ysgwydd Hwch (YH1-) in the Brecon Anticlinal region (Map C).

Vertical Distribution:

G.: U. Llandovery - Frasne (Boucot '75)

A. reticularis is a long-ranging species. It is common in both clastic and carbonate facies of shelf areas, but rare in the basinal successions in the Ludlow. The exception to this is in the Gypidula galeata beds (MEB) of Builth (Straw '37), where many A. reticularis were recorded, associated with a diverse shelly fauna of compound corals, bryozoa, and brachiopods, in limestone lenses of a mudstone sequence. Straw noted the current-sorted nature of some of these fossiliferous horizons; one (Straw '37 p 424) had the basal and top part composed dominantly of G. galeata while the middle was crowded with randomly-orientated bryozoans and Favosites.

The prevalence of A. reticularis (with S. euglypha) in units of the UBB Aymestry Limestone of the main outcrop was described by Newall ('66). The species is common throughout the shelf at this level, and

also in the LBB siltstones. Hurst ('75) found A. reticularis to be ubiquitous in his Much Wenlock Limestone carbonate communities, and Phipps and Reeve ('67) recorded that it was common too in the Woolhope Limestone.

A. reticularis declines and dies out in the ULB-LWB faunal changes at Ludlow (Holland, Lawson and Walmsley '63), and throughout the outcrop.

Ecology:

A. reticularis has an unequally biconvex (the brachial valve is more convex), costate shell, with a slight dorsal fold and ventral sulcus, and corresponding deflection of the anterior commissure. The ventral beak is incurved. Growth lines are prominent and commonly lamellose. Spiralia are directed dorso-medially. Spiriferids are inferred to be spirolophous (Rudwick '70) or deuterolophous (Williams and Wright '61).

The incurving of the pedicle beak during ontogeny results in the reduction or closure of the pedicle foramen in the adult shells. Several workers have commented upon the variability of the shell form in A. reticularis, which can be related to its environment.

Bowen ('66) described the development of notothyrial deposits in A. reticularis from agitated carbonate environments, while thinner shells with trails on the valve margins were found in individuals from argillaceous limestones that represented quieter conditions. Copper ('66, '67) interpreted atrypoid morphological adaptations to be designed for stabilising the shell. For example, frills and strong growth lamellae that are developed on atrypoids from fine clastic sediments are thought to have functioned to support and anchor the shell. The globosity of atrypoids is indicative of current strengths, with streamlined forms adapted for fast-flowing currents. Both workers favoured an orientation with the flatter, pedicle valve on the substrate for stability. However, Bowen et al. ('74) pointed out that shells with

trails would then have their commissures at, or below, the sediment surface, and therefore would be more likely to rest on the convex brachial valve.

Worsley and Broadhurst ('75) described a gregarious, clustered ecology for A. reticularis, in which steeply inclined individuals maintained stability by close juxtaposition with neighbouring shells, and by partial burial of the thickened, umbo region in the sediment. Juveniles were pedically supported, while the increased globosity and weight of the posterior part of the adult shell functioned as the main anchoring devices. The pedicle may have atrophied in mature forms.

Conclusions:

The LLB distribution of A. reticularis is confined to the shelf and shelf edge areas. The species diminishes in abundance above the Aymestry Limestone facies and limestone conglomerates of the SE inliers. In situ assemblages, containing many articulated specimens, are found in several areas in the Limestone facies. The majority of LLB occurrences are of broken, and disarticulated valves, however. In the top LLB to ULB of the areas of calcareous siltstone facies, there is a widespread, minor acme of A. reticularis and L. depressa; large valves are common, in calcareous nodular flags.

At Ludlow, clusters of articulated individuals (in calcareous siltstones) were mainly resting on the brachial valves. These populations seem analagous to those of Worsley and Broadhurst ('75). Complete shells in other assemblages were more dispersed, and variably orientated. Atrypoids display a wide range of morphological adaptations for different ecological strategies (Copper '66, '67). In the LLB, they are generally large and globose, with strongly-ribbed, lamellose shells; the pedicle foramen is inconspicuous. This form appears suited for maintaining position even if unattached in the adult stage. Many of the valves from the shelf edge sections are small compared with those in the SE inliers.

The higher abundance of A. reticularis in calcareous facies in the LLB, the smaller size of individuals in the shelf edge regions, and its absence from areas with laminated siltstone lithology suggest an intolerance of sedimentation. It may also reflect the need of juveniles for a hard site for pedicle attachment.

11. D. navicula (J. de C. Sowerby) Figs. 5.28 p291 , 5.27 p290

Leintwardine Beds Distribution:

D. navicula maintains its greatest concentration in the LLB in the shelf edge to Ludlow region, although occurring throughout the whole outcrop.

The basal LLB in the Shelderton area, which comprise irregular, very calcareous siltstones and shelly limestones packed with D. navicula virtually to the exclusion of other types, correspond to the "terebratulite" strata of Murchison (1854 - p 145). The concentration of these fossils is found to decrease slightly above the lower 5 m (approx; Lawnwell Dingle section Fig. 4.3 p110 LD/x to K, plus ? 1 to 2 m basal LLB not exposed), when other species become prevalent in some assemblages, but D. navicula remains abundant throughout the bottom 10 m (minimum) of succession. Populations of D. navicula from these beds were found to be very heterogeneous in the surveys carried out. (Ch. 6 p337ff.).

In the south of the Leintwardine region, and at Aymestrey, thinly flaggy, calcareous siltstones rest with sharp contact on the massive Aymestry Limestone. In the latter locality, the junction in the Main Quarry appears to be a clean-swept erosion surface, but there is no evidence of a similar unconformity at Mocktree Quarry or Bow Bridge. In all these sections, the basal LLB siltstones contain abundant D. navicula. Evidence of current action at this level at Aymestrey is provided by well-orientated, convex-up assemblages of shells, and the small ENE-WSW trending scour channels filled with disarticulated and broken shells. Fossils are mainly confined to discrete horizons in the sequence, commonly in lenticular deposits. This compares with the alternation of bedding-plane assemblages and beds containing more evenly distributed shells found at Shelderton.

A NW direction of sediment movement for the slumps at Lyepole Bridge Quarry indicates shelf to basin currents low in the LLB. The benthonic shelly fossils of the slump beds include numerous D. navicula valves, but the species is rare in the normally bedded units, and very scarce in areas of the laminated siltstone facies further west. The slump fauna is clearly derived from the shelf area.

Assemblages of D. navicula valves are common throughout the LLB in the shelf edge region. The species occurs even in the more poorly fossiliferous beds of the hLLB near Leintwardine (Whitaker '62), and in the "barren" channel-fill beds at Aymestrey (AY/A - above Ca). The

phosphatised conglomeratic horizons at the top of the LLB at Shelderton (SR/2-) have numerous D. navicula.

East of the Leintwardine area, the species nowhere achieves its maximum abundance until a more silty lithology has replaced the Aymestry Limestone facies (Map B). At Ludlow, D. navicula becomes abundant at a lower level in the west, where the facies are siltier. It is in the middle part of the succession at Ludlow and Wenlock Edge that D. navicula has its local acme. The fossil occurs in dense, often monospecific, accumulations throughout much of the LLB, in bands of the sheet laminated siltstone facies. Shells are more evenly distributed through other beds. D. navicula becomes relatively less prevalent higher in the sequence. At Ludlow, it extends, in the east, through into the ULB above the grayi-lauensis level, although it has disappeared in the west (MF/A-) about 5 m lower than this horizon.

The shelf inliers have a less consistent abundance of this fossil, but it is very common in parts of the succession of several areas. Typically, D. navicula is prevalent in bedding-plane assemblages in sequences where the dominant species alternate frequently, in the shelly calcareous siltstone facies.

In the high LLB (Map C), the abundance of D. navicula has declined in the shelf inliers. It has become increasingly common in the Llandovery area and SW part of the Brecon Anticlinal region, and is still very numerous at this level in the Ludlow and Leintwardine areas. D. navicula is one of the prevalent fossils in the shelly assemblages that enter the sequence in the uppermost strata of the Striped Flags of some sections (eg. Whimble (Wmb) Crickadarn Mill (CM)).

At the grayi-lauensis level (Map D), the species becomes common also in the areas of thickly-bedded calcareous siltstones of the Builth region. Its distribution over the basinal region has increased with the facies and faunal changes taking place in this part of the succession. In the areas of thinly flaggy beds to the north it is still limited in numbers. In areas of the shelf, there is a decrease in abundance of D. navicula in the ULB.

Vertical Distribution

Sp.: Elton-Gedinne (Tucker '68)

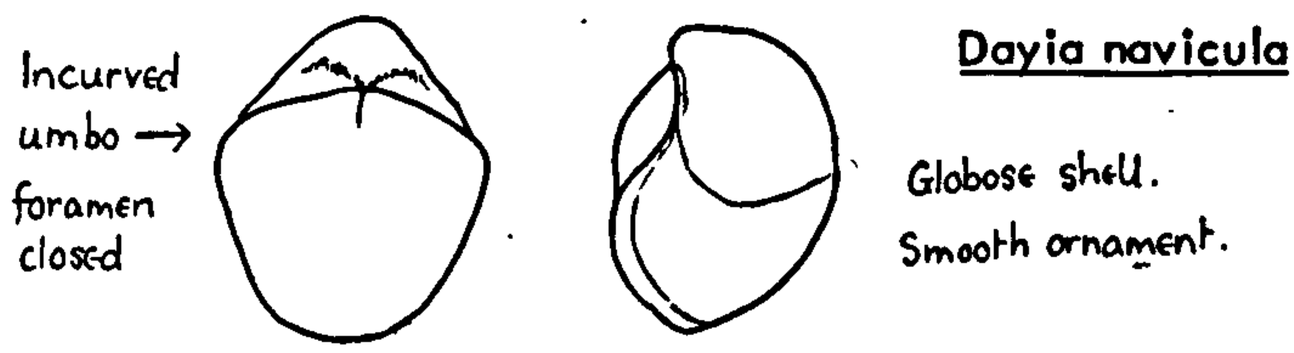
D. navicula is a long-ranging species, which is a prevalent fossil in sequences at several stratigraphic levels in the Ludlow Series.

The species is a minor constituent of shelf faunas below the LLB, when there is a marked increase in abundance. It is in the thick clastic successions of the basinal areas that D. navicula is most common below the leintwardinensis zone.

D. navicula is very common in the turbiditic siltstones of the Bailey Hill Beds of Knighton (Holland '59) and Wilsonia Grits of Kerry (Earp '38) in the nilssoni-scanicus and tumescens zone beds. Shells are concentrated in the shelly soles of the turbidite units. In the Builth region, the species is prevalent with S. ludloviensis in the Cyrtoceras Mudstones (nilssoni-scanicus beds), in fossiliferous horizons of slumped beds, but is rare in the interbedded, graptolitic shales (Straw '37). These basinal occurrences indicate that D. navicula is not indigenous to these areas, but has been transported in by turbidites and slumps.

D. navicula rarely extends above the Leintwardine Beds in the shelf inliers, following the decline in abundance seen in the upper part of the LLB and ULB. The species extends progressively higher in the succession in areas further W and NW. At Ludlow, it remains fairly common into the basal LWB before dying out (Holland, Lawson and Walmsley '63 - p 120) whereas at Builth (Straw '37) it is numerous in assemblages up to the top of the LWB. D. navicula is uncommon in the areas of thinly flaggy laminated siltstones to the north at this level. At Kerry, where Earp ('38) selected the species as the index fossil for the beds above the "M". leintwardinensis Shales, D. navicula does not become common until the upper part of the Dayia Beds (LWB), when more massive, irregularly-bedded siltstones have replaced the thinly flaggy lithology. The spread of shelly faunas into the basinal areas correlates closely with the facies change. D. navicula dies out in these areas to leave the characteristic UWB fossils.

Ecology:



D. navicula is a small, smooth atrypidine brachiopod, with an unequally biconvex shell. The pedicle valve is more strongly convex,

with an incurved beak, and has secondary thickening in the posterior part. The shell has a ventral fold and dorsal sulcus, most marked in the anterior region. The spiralia, connected by a long jugum, are directed laterally.

The incurvature of the umbo during ontogeny reflects the loss of a functional pedicle. The shell is adapted for resting freely on the substrate on the pedicle valve, stabilised by the weighting of its posterior region (Tucker '64).

Tucker ('64) described thin limestones, from the lower part of the LLB in the Leintwardine area, which contained closely-packed shells of D. navicula almost monospecifically. The lower part of one bed had mainly articulated shells, while disarticulated, pedicle valves dominated the upper layers. All growth stages were represented in the assemblages. The limestone population was considered to represent an in situ colony, composed of a lower, life assemblage and a winnowed deposit above. Tucker concluded that quiet, sediment-free waters were required by D. navicula.

The sequences considered by Tucker were examined in this study, and population surveys were carried out. The limestone beds are concluded to be coquinites, whose calcareous matrix is secondarily derived from the closely-packed shells. Some assemblages contain many articulated individuals, others are composed of pedicle valves. The former have probably not been transported far. The abundance of D. navicula in beds between the plane assemblages and shell lenses supports a local origin for the current accumulations here. The facies preference of D. navicula observed in this survey, in contrast to Tucker's conclusions, is for silty lithologies.

Conclusions:

The LLB distribution shows the greatest abundance of D. navicula in the Ludlow and Leintwardine sequences, although it is also very common in the shelf inliers. Population surveys suggest that the species is indigenous to the former regions. It becomes much more numerous above the Aymestry Limestone facies (see Fig 5.27 p290) in the calcareous siltstone facies. The species is abundant with benthonic faunas in the shelf, and is restricted to the slumped beds at Lyepole Bridge Quarry. This distribution, and the scarcity of the species in the laminated siltstones further west, indicate that D. navicula shells in the latter areas have been transported in, and the local environment was adverse for colonisation by benthos.

Below the LLB, D. navicula is present though not common, in shelf sequences (eg. at Ludlow - Holland, Lawson and Walmsley '63 p 153). It is widespread and locally common in basinal areas, but in assemblages found in slumps and turbidites. that may represent extensive transport. Therefore, the locus of the D. navicula distribution is not readily identifiable at this level. The confinement of D. navicula to horizons among sparsely fossiliferous beds that have a mainly pelagic fauna indicates that the species did not inhabit these basinal areas.

D. navicula was adapted for resting freely on the convex pedicle valve, stabilised by the posterior thickening of the shell. The distribution of the species indicates that it was tolerant to the silty environment of the distal shelf region, and hence probably to sedimentation. The "banks" at Shelderton in the basal LLB suggest that it lived gregariously; individuals could maintain their position against neighbouring shells. (Such a strategy was described for Atrypa by Worsley and Broadhurst '75). The small, smooth shell and unattached habit, indicate that D. navicula would not be resistant to strong turbulence.

The vertical distribution of the species shows its progressive westward extension, with other shelly fossils, into the basinal areas. Maps C and D show this spread, with the corresponding decline in abundance of D. navicula in the shelf inliers. The continuing rare presence of the species in the thinly flaggy siltstones of the northern areas (eg. Kerry) indicate that conditions here were still unfavourable for colonisation by benthos. The species dies out later in the western sequences, when the UWB fauna becomes cosmopolitan.

12. H. elegans (Muir-Wood) Fig 5.29 p 292

Leintwardine Beds distribution:

The distribution of the species is confined to the shelf and shelf edge areas. It is very common in the basal part of the LLB throughout this region (Map A), but declines in importance in the higher beds.

H. elegans is common in the conglomeratic limestones of the LLB in the SE inliers. In the sequences of Aymestry Limestone facies, the species generally becomes more common with the lithological change to more thinly bedded calcareous siltstones. It is found in monospecific assemblages comprising thin shell limestones. Many of the specimens are still articulated. At Perton, the main occurrence of H. elegans is in

the Limestone facies, however. Here, it is an important constituent of the fauna of the shelly conglomeratic bands, but is not common in the interbedded siltstones.

In the main part of the LLB (Map B), the distribution is centred further east, in the shelf inliers. H. elegans is fairly common through the succession at Chances Pitch, usually in thin shell limestones. In the other sections, there are some minor acmes, but it is not consistently present.

Maps C and D show a later expansion in abundance in several shelf inliers at the top of the LLB and in the ULB. Its areal coverage has extended slightly further west in the ULB, but it is still only common in the shelf inliers, and in the shelly calcareous siltstone facies.

Vertical Distribution:

H. elegans is a long-ranging species. Its abundance appears to vary considerably, locally, in the shelf areas, although it is consistently present throughout the Ludlow Series. In the basinal sequences, it is restricted to the Eltonian and Bringewoodian, except for rare occurrences in the UWB of Builth (Straw '37).

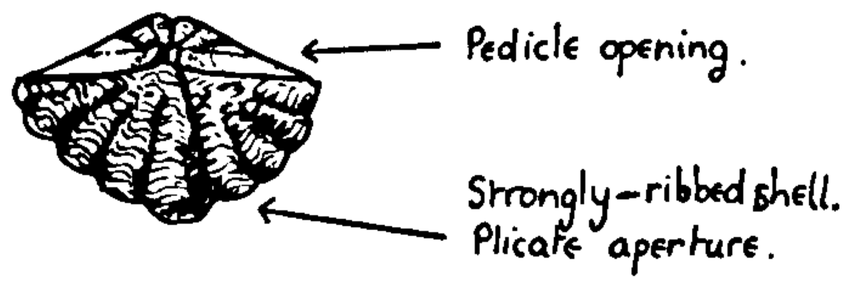
In the Malverns, H. elegans was listed as 'fairly common' or 'common' through the entire Ludlow series (Phipps and Reeve '67), and as 'abundant' in the Wenlock Limestone. At Perton though, its main concentration was found in the LLB (Squirrell and Tucker '60), and it was only a minor constituent of the fauna at some other levels, (including the Wenlock Limestone). Similarly, the very common occurrence of H. elegans in the Bringewood Beds of Wenlock Edge (Shergold '66) corresponds with its presence in small numbers at Ludlow (Holland, Lawson and Walmsley '63) and absence from Leintwardine (Whitaker '62), in similar facies sequences. Thus, the species abundance shows considerable local variation across the shelf areas. It persists into the UWB in many areas, and at Ludlow, it was noted from shell bands of the topmost beds (Holland, Lawson and Walmsley '63 - p 146).

In the basinal sequences, it is present in the shelly soles of the tumescens zone, turbiditic,siltstones (Holland and Lawson '63) at Knighton (Holland '59) and Kerry (Earp '38). The highest abundance at Builth (Straw '37) is in the "Atrypina" Beds (also tumescens zone), where shelly lenses occur among the sparsely fossiliferous, fine shales. At Cwm Craig Ddu (Straw '53), H. elegans is confined to slumped beds

within a sequence of shales which have a restricted, graptolitic fauna, at the nilssoni-scanicus level. The distribution of the shelly fauna in these basinal successions suggests that the assemblages have been transported into the area, and were not indigenous to it. The shales between the fossiliferous units have limited, mainly pelagic, faunas.

Ecology:

Howellella elegans



H. elegans is a small, biconvex delthyridid, with a strong smooth fold and sulcus, and lateral plications. The hinge line is slightly less than the maximum width of the transverse shell. The more convex pedicle valve has an apical foramen. Spiralia are directed laterally or posterolaterally (Boucot et al. '65).

This species is assumed, because of the open pedicle foramen, to have been pedically-attached. The plicate commissure may be a device for exclusion of sediment particles from the shell - comparable to the zig-zag deflections of rhynchonellids (Rudwick '64). Costae on the shell will, additionally, serve to strengthen it. There is a pronounced median fold and sulcus, interpreted to be for separation of the inhalent and exhalent currents (Rudwick '70). The alate shape of the shell could, however, indicate that it rested on the substrate, because the transverse extensions will produce a "snow-shoe" effect to prevent the shell sinking into the sediment. Similar adaptations are seen in many spinferoids (Rudwick '70).

Conclusions:

The LLB distribution shows H. elegans to be restricted to the shelf and shelf edge areas. The highest and most widespread abundance is at the base of the LLB (Map A). The common occurrence of articulated shells in monospecific assemblages may indicate their local derivation, but may also reflect a resistance to disarticulation of the plicated shell. In the main part of the LLB, H. elegans is consistently common only at Chances Pitch.

The species distribution in the rest of the Ludlow Series is similar, with the main concentration occurring in the shelf sequences. Basinal assemblages with H. elegans are considered to have been transported in from other areas; shell horizons are concentrated in slumped beds and turbidites. Large local variations in abundance are found across the shelf region. There seems to be no clear relationship between facies type and abundance in clastic and carbonate Ludlow shelf environments.

The open apical foramen suggests a pedically-attached mode of life. The strong ribbing and the plicated commissure indicate a resistance to agitated environments, and are comparable to the adaptations seen in the LLB rhynchonellids. Although the alate shell shape might also be interpreted as adapted for supporting the shell on a soft substratum, the distribution maps show that H. elegans is infrequent in the fine, laminated siltstone facies. Possibly, the pedicle merely anchored the shell, which rested on the substrate. The widespread persistence of the species into the UWB, when it extends westwards in areal distribution to Builth (Straw '37) suggests a tolerance of conditions in more proximal shelf environments.

13. H. canalis (J. de C. Sowerby) Fig 5.30 p293

Leintwardine Beds Distribution

H. canalis is restricted in distribution to the shelf region. It is most common in the calcareous shelly siltstone facies of the SE shelf inliers.

At the base of the LLB (Map A), H. canalis was reported to have an acme in the Aymestry Limestone facies of Wenlock Edge (Shergold and Shirley '68). At Ludlow and Woodbury, the species is only numerous at this level, while S. Woolhope (Squirrell '56) and Chances Pitch also have acmes in the lower part of the LLB. H. canalis was commonly recorded in this study, from calcareous siltstones. At Ludlow (MF/A-) and Chances Pitch, several assemblages of articulated specimens were found, including clusters with umbo-down shell orientations which may be in situ populations (as in Ziegler et al. ('66) for pentamerids).

In the rest of the LLB (Maps B and C), H. canalis is common only in the shelf inliers, especially Woolhope, and the Llandovery-Llandeilo region (Potter and Price '65). However, the ULB (Map D) shows a much

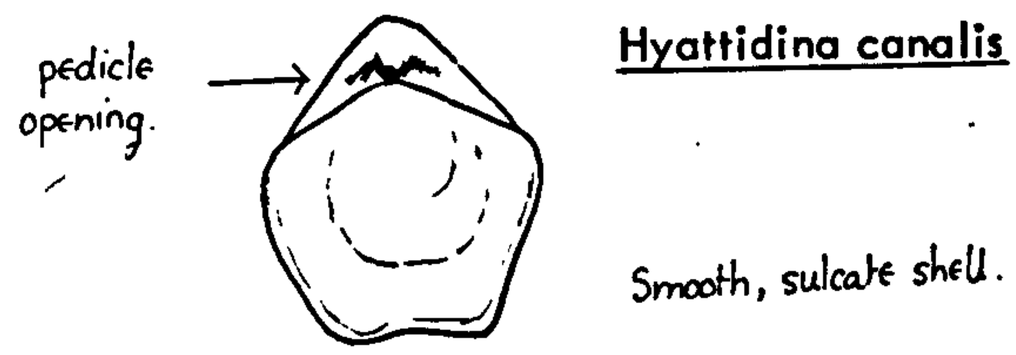
increased abundance in these same areas, corresponding closely to the acme of S. ornatella at this level.

Vertical Distribution:

G.: Ashgill-Ludlow (Boucot '75)

H. canalis is reported to be present in the Bringewood Beds of a few shelf areas (for example, at Woolhope (Squirrell and Tucker '60) and the Malverns (Phipps and Reeve '67)), but is not common anywhere until the Leintwardine Beds. It declines and disappears in the ULB-LWB faunal changes.

Ecology:



H. canalis is a small, smooth athyridacean, with an unequally biconvex shell. The larger, more convex pedicle valve is truncated by a circular foramen. There is a ventral sulcus and dorsal fold. Spiralia are laterally directed.

The presence of an apical foramen suggests that there was a functional pedicle to support and anchor the shell. In living articulates, the median deflection of the commissure produced by the fold and sulcus marks the position of the exhalent aperture. The thin, smooth shell is fairly globose; it shows no strengthening adaptations to withstand turbulent conditions.

Conclusions:

The distribution of H. canalis shows that it is restricted to the shelf areas. In the Leintwardine Beds, it is most common in the basal LLB and in the ULB.

The shell structure is consistent with a pedically attached and supported habit. LLB assemblages which are possibly in situ suggest that the shells were positioned umbo-down in a clustered group, when some stability could be derived from neighbouring individuals.

Brachipods: Distribution Controls

Articulate and most inarticulate brachiopods are sessile, epifaunal, ciliary suspension feeders. The exception to this are the lingulids, which have adopted an infaunal mode of life (see p 180 ff.). Only these can change their attachment sites and re-establish themselves if uprooted. The distribution of other brachiopods will therefore depend upon the success of the larvae in settling, and on the maintenance of position by the adult.

Dispersal of brachiopods is achieved by a free-living, pelagic larval phase, during which a suitable site for colonisation must be selected. In most Recent articulates this stage is very short, in some cases only a few hours (Rudwick '65). The patchy distribution of some species was related by Rudwick ('62(a)) to the limited power of dispersion. Shell clusters were each composed of similarly-sized individuals, and probably represented single spatfalls in the vicinity of the parent population. In contrast, some inarticulate brachiopods, for example Lingula and Discinisca (but not Crania), have a much extended larval period lasting up to several weeks. These larvae are adapted for actively swimming and feeding, and are frequently found among mid-oceanic plankton (Rudwick '65). The possible extent of dispersion is evidently much greater.

All living brachiopods are permanently attached to the substrate, generally by a pedicle, or more rarely, cemented (Rudwick '65). In some fossil forms, though, the closure of the pedicle foramen, or its constriction, during ontogeny indicates that the adult form rested unattached. Recent Neothyris has an anchoring pedicle, but internal thickening of the posterior part of the shell ensures its stability even if the pedicle becomes detached (Rudwick '65). Similar shell thickening is found widely among fossil brachiopods (eg. Pentamerus - Ziegler et al. '66; D. navicula - Tucker '64). A different strategy for unattached forms is shown by the large surface area to volume of many strophomenid shells (eg. leptostrophids), and alae of spiriferids, both of which will have a "snow-shoe" effect on the substrate. Unattached shells are unlikely to be distributed in turbulent areas, unless large and heavy like Kirkidium (Newall '66), because of their susceptibility to current scour and inversion.

The ciliary feeding mechanisms of all living brachiopods are very uniform. Lophophores serve both to initiate water flow through the mantle cavity and to filter food from the inhaled currents. It is in the form of the lophophore and circulatory current systems that there is diversity. The lophophore is supported by a hydrostatic skeleton, often supplemented by a calcareous brachidium. The latter is commonly preserved in fossils. However, Rudwick ('70) pointed out that the forms of the lophophore and the brachidial apparatus need not correspond directly, so that reconstruction of the feeding structures of extinct forms is hypothetical.

It is a feature of most suspension-feeders that feeding is a non-regulatory process. Generally, the rate of water-flow inside the mantle-cavity appears to be independent of the particle concentration, and to be controlled by the structure and size of the lophophore (Jørgensen '66). Rudwick ('70) noted some evidence in brachiopods that the rate of filtration of nutrients may be geared to their concentration in the water, but experimental studies in aquaria have produced inconsistent results. (eg. Atkins ('59) found Platidia spp. shells gaping open with no current system operating, and McCammon ('71) reported erratic rates of flow in Terebratulina septentrionalis). The size and complexity of the lophophore are directly related to the dimensions of the individual. Because metabolic requirements increase volumetrically but filtering capacity is a function of the filament area, the lophophore must become relatively more complex during ontogeny (Rudwick '70). The adult size of the species will largely control the final degree of complexity.

Fursich and Hurst ('74) discussed the lophophores of articulate brachiopods. They argued that the shell-shape is indicative of the lophophore type, taking Grant's ('72) assumption that the lophophore will tend to fill the available space, which is usually the greater part of the shell chamber. Secondly, information can be derived from the supporting structures (although Rudwick's ('70) caution about the brachidial skeleton was noted). It was concluded that the orthids, strophomenids and rhynchonellids had less complex lophophores than the spire-bearing spiriferids. From a comparison of the mantle cavity size of the concavo-convex to weakly biconvex shells of strophomenids and

orthids with the more bulbous, rhynchonellid shells, it was inferred that the latter probably had larger lophophores.

The current systems and feeding attitude vary with the lophophore type (Rudwick '62(~~b~~), '65). In the simpler, trocholophous and schizolophous conditions in the development of living brachiopods, there are median inhalent and lateral exhalent currents. The shell gapes widely with the filaments projecting forward between the valves (Fig 5.31-a, p236). In the spirolophous stage, Rudwick described the reversal of the circulation to lateral inhalent and median exhalent currents (Fig 5.31-b). Spiriferids were considered by Rudwick ('65) to have spirolophes coiled parallel to the spires, and hence in various directions (for example, dorsally directed in Atrypa, but laterally in Davia and Howellella), with water flowing either into or out of the spires. However, Williams and Wright ('61) proposed a double loop on the brachial axis - a deuterolophe - which would involve a more complicated circulation system. The gape of the shell decreases relatively during the ontogenetic stages and is not wide in mature individuals (Rudwick '62). Many species also develop a median deflection of the commissure, which invariably marks the position of the exhalent aperture, but may direct the current either towards or away from the substrate (Rudwick '65). The fold and sulcus tend to separate the inhalent and exhalent currents, which may be advantageous in quiet-water conditions, to prevent recirculation of filtered water and waste products.

Studies on living brachiopods provide conflicting views on the nutrient source for articulate brachiopods. Rudwick ('62) observed that diatoms and dinoflagellates, after selection by particle size, are mechanically accepted by the lophophore, and transferred in the food groove to the mouth. McCammon ('69, '72) proposed, alternatively, that dissolved and colloidal organic matter constitutes the principal food. More recently, Cowen ('71), and Suchanek and Levinton ('74) have pointed out that these mechanisms are not mutually exclusive. The latter study investigated the gut contents of brachiopods and bivalves found together at various depths. It showed that the two groups had similar ratios of organic to inorganic particles in the guts, but that the actual ratios varied at different depths. They concluded that the brachiopods and bivalves fed in the same way, and their food source changed according

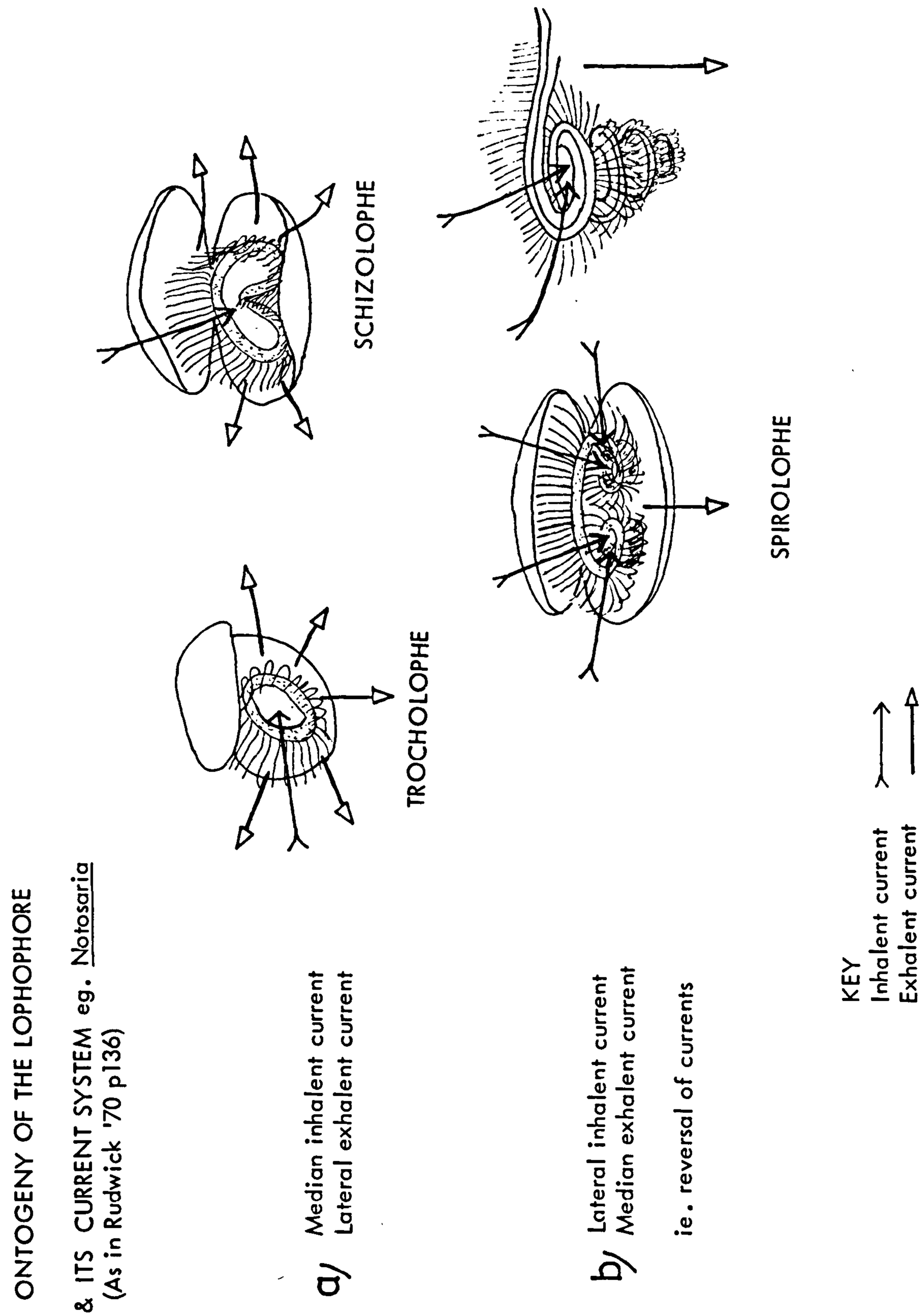


Fig. 5.31 : Ontogeny of the lophophore, and its current system.

to its abundance and to depth. In the present oceans, there is a higher concentration of particulate organic matter in coastal and inshore waters than in the open ocean, where there is little suspended material. McCammon's ('69) specimens were dredged from shelf and abyssal depths, but Rudwick ('62) worked on sub-tidal individuals.

For the lophophore to function efficiently, silt must be kept out of the mantle chamber. There is a ciliary rejection mechanism which separates to remove excess particles from the shell before it closes. Then, as the shell snaps shut, the outflow of water expels unwanted sediment (Rudwick '62). Living brachiopods regularly snap the shell shut and immediately re-open, with little interruption to feeding. Pedically-attached forms swivel the shell to dislodge sediment (Rudwick '62, Thayer '75(a)). Rudwick ('62(a)) commented on the intolerance of Recent articulates to sedimentation, particularly the smaller individuals whose apertures are closer to the substrate. Geniculation of the shell, as in Leptaena, and increasing convexity of the lower valve in ontogeny, like Dayia (Tucker '68), serve to raise the commissure off the sediment surface. Bowen et al. ('74) suggested that the flat stropheodontids may be able to swim for short distances, in a pectinid manner, to rid the shell of sediment; the proximity of the commissure and substrate suggests that these shells would be very susceptible to burial.

Setae are chitinous bristles which extend out from the mantle edges. They act as tactile sense organs. If particulate matter touches either the setae or mantle edge the shell snaps shut (Rudwick '62, '70). In living brachiopods, the setae commonly correspond in position and spacing with radial costellae, although there is no consistent relationship. The setal density remains constant during ontogeny by intercalation or branching. Similar patterns of radial costellae on the shells of strophomenids and orthids were considered likely, by Rudwick ('70), to relate to the setal positioning. The setae of living brachiopods may be close-spaced and short, forming a sensitive 'fringe', or be longer and fewer, when they create a 'grille' across the gape, as in Notosaria (Rudwick '70). Plication of the aperture, which is a feature seen in many different groups, and the development of apertural spines in some rhynchonellids (eg. S. wilsoni: Westbroek et al. '75), are interpreted as further protective devices to prevent the entry of unwanted material into the shell (Rudwick '64). They have the advantage

of permitting feeding to continue in spite of suspended sediment in the water, and therefore are regarded as adaptations for agitated environments. Of the LLB forms, S. wilsoni, M. nucula and H. elegans have plicated apertures. The setae of lingulids are thick and close-spaced. They are considered to be specially adapted for burrowing (Thayer and Steele-Petrovic '75).

Rudwick ('62(a)) found living brachiopods were more tolerant of turbid conditions than of active sedimentation. However, the distribution of species was largely determined by the available sites for anchorage. A few living forms can anchor directly into soft substrates (Rudwick '61), but most require a hard site for pedicle attachment (Neall '70, Foster '74). McCammon ('73) found Magellania venosa to be extremely tolerant of temperature and depth variations, and insensitive to light, but its distribution was limited mainly by substrate and current velocity. Secondary factors, such as 'baffling' by plants which increased the turbidity and prevented colonisation of otherwise suitable environments, modified the distribution. Neall's ('70) study of Neothyris also indicated the effects of local conditions. The wider areal distributions of Recent brachiopods are not well-known. Foster ('74) described a greater diversity and abundance than has previously been attributed to the Antartic Region, where the number of species remained high down to 1000 m depth, then decreased below. In the Ross Sea, the highest diversity was on the seaward side of the edge of the continental shelf (average depth 550 m). Pedically-attached forms, even at depths over 2000 m, were on hard sites on substrates. Brunton ('75) noted that Zezina's ('70) review of brachiopod distributions showed that more than 50% of Recent species (of 279 recognised) are known in temperate waters, from the edges of the continental shelf regions down to 500 m.

Homeomorphy displayed in species living in the same area suggests environmental control. A striking example is the deep-sea assemblage from the Baja Plain (Cooper '72), where an impunctate rhynchonellid (Neorhynchia), a punctate long-looped dallinid (Notorygmia), and punctate short-looped terebratulid (Abyssothyris) are all externally alike. They are thin-shelled, smooth, sulcate and globose. Hurst and Fursich ('74) commented that, in contrast, Rudwick's ('62) intertidal rhynchonellids and terebratulids are mostly ribbed and have large pedicle openings. On the basis of morphological adaptations seen in Silurian brachiopods,

LLB ARTICULATE BRACHIOPODS : RELATION OF SHELL FORM, LIFE HABIT & FEEDING STRUCTURE

Adaptations:

1 For TURBULENT conditions - Pedically-attached shells with strong ornament, plicated apertures, & narrow feeding gape.
eg. S. wilsoni, M. nucula, H. elegans

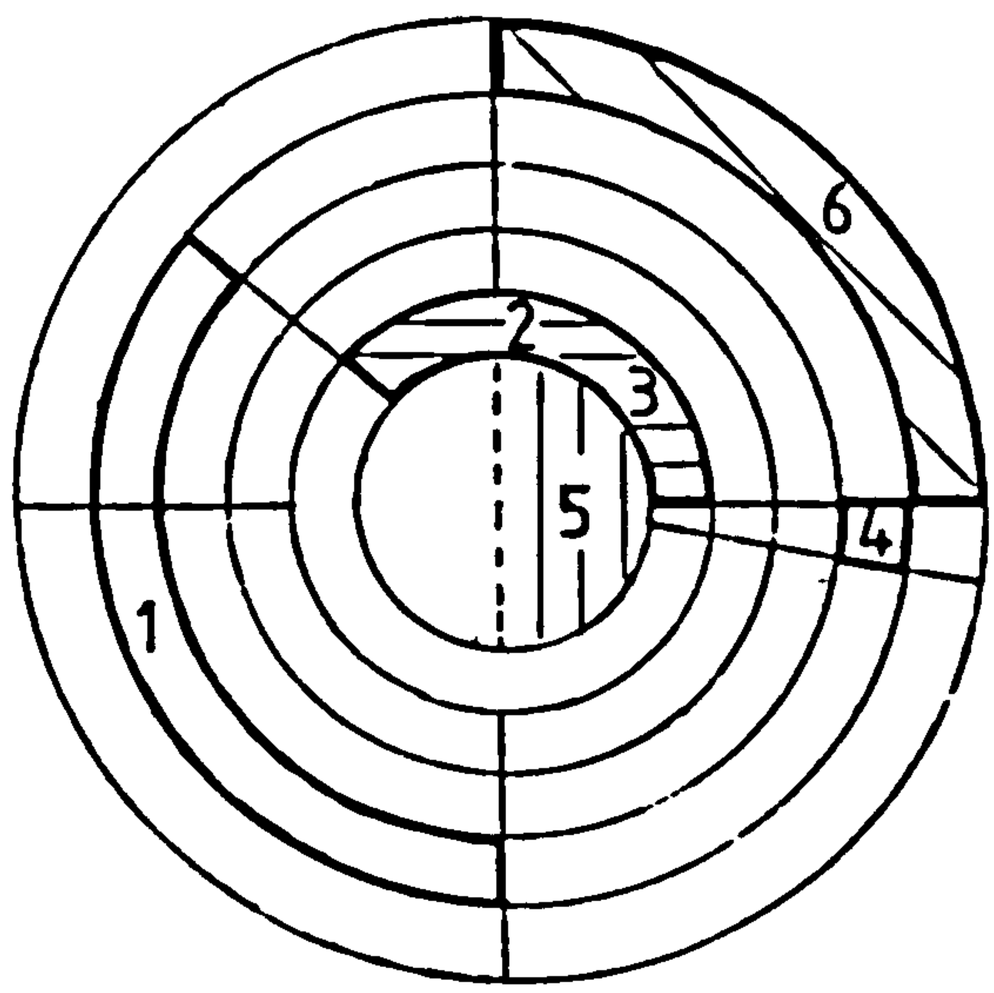
2 For SOFT SUBSTRATE - free, with large surface area cf. volume
eg. strophomenids, A. reticularis

3 For QUIET conditions - free, & small size.
eg. S.ludloviensis, D. navicula

4 For CALCAREOUS SUBSTRATES - large sized shells with strong ornament
eg. L. depressa, A. reticularis, S. wilsoni

5 Indication of INTOLERANCE TO TURBIDITY - Wide feeding gape
eg. strophomenids & orthids

6 Indication of INTOLERANCE TO SEDIMENTATION - Free on the substrate, with aperture close to the sediment surface
eg. flattened strophomenid shells - S. ornatella, L. filosa



Key to Fig. 5.32

LLB Articulate Brachiopods: Relation of Shell form, Life habit & Feeding structure

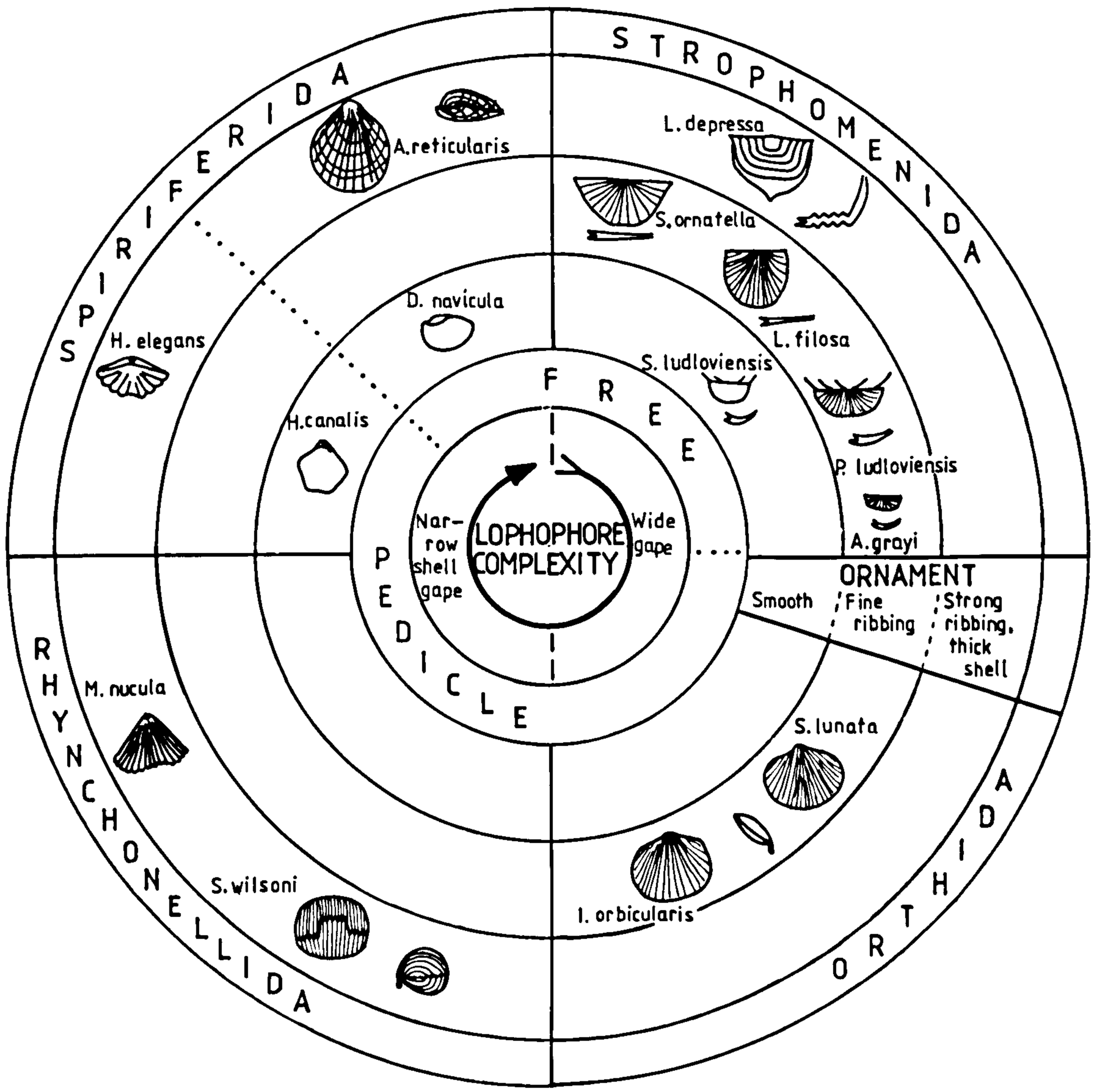


Fig. 5.32

Hurst and Fursich ('74) distinguished three groups, suited to turbulent, quiet-water, and soft-bottom conditions. A comparable diagram has been devised for the LLB articulate brachiopods, in which structural features are related to environmental tolerances: Fig 5.32

LLB Brachiopods: Morphology, habit and feeding structures: Fig 5.32

The distribution of sessile, epifaunal articulate brachiopods will depend upon their ability to maintain position in a suitable environment for feeding, and to reproduce successfully. The limited power of dispersal, and greater susceptibility of juveniles to adverse conditions will be a controlling factor in further colonisation.

a. Lophophore complexity:

The filtering capacity of the lophophore is directly related to its size. If food is a limiting factor, the efficiency of the structure will be important. The increasing complexity of the lophophore (Hurst and Fursich '74) is shown on the diagram together with the change in feeding attitude from a wide gape in simpler forms to a narrow separation of the valves in the groups with larger lophophores (Rudwick '62). This may correlate with an intolerance to silt-laden water in orthids and strophomenids. They are inferred to have had closely-spaced setae for silt-detection (Rudwick '62); but frequent interruption to feeding may prevent adequate assimilation in turbid environments. Among the forms which have smaller gapes, M. nucula, S. wilsoni and H. elegans show adaptations to prevent sediment entering the shell during feeding (for example, the plicated apertures, and marginal spines).

b. Attachment:

Pedically-attached forms generally require a hard site on the substrate. The pedicle may serve only to anchor the shell, but may also support it. Species with a large foramen (eg. M. nucula, H. elegans) are usually inferred to have had a strong pedicle (although Thayer ('75(a)) has pointed out that there is no direct relationship between size and strength). Unattached forms - strophomenids, and some spiriferids - show a variety of ecological strategies. For instance, strophomenids characteristically have wide, flat shells for resting on soft substrates by a "snowshoe" effect, while D. navicula has a thickened umbo on the pedicle valve for stabilisation. Flat strophomenids might be expected to be particularly intolerant to sedimentation because the commissure is so close to the substrate.

c. Ornamentation:

Ornamentation ranges from smooth thin shells (eg. D. navicula, S. ludloviensis) to thick, strongly-ribbed forms (eg. S. wilsoni, A. reticularis). There is a corresponding increase in size from the former to the latter.

The outer circle of species on the diagram includes the shells with strong ornamentation. The globose, ribbed, pedically attached forms - M. nucula, S. wilsoni and H. elegans - all have plicated, sulcate apertures. They are well-adapted for living and feeding in turbulent environments. The large, thick, inflated shell of A. reticularis is either unattached or weakly tethered in the adult form, but has internal thickening in the umbonal region for stabilisation. The form suggests a resistance to current scour, and also to sinking into the sediment. L. depressa has a large, ribbed, concavo-convex shell, with pronounced geniculation, and high ratio of surface area to volume. Big, thick shells are indicative of calcareous environments where there is free calcium carbonate for secretion (eg. Kirkidium in Aymestry Limestone). The larger thicker shells of the LLB A. reticularis in calcareous than in silty strata is consistent with such environmental control.

In the middle circle, the ornamentation is fine ribbing. This group contains the orthids and majority of strophomenid species. The former are pedically attached, while the latter rested free on the substrate (- A. gravi may have been epiplanktonic, however). The shell shape varies from weakly biconvex to concavo-convex. All these species are inferred to have gaped widely during feeding.

The inner ring includes the smooth, thin-shelled forms, which are small species. D. navicula and H. canalis are both sulcate spiriferids, the former resting freely on the sediment, but the latter being pedically-anchored. S. ludloviensis is a small chonetid, whose hinge spines may act as stabilisers or for attachment to algal vegetation. These forms are considered to be adapted for quiet environments.

C. TRILOBITES:

1. Calymenids: C. puellaris and C. lawsoni Fig. 5.33 p294

Leintwardine Beds Distribution:

a. C. puellaris (Reed):

C. puellaris is one of the faunal indices for the ULB. At the stratotype on the Whitcliffe, Holland, Lawson and Walmsley ('63) reported it to appear first in the thin fossiliferous seam taken to mark the base

of the ULB division. They recorded the species to be fairly common only in these beds. In this study, at Sunnyhill Quarry (SY/B-), also in the eastern part of the Ludlow anticline, C. puellaris becomes common rapidly at the level (SY/B-M) taken to mark the LLB-ULB boundary. However, further west in this area, in section MF/A-, C. puellaris (including one complete specimen) is present in the highest LLB, although it is not common at this level.

In the SE inliers, the species first appears lower in the succession. At May Hill, fairly large skeletal elements occur commonly in the upper 3 m of the U. Blaisdon Beds, usually in very fossiliferous limestone bands. Of nine cranidia measured, 6 from May Hill and 3 from Ludlow, those from May Hill were bigger (in length and width). Lawson ('55) recorded C. puellaris to be fairly common also in the Lower Longhope Beds, which are approximately equivalent to the ULB.

Slightly further north, Squirrell ('56) found that C. puellaris was common in the top strata of the L. Yatton Beds (LLB), along with proetids; trilobites became relatively numerous at this level. The species' range extended into the basal part of the U. Yatton Beds, where it was rare. This higher division included the S. ornatella acme, and correlates with the ULB. Tucker ('58) noted a similar distribution in the northern half of the Woolhope inlier, with the acme of C. puellaris occurring in the top siltstones of the LLB, below the S. ornatella division. At Perton (PL/A-, (LC)), C. puellaris is present in the top 5 m of the LLB, but becomes more common only in the top 2 m.

The Chances Pitch section (CP-) has calymenids consistently present through the upper 5 m of the LLB. C. puellaris (first positively identified in CP-α (LC)) is common together with proetids in plane assemblages of the calcareous laminated siltstones, especially in the top metre of section. At Woodbury Quarry, C. puellaris was not identified (LC) until the level of the LLB-ULB boundary. Phipps and Reeve ('67) found the species to be fairly common in the Woodbury Shale member (= ULB) of the Malverns.

At Usk, Walmsley ('59) recorded the acme of C. puellaris to occur in the L. Llangibby beds (= ULB), where S. ornatella was abundant. The species first appeared in the highest LLB, but was almost confined to the ULB.

In the shelf edge region C. puellaris was not found in the LLB, although it is recorded from the ULB of Leintwardine (Whitaker '62), and becomes fairly common in the ULB at Aymestrey. The species was found in calcareous siltstones close to the LLB-ULB boundary at Clawdd British (CB-) and Crickadarn Mill (CM-) in the SW region.

b. C. lawsoni (Shirley)

In the Leintwardine area, C. lawsoni becomes very common towards the top of the hLLB in bands containing close-packed accumulations of skeletal elements and in which other fossils are rare. The size of individual elements is very variable in these assemblages. At Mocktree Quarries, horizons with C. lawsoni were examined in the channel-fill beds of MQ/A-, lying directly above the UBB Limestone, and in MQ/8-, where the hLLB were banked against the UBB Limestone. In the former section, the band was little below beds with N. lauensis and N. confluens (DJS), while the latter assemblage included neobeyrichiid ostracodes (LC). The ostracodes indicate a level at the LLB-ULB boundary for the calymenid bands.

In the Shelderton Road section, the highest part of the LLB is rich in trilobites, particularly proetids and encrinurids. C. lawsoni was found occasionally in the assemblages, but was not common. Whitaker ('62) did not record the species (= "Calymene sp. nov.") from the ULB at Leintwardine, but had C. puellaris 'very common' at this level. Siveter ('74) notes the presence of C. lawsoni in the ULB at Leintwardine. In section SR/2-, C. lawsoni was identified (DJS) from the phosphatised conglomerate band (SR/2-g) taken to indicate the ULB here, at the level where N. lauensis (DJS) first appeared.

At Aymestrey, bed Ay/A-Ea, which is not far above the conglomerate (Ay/A-Ca) where there is a sudden faunal change, contained a large articulated thorax and pygidium of C. cf. lawsoni (DJS). The equivalent, poorly fossiliferous strata on the Bengry Track yielded a cranidium of C. lawsoni (JDL collection). These beds are interpreted as channel-fill hLLB, comparable to those at Leintwardine (p 131). Phosphatised pebble-beds occur higher in the sequence, at the level where N. lauensis enters and is common (Penn, in Lawson '73(a) p 262). Above this C. puellaris is common, and not C. lawsoni (Lawson '73(a)).

In the basinal sequence at Kerry, two calymenid cranidia from the level where N. cf. lauensis and N. scissa (DJS) entered the fauna (in PylD/8-) were identified as C sp., cf. lawsoni (DJS).

C. lawsoni has been reported from the LLB at Ludlow (Shergold and Shirley '68, Lawson and Whitaker '69). A Acranidium from the middle LLB at Chances Pitch (CP-Xa) was identified as Calymene sp, but nearer to lawsoni than puellaris (DJS). Records of Calymene cf. beyeri from Woolhope (Squirrell and Tucker '60) at this level, and from the Malverns in the LLB and ULB (Phipps and Reeve '67) were included tentatively by Siveter ('73) in his synonymy for C. lawsoni. (They have been plotted in the faunal distribution maps for C. lawsoni). Further work needs to be done before firm conclusions on the species' distribution can be reached, but it appears that C. lawsoni shows a comparable distribution pattern to C. puellaris, appearing earlier in the SE.

c. Calymene sp.

Elements of unidentified calymenids are fairly common in the shelly limestones of the middle LLB at Perton. The sequence at Woodbury Quarry also yielded several calymenid skeletal elements which could not be specifically determined (LC).

Vertical distributions:

The two LLB species are the last calymenids in the British succession (Siveter '73). C. puellaris has a widespread distribution in Britain (the Welsh Borderland and Lake District), Gotland and Scania. Its vertical range is limited everywhere, from a fairly high level in the Leintwardine Beds to the LWB (Siveter '73). C. lawsoni occurs most commonly in the hLLB of the Leintwardine area. Its range extends from the UBB to LWB (Shergold and Shirley '68).

Distribution Maps:

Calymenids are not found in the basal conglomeratic facies or Aymestry Limestone (Map A). In the main part of the LLB (Map B), C. lawsoni (including C. cf. beyeri records) has a fairly wide, though not common, distribution through the shelf regions. C. puellaris enters the fauna fairly high in the LLB in the SE shelf inliers. (It is also recorded by Shergold and Shirley ('63) in their High LLB at Wenlock Edge). Map B shows the more northerly distribution of C. lawsoni, further towards the shelf edge than C. puellaris. In the top LLB of Map C, C. lawsoni is common at the shelf edge region, while C. puellaris has extended further NW across the shelf, and is fairly common in several inliers. In the ULB, at the gravi-lauensis level (Map D), the abundance of calymenids has greatly increased. Their distribution is cosmopolitan

over the outcrop, although few occur in the thinly flaggy siltstones of the northern basinal region. C. puellaris has considerable areal coverage at this level, having extended further north and west over the area. The much greater distribution and abundance of calymenids at this level suggest the widespread existence of suitable environments. The restraints to their colonisation of the basinal areas have diminished in the higher part of the Leintwardinian.

2. Encrinurids: E. stubblefieldi (Tripp), E. rosensteinae (Temple, Tripp and Gass). Fig. 5.34 p295

E. stubblefieldi, a species of the punctatus group, forms one of the faunal indices for the ULB. At the stratotype, Holland, Lawson and Walmsley ('63) recorded the species from the basal bed of the division. It occurs fairly commonly only in the ULB in the type area. It is recorded from the L. Underbarrow Flags (ULB) of the Lake District (Shaw '71).

E. rosensteinae, of the variolaris species group, is found together with E. stubblefieldi in the Ludlow and Leintwardine areas. The two species appear to have co-existed.

Leintwardine Beds Distribution:

Encrinurids of both species become common in the top few metres of the LLB at Leintwardine (Shelderton Road section SR/2-), in calcareous siltstones which have a rich trilobite fauna. This is the only area where the acme for the genus occurs below the ULB. Here, although encrinurids extend up into the ULB, they are not common at this level (Whitaker '62).

To the east, at Ludlow, encrinurids (again of both types) appear in the topmost LLB at MF/A-, but become rapidly much more numerous in the more thickly-bedded ULB. A similar distribution, with the acme in their hULB (= ULB at Ludlow), was noted by Shergold and Shirley ('68) for Wenlock Edge. At Aymestrey, encrinurids are found commonly in the fossiliferous seams of A. gravi and N. lauensis in the ULB.

At Ysgwydd Hwch (YH1-), encrinurids come into the fauna at the gravi-lauensis level. Straw ('37) recorded their occurrence in the "C". gravi beds at Builth, together with N. lauensis, but here and at Aberedw, they appeared first in the transition beds just below the N. lauensis level (Straw '37).

In the shelf inliers, E. stubblefieldi occurs at the base of the ULB at Woodbury Quarry, but was not found in the other areas. Records from the ULB are shown in Map D. Like the calymenids they show a much wider areal distribution at the gravi-lauensis level, suggesting an extension of favourable conditions. In contrast to the calymenids, the original locus of distribution is at the shelf edge, and the ULB spread has involved a "shelf-ward" shift in their range. They remain most common in the thickly flaggy siltstones and calcareous siltstones of the main outcrop, however. No specimens were found in the thinly flaggy siltstones of the northern basinal region.

3. Proetids: P. obconicus (Lindström) and W. ludlowensis (Alberti) Fig 5.35

UBB and Leintwardine Beds Leintwardine Beds (Owens '73)

The species of proetid usually found in the LLB is P. obconicus, which has a wide distribution in the shelf and shelf edge regions. W. ludlowensis occurs less commonly, mainly in the Ludlow and Leintwardine areas (and Wenlock Edge - Owens '73), but also in other shelf and shelf edge localities. However, it was only recorded separately if cranidia were found, so that the distributions shown (in Fig. 5.35p296) are minimal; all other skeletal elements were recorded as 'proetid'. The two types are commonly present in the same beds, and so, appear to have co-existed.

Proetids are present but relatively uncommon in the Aymestry Limestone facies (Map A), but above this (Map B), have a fairly ubiquitous distribution throughout the areas of calcareous siltstone facies. They are never numerous, but are found consistently in shelly limestones through the LLB. Towards the top of the LLB, their abundance increases markedly in several areas (Map C). This corresponds to a general increase in diversity of the fauna at this level.

At Ludlow and Leintwardine, proetids become very common in some bands, together with graptolites, beyrichiacean ostracodes, and A. gravi. A few beds at Leintwardine have monospecific assemblages of skeletal elements of varying sizes, comparable with the calymenid (C. lawsoni) deposits at a roughly equivalent stratigraphical level at Mocktree Quarries (MQ/A-, and MQ/8-). P. obconicus is the prevalent species of proetid, but W. ludlowensis is also present. Several complete specimens of P. obconicus were found at Ludlow (in MF/A-), and Shelderton Road section (SR/2-).

Similar increases in abundance of proetids in the topmost LLB were noted at Ysgwydd Hwch (YH1-), Woodbury, and Chances Pitch. Squirrell ('56) mentioned the relatively common occurrence of proetids with C. puellaris at this level at S. Woolhope.

The abundance of proetids diminishes again at the grayi-lauensis level at Ludlow (Holland, Lawson and Walmsley '63) and Leintwardine (Whitaker '62). In several shelf inliers, proetids are present in the S. ornatella (= ULB) beds. At Builth, Straw ('37) recorded the acme for proetids in the basal "C" grayi beds at the N. lauensis level, and an increase in their abundance coincides with this horizon also at Crickadarn Mill (CM-, (LC)).

Thus, the acme of abundance of proetids occurs at a slightly lower level than that of encrinurids and calymenids.

4. Other trilobites:

The increase in abundance of trilobites in the top LLB is accompanied by greater diversity. Odontopleurids of Leonaspis sp. (ATT), and otarionids - Otarion cf. diffractum and Harpidella aff. novella (RMO), are found at Ludlow and Shelderton at this level. (O. cf. diffractum is also present lower in the LLB of the Leintwardine area, for example, TL5/-, NE of Wassell Barn). At Ludlow, a lichid - Hemiarges sp. (ATT) - was found at the LLB-ULB boundary at Sunnyhill Quarry (SY/B-M). Another lichid - Acanthopyge sp. (ATT) was found at May Hill, in the conglomeratic bed (LH-I) taken to indicate the base of the ULB; several specimens of C. puellaris and proetid pygidia were also present in this band.

Acastella spinosa was identified (LC) in the top LLB at May Hill (LH-Aa) and Shelderton (SR/2-a). It is recorded from Usk at this level (A. cf. spinosa) and from the ULB (Squirrell and Downing '69, p 310). Acaste sp. occurs in the ULB at S. Woolhope (Squirrell '56). A. spinosa is found mainly in the UWB, so that the LLB specimens represent early appearances of the species.

Trilobite ecology:

Most trilobites are thought to have been vagile benthos. The morphological diversity can be related to the various modes of life and feeding habits. Functional adaptations for crawling, swimming, and burrowing into soft sediment were described by Bergstrom ('73), who inferred that the class included deposit-feeders, scavengers and active predators.

Proetids are considered, from their distribution to have lived in shallow water, sometimes in "reef" environments (Fortey and Owens '75). The order maintains a conservative morphology throughout its geological range, with a few morphotypes appearing repeatedly during evolution. This suggests that different groups occupied the same ecological niches successively from the Ordovician to the Permian. The greatest abundance of proetids is found in limestones, but they are not confined to that lithology (Fortey and Owens '75).

The proetid ecological preference for calcareous environments makes a burrowing habit unlikely. The morphology of proetids - the convex profile, and small size - does not appear adapted for this mode of life, nor for vigorous swimming or hunting. It is considered that proetids were probably deposit-feeding or scavenging forms, either crawlers or slow-swimmers.

Bergstrom ('73) proposed that Flexicalymene burrowed into soft sediment. He related the structure of the limb, which has a distal, comb-like fringe of spines on the exite (Bergstrom '69) and is inferred to have had strong musculature, to the geometry of some Cruziana trails. Also, he noted the reported occurrence of Flexicalymene meeki in burrows of the Cruziana type. However, other calymenids are typical of limestones; for example, Calymene blumenbachii is very common in the Much Wenlock Limestone of Dudley. A burrowing habit is improbable in this environment. Pronounced niche diversification may be developed in calymenids, with various modes of life being adopted. The fairly small eyes suggest that calymenids were not active predators.

Encrinurids have a convex tuberculate cephalon, with stalked eyes. This morphology appears adapted for a position partially buried in the sediment, when the ornamentation will help to camouflage the trilobite. Such a strategy is appropriate for a predatory animal.

Conclusions:

The Leintwardine Beds distributions show the restriction of the trilobite fauna to the areas with benthonic faunas. In the ULB, the westward extension in their occurrence indicates environmental changes in the basinal region. The abundance and diversity of the trilobite fauna increases at the top of the LLB, and reflects more favourable conditions at this time. Trilobites are numerically important in some ULB assemblages.

Trilobites are vagile benthos, adopting various ecological strategies. The proetids become more common above the Aymestry Limestone facies, in shelly limestone bands of the calcareous siltstone facies. There is a widespread acme at the top of the LLB, when the greatest abundance is in the Ludlow and Leintwardine areas. Complete specimens from this level in calcareous siltstones of both regions show that the trilobites were indigenous. At Leintwardine, proetids were uncommon in the channel-fill beds, but very common in the sequences of the normal succession. Proetids become less common at the gravi-lauensis level. The preference for calcareous environments described by Fortey and Owens ('75) is not consistent with the LLB distributions, except for the concentration of skeletal elements in shelly limestones. The concentration of proetids in the top LLB is highest in more distal shelf environments (ie. Ludlow to Leintwardine), in clastic facies. Proetids and warburgellids frequently occur together in assemblages, which suggests that they have similar modes of life.

The calymenids C. lawsoni and C. puellaris both appear lower in the succession in the SE. The species seem to be mutually exclusive. C. lawsoni has its acme of abundance in the high LLB. Horizons with profuse skeletal elements of C. lawsoni (DJS) in the Leintwardine area, and the articulated thorax and pygidium of C. cf. lawsoni (DJS) at Aymestrey, indicate that individuals lived in the shelf edge areas. These occurrences are in channel-fill hLL beds. The species is not common at Shelderton in the normal LLB succession. Whitaker ('62) commented on the greater variety of fauna within the channels than was found in the intervening, more exposed, shelf areas. The distribution of C. lawsoni may reflect a preference for more sheltered conditions in the canyon-heads. C. puellaris is most common and widespread in the top LLB-ULB. The complete specimen from high in the LLB at Ludlow (MF/A) must be locally derived, so that the species was indigenous here. The associated fauna in these calcareous siltstones includes shelly benthos and graptolites. In the shelf inliers, calymenids are usually found in richly-fossiliferous limestome bands of the calcareous shelly siltstone facies.

The two calymenid species have comparable distribution patterns, with C. lawsoni appearing before C. puellaris in the succession. Their

vertical and lateral ranges overlap but they are not found in the same beds. This may reflect different ecological preferences, or might indicate competitive exclusiveness. Both species "migrate" with time towards the shelf edge region after appearing first in the shelf inliers.

Encrinurids have a LLB distribution centred in the shelf edge region. They typically occur in silty lithologies. At Shelderton (SR/2), proetids are abundant in the same sequence. Encrinurids become more common and laterally extensive in the ULB, particularly in the thickly flaggy, gravi-lauensis beds. The distribution pattern is very different from the calymenids; encrinurids do not appear in the shelf inliers until the ULB. The two encrinurid species are often found in the same beds, so that they, like proetids and warburgellids, seem to have co-existed. The association with silty lithologies is consistent with the ecological strategy suggested, of being camouflaged within the surface sediment, and perhaps predatory.

The characteristic occurrence of calymenid and proetid skeletal elements in the shelf inliers is in shelly limestones. However, these trilobites appear indigenous in calcareous siltstone beds of Leintwardine and Ludlow. Many of the fossiliferous limestones are lenticular coquinas, when the calcareous matrix may be secondary. At Ludlow, disarticulated skeletal elements of trilobites are commonly found in bedding-plane shell assemblages, but the few, complete trilobites were found at different levels. It is possible that the usual association of calymenids and proetids with limestones in the shelf inliers reflects a preservational bias. Otherwise, an independence of facies must be assumed, in view of the distribution of locally-derived individuals in silty lithologies.

Towards the top of the LLB and in the ULB, a few lichids, odontopleurids, otarionids and dalmanitinids enter the fauna. The increase in diversity of the trilobites accompanies the greater abundance and distribution of the common species; conditions had clearly become more favourable for these vagile benthos.

D. OSTRACODES: Beyrichiaceans, and non-palaeocope forms (mainly B. siliqua) Figs. 5.36p297, 5.37p298, 5.38p299.

(Beyrichiacean identifications by DJS shown in Fig .5.39p251).

Ostracodes form minor components of the fauna throughout the LLB. Records of their abundance are relative and very approximate; also minimal, since microfossils are particularly liable to be missed in

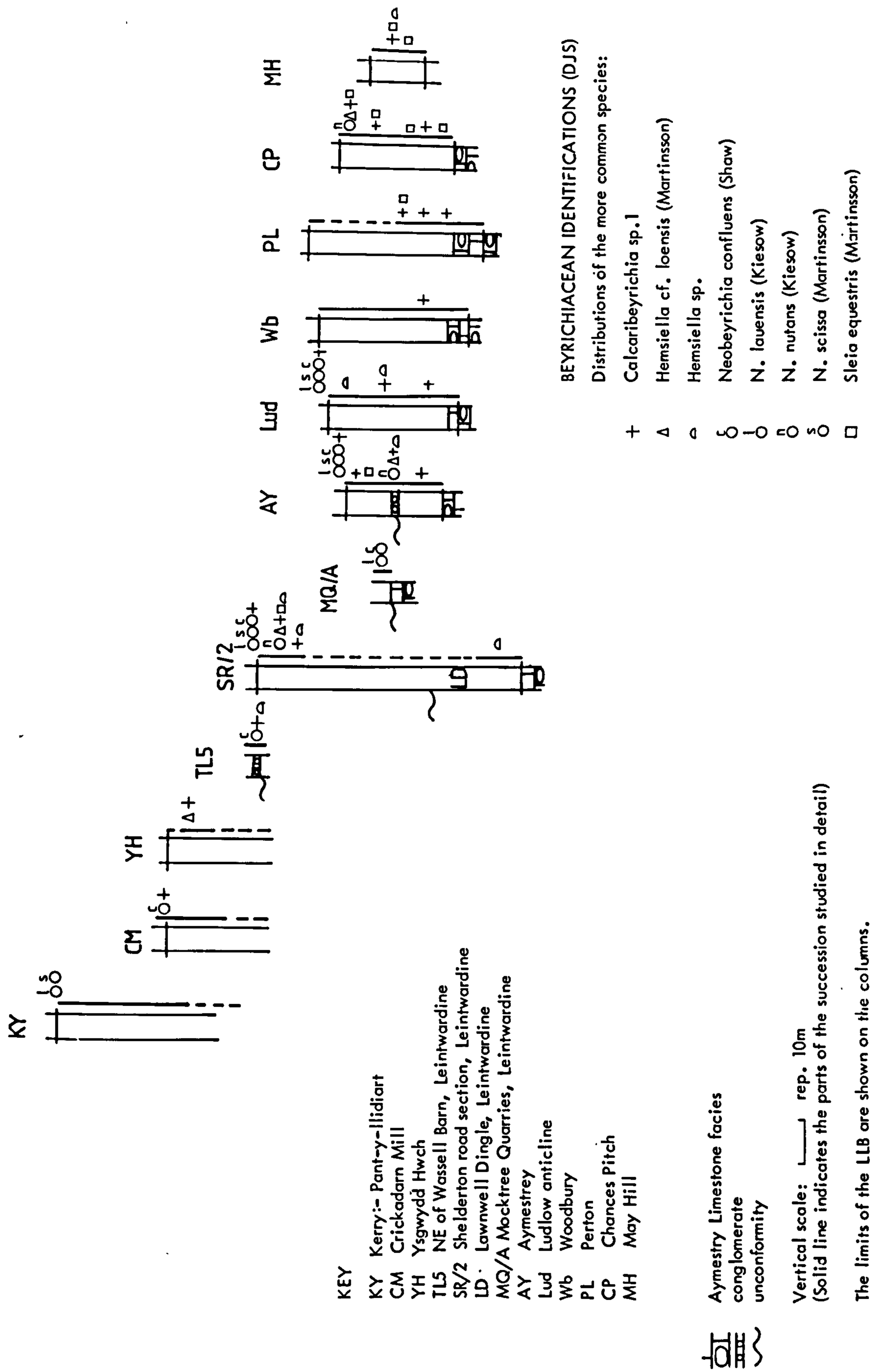


Fig. 5.39 : Beyrichiacean identifications (DJS).

field examination. However, the distributions of the beyrichiacean and smooth ostracodes are significantly different. The former are cosmopolitan through the main part of the LLB (Maps A and B). They increase in abundance in the highest part of the LLB (Map C), when they become most common in the shelf edge, Ludlow and basin regions. Non-palaeocopes are mainly found in shelf areas. Their distribution changes little through the LLB. The difference becomes more pronounced if individual species of beyrichiaceans are considered. The vertical range chart (Fig 5.39) shows the detailed distribution of identified forms.

Smooth forms (which were not identified separately) are common constituents of faunas in shelly limestone bands. Calcaribeyrichia sp. 1 and Sleia equestris are found more rarely, in the same beds in shelf successions. At Ludlow and the shelf edge regions in the middle part of the LLB, Hemsiella sp. is the typical beyrichiacean species. It is very common in plane assemblages of S. ludloviensis and small D. navicula valves, in the sheet-laminated siltstone facies (for example, MF/F-).

In the higher strata of the LLB at Ludlow and Leintwardine, beyrichiaceans become very common and more diverse. At Shelderton (SR/2-), they are often found in siltstones in "nests" and plane assemblages with A. gravi, separate from shell layers. They occur abundantly from a lower level in the succession than farther east at Ludlow. Hemsiella sp. is the most frequent species, but Calcaribeyrichia sp. 1 and smooth ostracodes are also associated in the assemblages.

Towards the top of the LLB, the diversity, as well as the abundance, of the beyrichiacean ostracodes increases. In addition, neobeyrichiids appear with the other ostracodes in the A. gravi-rich seams. At Shelderton, N. nutans is the first species of neobeyrichiid to enter the fauna. At a slightly higher level, N. lauensis, N. confluens and N. scissa are found. This latter horizon (which is a phosphatised conglomerate band SR/2-g) was taken to indicate the ULB here. At Ludlow and Aymestrey, an equivalent increase in diversity of species accompanies the appearance of N. lauensis (Swater '74). The ULB has a very rich beyrichiacean fauna compared with lower and higher divisions. The N. lauensis fauna forms a widespread marker horizon throughout the basinal areas and extending eastwards to Ludlow. The ULB ostracodes occur in impersistent, thin fossiliferous seams with A. gravi, comparable

in composition to assemblages of the topmost LLB. The appearance of N. lauensis is closely linked to the facies change to the more massively-bedded, calcareous siltstones of the "C" grayi flags (Map D). However, the horizon also extends into the thin, laminated siltstones of Kerry (PylD/8.).

Ecology:

Martinsson ('62) proposed that beyrichiid ostracodes were benthonic, but because of the wide range of facies in which they are found, suggested that they may have lived among algal vegetation. The majority of Recent ostracodes are vagile, benthonic, filter-feeders, utilising detritus as the principle food source (Barnes '68).

The areal distribution and abundance of beyrichiacean ostracodes of the N. lauensis fauna and, to a lesser extent, of the high LLB beyrichiacean fauna, is more consistent with a pelagic habit. The LLB and ULB assemblages are comparable in composition, and both occur in siltstones, crowded into "nests" and thin fossiliferous lenses. This suggests the associations are ecologically equivalent, which supposes similar modes of life for various different genera and species. (Also, the morphological and distributional alikeness of the neobeyrichiid species suggests little niche differentiation). The characteristic association with A. grayi is reflected by the parallel distribution pattern of the brachiopod. A. grayi - beyrichiacean ostracode assemblages are frequently found at separate levels from benthonic shelly faunas. This indicates a different derivation from the shelly benthos for these assemblages.

Among the beyrichiacean ostracodes, the adoption of different ecological niches must be anticipated, so that the single distribution map is an over-simplification. Calcaribeyrichia sp. 1 and S. equestris are both commonly associated with shelly fauna in limestones of the shelf sequences. The former is also widespread in the basinal and shelf edge beyrichiacean assemblages. This species is large and tuberculate, and it is conceivable that the more robust form could explain its preservation in the more turbulent shelf conditions while other, more delicate, forms have been selectively destroyed. Such an argument was suggested by Rickards ('75) to account for the lateral distribution of various Llandovery graptolites, only the stronger forms being preserved in shelf areas. However, the neobeyrichiid species are also large and

tuberculate, but these are extremely rare in the shelf inlier sequences, and with benthonic shelly faunas. Therefore, the distribution pattern of the top LLB and ULB beyrichiacean assemblages is considered to show an original bias.

Calcaribeyrichia sp. 1 and S. equestris, like the non-palaeocope ostracodes which are typically found associated with benthonic fossils in calcareous facies, appear to have been benthonic. Similarly, Hemsiella sp. is found in abundance in shelly assemblages of the calcareous siltstones (LLB) at Ludlow. But it is also a major constituent with Calcaribeyrichia sp. 1 of the top LLB ostracode "seams" at Shelderton. Both continue to be found in the higher, neobeyrichiid faunas. Therefore, it appears probable that the ostracode assemblages are of benthonic forms. The basinal distributions could then be explained by the ostracodes (and A. gravi) being associated with algal vegetation, and being transported with detached plants. The scarcity of ostracodes, except concentrated in horizons, in the laminated siltstone sequences indicates that they were not indigenous to these areas. N. lauensis has its main abundance in the massively-bedded calcareous siltstone facies (Map D).

The A. gravi-ostracode assemblages are commonly closely-packed associations of disarticulated valves and carapaces, many of which are unbroken. The lenticular nature of the seams shows that they have been accumulated by gentle bottom currents, perhaps during a period of standstill in deposition of sediment.

Conclusions:

The distribution of the non-palaeocope ostracodes suggests that these were benthonic forms, preferring calcareous facies. The beyrichiacean ostracodes include species (eg. Calcaribeyrichia in calcareous deposits, Hemsiella in silty facies) that appear benthonic, and which are also common in the discrete, ostracode and ostracode-A. gravi, assemblages of the top LLB and ULB. By inference, these latter faunas are also benthonic, therefore. It is not until the top part of the LLB that A. gravi-ostracode assemblages begin to occur in the laminated siltstone facies; below this, scattered individuals are found here infrequently. The main abundance in the basinal region is in the ULB "C" gravi beds siltstones, alternating with shelly faunas. The distributions indicate an original preference among many beyrichiacean

species for silty, distal shelf environments (eg. neobeyrichiids). The occurrences of assemblages in some laminated siltstone sequences (eg. N. lauensis fauna at Kerry - PylD/8) which have a sparse, mainly pelagic, fauna, may be explained by transport of the ostracodes with detached algal vegetation. The westward extension of beyrichiacean distribution, and facies change to thick, calcareous siltstone flags, at the top of the Leintwardine Beds suggests an environmental change at this level.

E. BIVALVES:

1. F. amygdalina (J. de C. Sowerby) Fig. 5.40 p300

In the Treatise (Cox et al. '69), Sedgwickia and Fuchsella were synonymised and placed in the Grammysiidae. L.F. Marsh ('76 - pers. comm.) intends to re-separate them as distinct genera and to refer to this species as Fuchsella amygdalina.

Leintwardine Beds distribution:

The distribution maps A-D show the absence of F. amygdalina from the basinal areas of thinly-bedded, laminated siltstones, but its cosmopolitan distribution over the shelf. Through most of the LLB, the species is confined to the shelf and shelf edge regions (Maps A and B), but at the top of the LLB, it spreads further westwards into the SW, Brecon Anticlinal, sequences (Map C). At the grayi-lauensis level (Map D), F. amygdalina becomes very common in the thickly-bedded siltstones of the "C" grayi Beds.

In the basal LLB (Map A), F. amygdalina is not common in the Aymestry Limestone facies, but increases in abundance in the siltier beds above. For example, a few valves were found in the lowest, Davia-rich limestones at Lawnwell Dingle (Leintwardine), but assemblages of scattered, convex-up shells occurred in the calcareous siltstones slightly higher in the succession. In the thinly-bedded LLB siltstones at Aymestrey, there are frequent plane assemblages of single valves of F. amygdalina (sometimes aligned - see p 370-1), usually separate from the horizons with abundant brachiopods. Bands of bivalves, including F. amygdalina, occur in the siltstones interbedded with the conglomeratic limestones at Perton. Similarly, at May Hill (WG-), bivalves are important constituents of the fauna from the muddy siltstones of the L. Blaisdon Beds, but are uncommon in the brachiopod - and bryozoan-rich faunas of the conglomeratic limestone beds. There are occasional

articulated specimens, which cannot have been moved far, in these fine clastic sediments at May Hill.

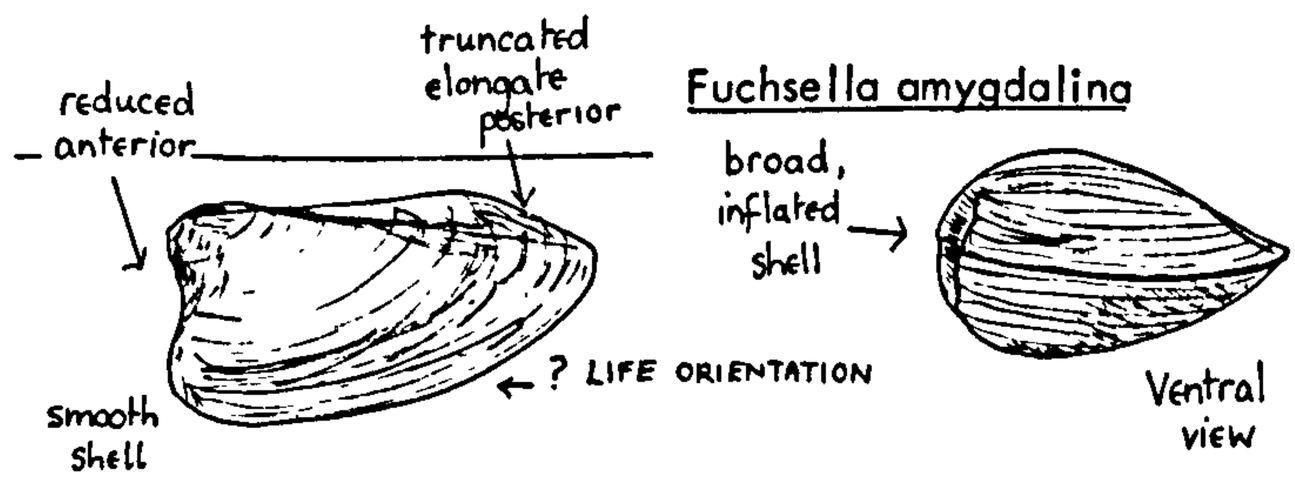
The more widespread occurrence of F. amygdalina in the main part of the LLB is shown in Map B. Plane-assemblages of separate, convex-up valves are common in the sheet-laminated siltstone facies at Ludlow, and some articulated specimens are found in the beds between shell horizons. Bivalves dominate the assemblages of numerous beds in the calcareous siltstones of the SE shelf inliers. Although the majority of shells are disarticulated, infrequent articulated individuals occur in all these sequences. Bivalves are much more common in the siltstones than in the interbedded shelly limestones of the calcareous siltstone facies.

In the Brecon Anticlinal region, a slumped bed fairly high in the leintwardinensis Striped Flags at Cwm Hely Dingle (CHD-) contained numerous articulated individuals of F. amygdalina. Many were orientated with the hinge uppermost, apparently in life position (see Ecology). The fauna of this bed contrasted greatly with that in undisturbed beds above and below, and had apparently been carried downslope, in a viscous sediment flow, from a shallower area.

Map C shows the westward spread of shelly faunas and calcareous siltstone facies at the top of the LLB. F. amygdalina enters the fauna in several of the basinal sequences in the SW (CTDI-, CM-, YH1-). It is very common at Ysgwydd Hwch (YH1-), where it is found in monospecific assemblages of valves, but also scattered in beds between the fossiliferous horizons. The species has a wide distribution in the areas of calcareous siltstone facies at this level, and is prevalent in many assemblages.

Map D shows an increased abundance of F. amygdalina in several areas of the shelf, and in the "C" gravi Flags of Builth (Straw '37). At Crickadarn Mill (CM-), individuals are large, and articulated specimens are fairly common.

Ecology:



F. amygdalina has a moderately inflated, equivalve shell, which is elongated posteriorly and has a flattened posterior margin. Some of the

articulated LLB specimens were positioned with the sagittal plane vertical and hinge uppermost, lying perpendicular to the bedding (- see above). This is presumed to be a life orientation.

Bambach ('71) described a similar attitude for Grammysia oblicua, which he interpreted as its life position. The ecology of this species was discussed in relation to the morphological features of the shell. An anterior-ventral gape in the shell was considered to be for protrusion of a byssus, while a dorsal posterior gape would facilitate efficient feeding in a semi-infaunal, non-siphonate form. The shells were orientated with the prominent keel parallel to the bedding - this would serve as an additional stabilising device. F. amygdalina does not have a diagonal carina, however, and has no pronounced gapes on the shell.

Stanley ('72) commented that many Palaeozoic pholadomyaceans have an elongate shape that cannot be definitely recognised as either endobyssate or free-burrowing. He suggested that the presence of a ventral (byssal) sinus was indicative of an endobyssate strategy, because it would reduce the mantle cavity space available for the foot. The Treatise notes an entire pallial line in Sedgwickia.

For a burrowing mode of life, the shell form and its relative convexity correlate closely with the rate and depth of burrowing. The shape of F. amygdalina is not streamlined for rapid burrowing, nor does it have the very elongate shape of deeper-burrowing bivalves (Kauffman '69). The weak external ornamentation of the shell is consistent with a burrowing habit, because ridged and carinate shells retard penetration of the sediment (Trueman, Brand and Davis '66). Therefore, F. amygdalina may be a fairly slow, shallow-burrower: L.F. Marsh (pers. comm. '76) considers the morphology to reflect such a mode of life.

From the LLB evidence of the life orientation, and the lack of features associated with an endobyssate strategy, it appears most likely that F. amygdalina was a slow, shallow-burrowing species.

Conclusions:

The occurrence of articulated specimens of F. amygdalina at Ludlow and in the shelf inliers indicates that the species was indigenous at least to these areas throughout the LLB. Its abundance declines westwards from Ludlow, and only disarticulated valves were found; whether F. amygdalina lived in the shelf edge region, or the fossils

are all derived from other areas, cannot be determined. The common distribution of F. amygdalina (and other bivalves) in assemblages separate from those dominated by brachiopods is interesting. It could be an original feature of the areal distributions, or result from differential transport or breakage effects. It may reflect the extent of the current disturbance which accumulated the shells, though; to exhume living, infaunal or semi-infaunal, forms the top sediments must be removed or reworked, while disturbance of just the sediment-water interface will only affect epifaunal forms, such as brachiopods, and the shells of dead infauna (which tend to come to the surface).

At the top of the LLB, the presence of infrequent articulated specimens as well as single valves at Crickadarn Mill (CM-), and Ysgwydd Hwch (YH1-) shows that F. amygdalina now inhabited this region. The species increases in abundance, and articulated individuals become fairly common in the "C" gravi Beds (ULB) of the former locality, which suggests that conditions became increasingly favourable in this region.

2. G. cymbaeformis (J. de C. Sowerby) Fig. 5.41 p301

Leintwardine Beds distribution:

G. cymbaeformis is restricted mainly to the shelf region, occurring most commonly in the SE inliers.

In the basal LLB (Map A), the species is rare in the Ludlow and shelf edge (Leintwardine, Aymestrey) sections. It is found in bands in calcareous siltstones at Perton, both with other bivalve species and monospecifically. The assemblages are composed of single valves. The Woolhope inlier is the only area where G. cymbaeformis is common at this level. At May Hill, the species is found in some of the muddy siltstones that are interbedded with the conglomeratic limestones, but is less common than F. amygdalina.

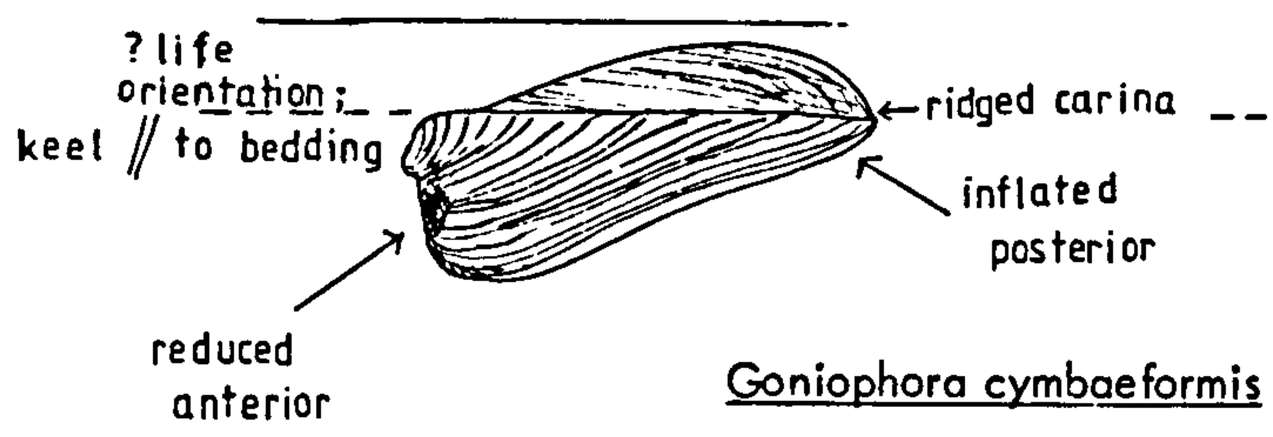
The distribution pattern remains similar in the main part of the LLB (Map B). G. cymbaeformis is consistently present (in small numbers) in the upper half of the succession at Ludlow, and becomes fairly common in assemblages in the higher beds at Woodbury. The latter occurrences are often with F. amygdalina in faunas dominated by bivalves, and in the siltstones; specimens are disarticulated.

Map C shows the spread of the distribution into the SW of the outcrop, comparable to that shown by F. amygdalina at this level. G. cymbaeformis forms a minor element of the fauna at Ysgwydd Hwch (YH1-) and

Crickadarn Mill (CM-), occurring in bands with F. amygdalina. In the ULB of Map D, the main concentration is in the SE shelf inliers. Like F. amygdalina, G. cymbaeformis is much less common in the northern shelf areas at this level.

Rare articulated individuals were found. These came from the LLB at Perton, in bivalve-rich siltstone bands, and from the topmost LLB on the Whitcliffe (at the stratotype for the base of the ULB) at Ludlow. These specimens must have been locally derived, and indicate that the species was indigenous then to these areas.

Ecology:



Goniophora cymbaeformis

G. cymbaeformis has an anterior beak, curved inwards and forwards, and an elongated posterior region with a broad, flattened margin. The shell has a carina running diagonally from the hinge to the postero-ventral edge. The maximum width of the shell is roughly midway between the dorsal and ventral margin, producing a wedge-shaped ventral profile.

Stanley ('72) considered this modiomorphacean genus to be endobyssate, because of the elongate, prosocline shell form, with its reduced anterior region. He interpreted the shell to have a broad byssal sinus on the ventral margin, and its profile is well-adapted for a semi-infaunal rather than an epifaunal, mode of life (- epibyssate bivalves, such as Mytilus, tend to have a ventral position for the maximum width). Stanley ('72 - p 194) illustrated G. sturtzi apparently preserved in life orientation. This attitude (see figure above) is very similar to that described by Bambach ('71) for Grammysia obliqua, with the keel parallel to the bedding, and hinge uppermost. The latter species is inferred to have been semi-infaunal, endobyssate, with the posterior margin projecting above the substrate (see F. amygdalina ecology). The strong carina of the Goniophora shell would tend to retard burrowing if the species were free-living (Trueman et al. '66), but will act as a stabilising device in an endobyssate form (Bambach '71).

From a consideration of the shell morphology, a semi-infaunal, endobyssate mode of life appears likely for G. cymbaeformis.

Conclusions:

The LLB distribution of G. cymbaeformis is centred in the shelf inliers, where it is found in bivalve-rich bands in siltstones. It spreads progressively further west, becoming more common in the upper part of the division at Ludlow, and then entering the fauna of some SW basinal sequences in the top LLB (eg. Ysgwydd Hwch YH1). It remains most numerous in the SE shelf inliers, however.

G. cymbaeformis may have been endobyssate. Its concentration in shelf areas suggests a preference for more proximal shelf environments than F. amygdalina, although the two species often occur together in beds in the shelf inliers.

3. Pteronitella spp.: P. retroflexa (Wahlenberg), P. reticulata (J. de C. Sowerby) Fig. 5.42 p302

Leintwardine Beds distribution:

Pteronitella spp. are found in areas of the shelf, mainly in the calcareous siltstone facies. Of the two species, P. retroflexa occurs more commonly, but both are found together in many assemblages.

Pteronitellids are fairly common in the basal LLB at Perton, in bivalve-rich bands in siltstones. They are infrequent in the interbedded shelly and conglomeratic limestones, though. Individuals are generally small. Some horizons include articulated shells, but most assemblages are composed of single valves. The lowermost LLB at Chances Pitch (CP-) had several bands with very large individuals of P. retroflexa. One bedding plane had many large specimens, a few of which were articulated (CP-Ca).

The distribution remains similar through the LLB (Map B). The species appear consistently in bivalve-rich bedding plane assemblages at Perton, Chances Pitch and Woodbury. Their abundance increases markedly in the higher part of the LLB at May Hill (LH-) and Woodbury. In the former locality, monospecific assemblages, some of which have mostly articulated individuals, become common. Map C, for the top LLB, shows the cosmopolitan distribution across the shelf at this level. Pteronitellids have become more numerous in the Llandovery-Llandeilo region at this level (Potter and Price '65).

In the ULB "C" gravi flags at Crickadarn Mill (CM-), P. reticulata, P. retroflexa, and Pterinea sp. (cf. tenuistriata) become very common in plane assemblages of large valves. The fauna of these siltstones

includes numerous bivalves, of several different species. Articulated specimens were not uncommon, which suggests that little transport of the shells took place before burial. The occurrence of pteronitellids here thus represents an extension of the areal distribution at this level.

4. Pterinea sp., cf. tenuistriata (M'Coy) Fig. 5.43 p303

Leintwardine Beds distribution:

Pterinea sp. has a distribution centred in the basin and shelf edge regions. Many of the specimens in the thinly-bedded, laminated siltstone facies are very small, and were not specifically identified. Most larger individuals were similar to P. tenuistriata (LC). Pterineids are uncommon in the shelf region, but occur occasionally through the LLB.

The thin siltstones (LLB) capping the Aymestry Limestone (UBB) at Aymestrey have occasional P. tenuistriata valves in the shell assemblages. Other occurrences are in the sparsely fossiliferous siltstones further west. Pterineids occur occasionally in sequences where the fauna consists mainly of graptolites, L. lata, and C. cornucopiae; benthonic shelly forms are rare in these beds. The former association of fossils is found sporadically through the succession in the poorly-fossiliferous leintwardinensis beds of the basin. At Lyepole Bridge, the undisturbed units between the shelly slumps have a fauna of abundant graptolites and L. lata, with pterineids. Articulate brachiopods are rare in these beds (cf. their abundance in the slump faunas).

Maps B and C show the continued distribution centred in the basinal sequences. In the top LLB, there is an incursion of shelly faunas into the Striped Flag facies, for example, in the SW Brecon Anticlinal region (YH1-, CM-, CTDI-), and at Leintwardine (SR-). The graptolite - L. lata - pterineid fauna still occurs in these sequences, in the beds between the shell horizons. This indicates a separate source for the two types of fauna. At this level, pterineids are found in the siltstones of the Llandovery-Llandeilo region (Potter and Price '65).

In the ULB (Map D), the thin flags of the N and NW of the outcrop (eg. Kerry) still have pterineids occurring sporadically; shelly fossils remain uncommon in these beds, and the faunas are sparse. In the "C" grayi beds facies and calcareous siltstones of the main outcrop, pterineids are still widely distributed. The Crickadarn Mill (CM-) sequence includes assemblages of very large P. cf. tenuistriata with pteronitellids.

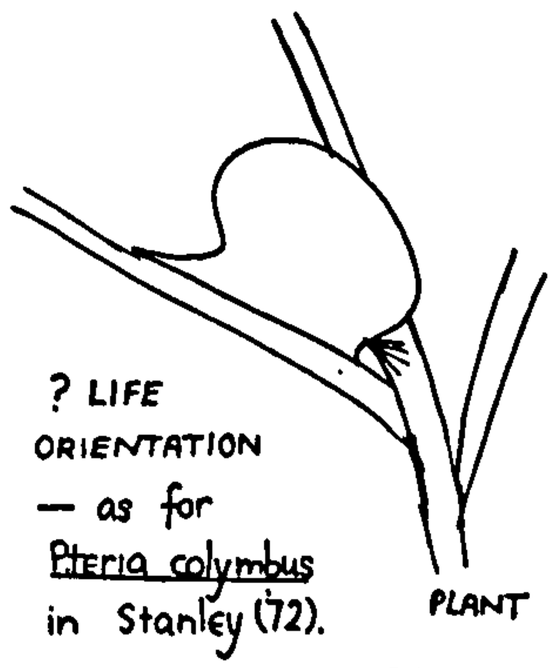
Pteriacean (P. retroflexa, P. reticulata, P. tenuistriata) ecology:

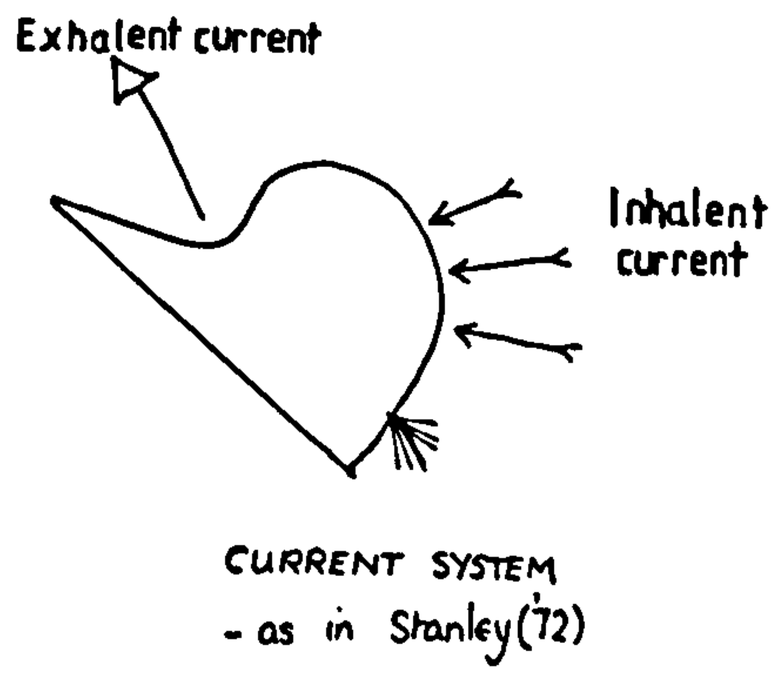
These bivalves are byssate throughout life (Newell '69, in Treatise). They have a byssal notch or sinus, associated with the anterior auricle, and a well-defined posterior wing. The shells are inequivalve, and fairly flattened. Stanley ('70, '72) interpreted the shell morphology as being adapted for an attached mode of life with the sagittal plane non-vertical (see below). In such Recent forms, the more convex valve usually lies uppermost. This allows the maximum contact of the flatter valve with the substrate, for maintenance of physical stability.

The pteronitellids have a greatly elongated hinge line posteriorly, while the anterior auricle of the shell is reduced and rounded. The shell is well flattened. Stanley ('70) considered the shell form to be related to feeding efficiency. The wing-like extension of the hinge line helps to separate the inhalent and exhalent currents, and the shell is streamlined to minimise current resistance. He suggested that these forms may be endobyssate, partially buried in the sediment, because epibyssate types commonly also have an elongated anterior auricle which acts as a fulcrum to prevent overturning of the shell (as in Recent pectinids), and are more markedly inequivalve.

Pterinea spp. have a less extended posterior auricle and a more developed anterior one than pteronitellids. The features are characteristic of epibyssate forms. The shell is thin in pterineids compared with the Pteronitella spp., and much smaller in size.

Stanley ('70) described the ecology of a Recent pteriid, Pteria colymbus (Röding) which has a considerably extended hinge-line posteriorly, and also a well-defined anterior wing. This species is found in shallow sub-tidal areas, attached to alcyonarians. Individuals cluster gregariously, attached to the central stalk, with the posterior auricles pointing upwards along the side branches of the plant.





The distribution of the two pteronitellid species is quite different from that of P. tenuistriata. The former are confined to the areas of shelf facies, while the latter occurs in the thinly-bedded, laminated siltstones of the basinal sequences.

Articulated specimens of P. retroflexa were found in the basal beds of Chances Pitch, May Hill (WG-), and Perton. They were rare compared with the number of single valves found, but indicate that the species lived in the vicinity. At May Hill (LH-), high in the LLB, and in the ULB, there were some bedding planes with many articulated P. retroflexa. At Perton, occasional complete specimens were found in the bivalve-rich bands of siltstone that occurred through the LLB succession. In the highest LLB at Woodbury and Perton, some pteronitellid valves covered with a net-like bryozoan were noted in assemblages.

The number of articulated individuals recorded must be a minimum figure, since the convex left valve, if lying convex-surface upwards, usually obscures the flatter right valve. The distribution of complete specimens indicates that the pteronitellids were indigenous in the shelf inliers in the LLB. In the ULB, articulated individuals (of both species) at Crickadarn Mill (CM-) in the Brecon Anticlinal, illustrate the increased westward extent for the distribution at this level.

P. tenuistriata, in the laminated siltstone facies, is usually found disarticulated. However, an articulated individual at Kerry (KY/1-C), and one at Aymestrey, are important because they suggest that some pterineids lived in these areas. The rarity of shelf occurrences may result from an original distribution centred in the basin region, but possibly the light, thin shells have suffered extensive breakage in the more agitated environments of the shelf region. P. tenuistriata is abundant lower in the Ludlow Series at Builth, in the Pterinea Beds of Straw ('37). Here, swarms of single valves (often dominated by one type of valve) of the bivalve occur on bedding planes of the laminated shales. Straw considered the valves to have been carried in and deposited as a "carpet" over a wide area.

The distribution of P. tenuistriata suggests that this epibyssate species may have been epiplanktonic, attached perhaps to floating algae. The small size and light, thin shell would be suitable for such a mode of life. The absence or scarcity of benthonic fauna in the laminated shales seems to indicate that conditions were inimical to bottom-dwelling forms. The abundance of the species does not increase from

the basin into the shelf edge and shelf regions. This, and the location of the articulated individuals, argues against all the pterineids having been transported extensively in from shallower shelf environments, where benthonic fauna are common.

Conclusions:

The distribution of Pteronitella spp., in areas with rich benthonic faunas, contrasts with the widespread occurrence of P. tenuistriata in sequences where benthonic forms are rare. The latter species must be epibyssate, but the distribution of the former does not distinguish between epi- and endo-byssate strategies. The spread of pteronitellids (including articulated specimens) into the SW basinal sequences in the ULB shows the development there of favourable conditions at this level.

5. Cypricardinia planulata (Conrad) Fig. 5.44 p304

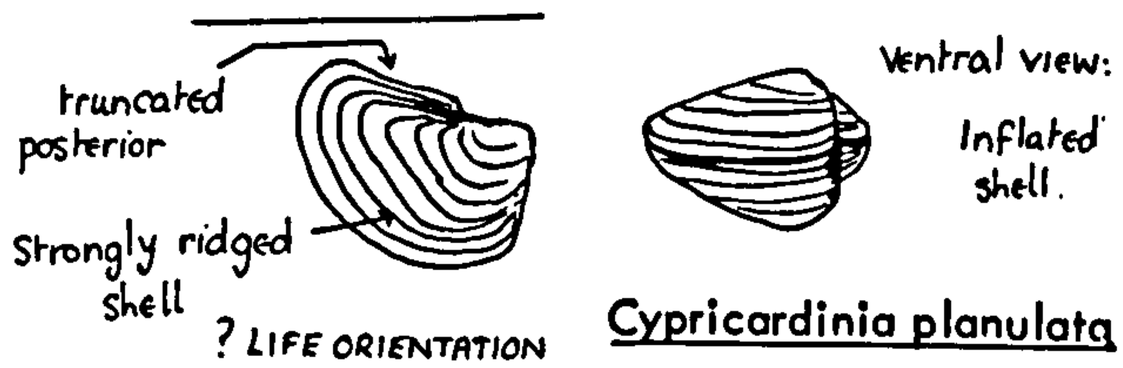
Leintwardine Beds distribution:

C. planulata has a distribution mainly in the shelf edge region. It occurs, but only rarely, in the shelf inliers at Perton, Woodbury and Chances Pitch (see Maps A and B) in the LLB. Straw ('37) recorded C. subplanulata (Reed) from the Lingula lata beds at Builth, but because only the upper part of this division is equivalent to the leintwardinensis zone, the record at this level is uncertain. C. planulata was not found in the basinal sequences studied.

C. planulata is found (as scattered, single valves) throughout the LLB at Ludlow. In the top few metres of LLB succession at MF/A, it is consistently present in small numbers. At a comparable level (Map C) at Shelderton (SR/2-), and at Wenlock Edge (in the bULB of Shergold and Shirley '68), it also forms a minor constituent of the fauna. These sequences have diverse faunas, including graptolites, trilobites, ostracodes, lingulids and many shelly fossils.

In the ULB (Map D), C. planulata is recorded only from Ludlow (Holland, Lawson and Walmsley '63) and Wenlock Edge (Shergold and Shirley '68).

Ecology:



C. planulata has a thick, inflated shell, with well-defined, concentric furrows. The umbones lie anteriorly on the elongate shell, which has a broad, flat, posterior margin. The simple pallial line has a shallow byssal sulcus. This species is small in size.

Stanley ('72) considered Cypricardinia to be endobyssate, living partially buried in the sediment, with the posterior margin uncovered. The thick shell, with its strong ornamentation is not well-adapted for penetration of the sediment in burrowing, but the furrows on the shell would serve to stabilise the shell within the sediment. The weight of the shell lends physical stability, but Stanley ('72) pointed out that, because the current velocity required to move a shell is proportional also to the square root of the shell diameter (Menard and Boucot '51), many small animals are unstable despite having a high density. The widespread occurrence of byssal attachment in juvenile forms illustrates this. Therefore, it is more probable that cypricardiniids were endobyssate than attached epifaunally.

Conclusions:

No articulated specimens were found, so that the species distribution is difficult to evaluate. However, the restriction of C. planulata to the shelf and shelf edge facies indicates a benthonic mode of life, and suggests that conditions in the areas of laminated siltstones were not suitable for colonisation. The more common occurrence in the shelf edge region suggests a preference for more distal shelf conditions.

6. C. cornucopiae (Goldfuss): (= C. interrupta) Fig. 5.45 p305

Leintwardine Beds distribution:

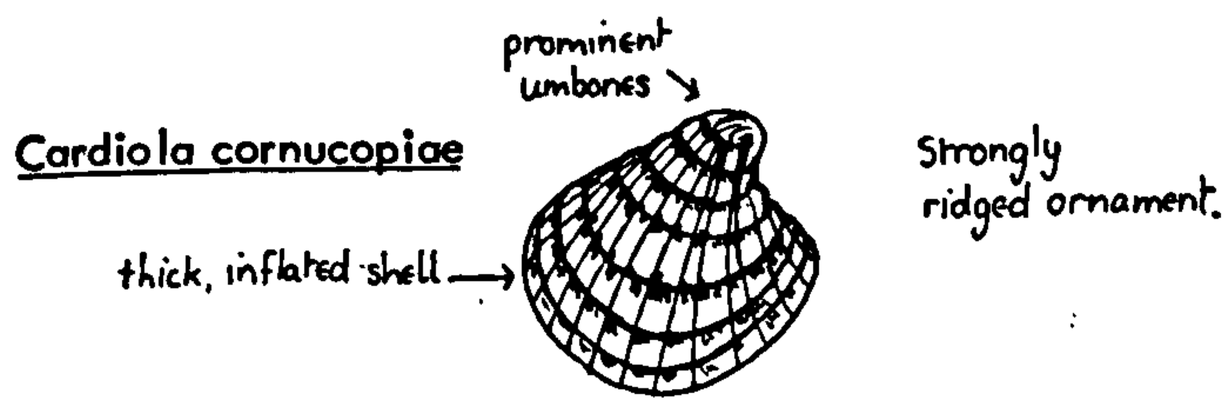
The distribution maps show the cosmopolitan occurrence of this species. Its abundance is low, and specimens occur singly in beds.

In the basinal siltstones, C. cornucopiae is found sporadically in sparsely fossiliferous sequences. The associated fauna includes graptolites, L. lata, and small pterineids: benthonic forms are rare. However, in the shelf areas, specimens are present with other shelly fossils. At Perton, Chances Pitch and May Hill, the species occurs in siltstones which contained other bivalves.

Articulated specimens were found in the LLB at Chances Pitch, Perton and Leintwardine (LD-). They were very rare; typically, single

or broken valves are present. The distribution of the complete individuals, and the association in some beds in these areas of C. cornucopiae with other bivalves, are important. They suggest that C. cornucopiae was indigenous to the shelf and shelf edge region, and in similar environments to other species of bivalves which are byssate or shallow-burrowing, benthonic forms.

Ecology:



C. cornucopiae has a thick, coarsely-ornamented, equivalve shell which is fairly inflated and has prominent umbones.

The mode of life is difficult to evaluate. The shell morphology is not clearly adapted for burrowing, nor for byssal attachment. Therefore, it may have been an epifaunal, free-living form (L.F. Marsh '76, pers. comm.). The occurrence of this fossil in basinal sediments is well-known (eg. Holland '59 p 453, Cocks et al. '71 p 126, Berry and Boucot '67). The lack of benthos in these sequences may indicate a planktonic mode of life for the species, byssally-attached to floating objects. Alternatively, Berry and Boucot ('67) proposed that Cardiola was benthonic, and thus that the Silurian graptolitic sediments in which it was common were deposited in shallow water.

Conclusions:

In the LLB, C. cornucopiae is infrequent in the basinal sequences, and typically occurs as isolated valves in beds which have no other benthonic fossils. It is unlikely to have been living benthonically there, because the large numbers of individuals required to form a breeding population would mean that shells would then probably occur together frequently. Therefore, a free-living or epiplanktonic mode of life, which can explain the widespread LLB distribution, seems likely.

BIVALVE DISTRIBUTIONS:

The distribution of bivalves in the LLB is very largely confined to the shelf and shelf edge regions. The exceptions are P. tenuistriata

and C. cornucopiae, which are found, fairly infrequently, in the sequences of thin laminated siltstones of the basinal areas.

The common LLB bivalve species are suspension-feeding types, and so are most of the other species that are found in small numbers in the shelf and shelf edge sequences (- epibyssate species such as M. mytilimeris, and forms (unidentified) with adaptations for infaunal habitats). Only nuculoids (eg. Nuculites antiquus) are thought to have been deposit-feeders. This is from a consideration of their morphology, adapted for rapid burrowing, and from analogy with modern representatives which have a similar structure (Stanley '72). However, N. antiquus is uncommon in the LLB (although it becomes more numerous in the ULB).

Stanley ('70, '72) noted that the maintenance of physical stability is of prime importance to bivalves. He regarded an endobyssate strategy as advantageous over free-burrowing in forms not adapted for deep or rapid burrowing, because of the lessened vulnerability to disinterment by waves and currents. This may apply to F. amygdalina and G. cymbaeformis. The pterineids and pteronitellids were clearly adapted for byssal attachment. C. cornucopiae may have been free-living or byssally attached; the morphology shows no adaptations for infaunal life.

Bivalves are filter-feeders, using a ciliary feeding mechanism. Steele-Petrovic ('75) described the closed-filament structure of the gills, and suggested that this can be easily blocked, in turbid conditions, by sediment particles. Recent suspension-feeding bivalves are relatively uncommon in soft muddy sediment, probably because of their intolerance to turbidity (Rhoads and Young '70).

The decrease in abundance of bivalves from the shelf to the basin in the LLB is matched by the diminution of other benthos. The nature of the substrate, which becomes finer-grained and muddier towards the basin, will be an important factor. However, the controls on distribution are complex. Parker ('63) stressed the variety of limiting factors, both physical and biological, affecting benthonic macroinvertebrates.

The occurrence of articulated specimens of bivalves is ecologically significant, because with death of the individual, the action of the ligament causes the shell to open. Therefore, articulated shells cannot have travelled far, and their presence shows that the species was indigenous to the area at that time.

At the top of the LLB, and in the ULB, the westward extension in the distributions of several benthonic bivalve species (including some articulated individuals - eg. F. amygdalina at Ysgwydd Hwch, YH1-) indicates an environmental change at this time.

F. GASTROPODS: Fig. 5.46 p306

Gastropods are minor elements of the LLB fauna in the shelf and shelf-edge regions, but are not found in the laminated siltstones of the basinal sequences. In the ULB, the distribution extends further west, into the "C" gravi beds of Builth (Straw '37), but not into the areas which have laminated siltstones at this level (eg. Kerry). The distribution maps show the three most common types: Bembexia lloydii (J. de C. Sowerby), Cyclonema corallii (J. de C. Sowerby), and Loxonema spp.

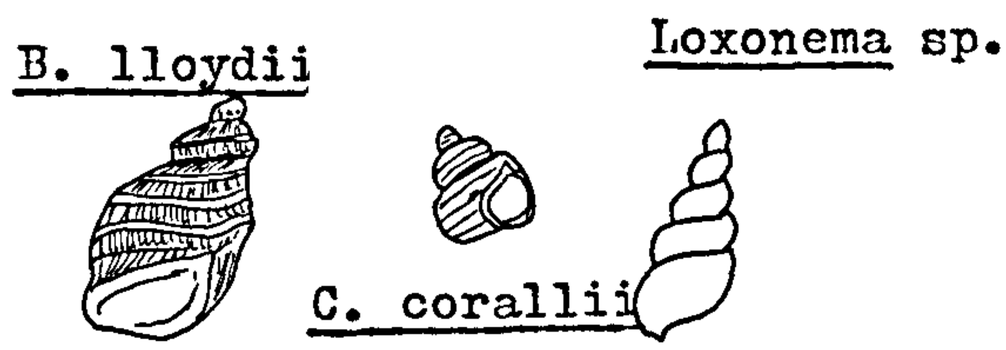
In the basal LLB (Map A), gastropods are uncommon except at Ludlow, where the three genera occur consistently in small numbers among the shelly faunas. B. lloydii occurs mostly in silty beds at Ludlow and at Leintwardine, but C. corallii is generally found in more calcareous bands. A few gastropods (unidentified) occur in the conglomeratic limestone beds; several of these specimens are bryozoan-encrusted, and form nodules. (~~eg. p~~

In the calcareous siltstone facies of the main part of the LLB (Map B), gastropods are widespread in their distribution, but still only minor members of the fauna. B. lloydii and Loxonema sp. tend to occur in silty lithologies, while C. corallii (often bryozoan-encrusted) is a fairly common component of shelly limestone faunas, especially at Perton. Towards the top of the LLB (Map C), the abundance of C. corallii and Loxonema sp. in the shelf inliers increases, and B. lloydii becomes fairly frequent at Leintwardine. In the SW of the Llandovery-Llandeilo area (Potter and Price '65), Loxonema spp. are very common.

The ULB shows a numerical increase in the gastropod abundance, with C. corallii and B. lloydii both quite common in the shelf inliers, and Loxonema sp. more important in the SW of the outcrop.

The facies preferences of the species remain similar throughout the Leintwardine Beds. The more common occurrence of B. lloydii and Loxonema sp. in the western part of the shelf (especially Map C) illustrates their tolerance or preference for silty environments.

Ecology:



These archaeogastropod species are thought, by comparison with living forms, to have been herbivorous vagile benthos. Recent archaeogastropods have unspecialised radulas, and are micro - or macrophagous herbivores. The LLB distributions are consistent with a benthonic mode of life. The absence of gastropods from the laminated siltstone sequences indicates that conditions in these areas were unfavourable.

B. lloydii and Loxonema are distributed mainly in silty facies, but are not found west of Aymestrey. Similarly, Bucanopsis expansus, which in the LLB has a very limited range, occurs in muddy beds with other benthos in the shelf edge region (eg. Leintwardine, Aymestrey, Crickadarn Mill and Ysgwydd Hwch) but is not found among the pelagic faunas of the laminated siltstones.

C. corallii, in contrast, is usually found in more calcareous beds, together with shelly faunas. It is not common in the shelf edge region. Many individuals are partially or wholly encrusted by bryozoa, in shell horizons that are lenticular, current-accumulated coquinas. P. globosa also shows a preference for calcareous environments, being characteristic of the UBB Aymestry Limestone, and disappearing gradually with the facies change to more silty lithologies in the basal LLB.

The common occurrence of Loxonema spp. in the shelly siltstones of the Llandovery-Llandeilo region was related by Potter and Price ('65) to environmental control. Loxonema spp. are most characteristic of the UWB and Downtonian faunas; for example, at Builth (Straw '37) in the "Holopella" conica beds (UWB), and Kerry (Earp '38) in the "Platyschisma" helicites beds (Downtonian). These gastropods are clearly tolerant of shallow, sandy shelf conditions. Potter ('60) noted a westward increase in the diversity and abundance of Leintwardine Beds gastropods in the Llandeilo area. This was accompanied by a depletion in the other benthos, and a coarsening of the facies with sandstones replacing the fine

siltstones typical of the Llandovery area. In addition, the Leintwardine beds thin from 165 m at Cwm Dwr to 4.5 m in the Cennen valley, where they overlie the red deltaic Trichrûg Beds (Potter and Price '65). The lateral faunal variation corresponds to the more sandy, shelf environment to the west. The vertical faunal composition also reflects this control; many elements of the Whitcliffe Beds fauna appear early here. P. ludloviensis, M. nucula, Loxonema gregaria and P. helicites are associated in the mollusc-dominated fauna of the Carn Powell facies beds (Bringewood) beneath the Trichrûg Beds (Potter and Price '65).

The LLB gastropod species appear to be facies controlled in their distributions. Many living gastropods are specific in their food requirements, for example, Littorina obtusata browses exclusively on fucoids, while L. neritoides eats blue-green algae (Morton '65). The gastropod distributions may therefore reflect those of various algae, indicating different food sources for the species.

The increased abundance of gastropods at the top of the LLB and in the ULB indicates that conditions were favourable at this level. Shell transport is difficult to assess. Bryozoan-encrustation may have started during life, but complete enclosure of the shell shows that the gastropod was dead. Such shells are common among the plane assemblages and lenticular deposits of the shell inliers, indicating periods of little sedimentation, when the shells became fully encrusted.

G. ORTHOCONES: M. bullatum (J. de C. Sowerby), K. angulatum (Wahlenberg), Cyrtoceras sp., L. ibex (J. de C. Sowerby) and unidentified orthocones — Fig. 5.47 p307

Orthocones have a cosmopolitan distribution in basin and shelf areas in the LLB. They are generally minor elements of the fauna. The highest abundance is found in the shelf edge region, where the diversity of types is also greater. Records for the ULB suggest that orthocones have become more numerous in the shelf faunas at this level.

The specific distributions are not significantly different. The size of the orthocones shows some lateral variation, however. Orthocones are among the more frequent elements of the sparse fauna of the basinal laminated siltstones. Specimens are characteristically small, and imploded. In the shelf edge and shelf sequences, orthocones have a scattered distribution. They vary in size, but are generally larger than the basinal specimens. Some are imploded, but others are merely

distorted to an ovoid cross-section.

Horizons with very large, bryozoan-encrusted orthocones are found in the top LLB at Shelderton. A similar assemblage forms the basal conglomerate (AY/A-Ca) of the channel-fill beds at Aymestrey. The orthocones are sometimes encrusted on both sides of the shell (seen from the moulds), showing that the bryozoan colonisation took place on the empty shell. All the bryozoan encrustation is considered to have occurred during post-mortem deposition.

Ecology:

The nektonic mode of life of orthocones can explain their distribution over the whole outcrop. The size difference between the basin and shelf areas could result from a less abundant food supply in the former. But, small shells will be more easily transported by currents after death, and could have been deposited in the basin selectively, from an original distribution in shelf and shelf edge areas.

The greatest frequency and diversity in the LLB is found in the shelf edge region. In the ULB of Crickadarn Mill (CM-), large orthocones (unimploded) of a variety of species became very common in the "C" gravi beds facies, among a bivalve-rich, "Whitcliffe-type" fauna. Orthocones are rare in the laminated siltstone faunas of Kerry (Earp '38) and Knighton (Holland '59) at this level.

The size and abundance of the orthocones suggests that, although their nektonic ecology can directly explain the cosmopolitan distribution, they may originally have been more common in the shelf and shelf edge areas. Food may have been a controlling factor in distribution. Orthocones were active predators, and therefore were limited by the geography of their prey.

Implosion of shells has been attributed to depth of water by Denton ('74). However, pressure of the sediment load could also cause the shell to collapse, and it does not seem feasible to separate the two explanations.

H. BRYOZOA Fig. 5.48 p 308

The distribution of bryozoa in the LLB is restricted to the areas of the shelf and shelf edge. They are not found in the laminated siltstone facies of the basinal sequences. In the ULB, bryozoa form elements of the shelly faunas further west, in the thickly-bedded calcareous siltstones of the "C" gravi beds, but are still uncommon in

the laminated siltstones to the north (eg. Kerry, Knighton).

Bryozoans were identified beyond categories for branching, stick-like forms, massive colonies, and encrusting types, except for P. lanceolata. The latter is a distinctive element particularly of the basal conglomeratic limestones of the shelf inliers.

In the SE, the limestone conglomerates contain numerous broken bryozoan colonies in the matrix, together with shells and bioclastic debris. At May Hill, some colonies were encrusting the lithoclasts, and several shells were enclosed in bryozoa too (eg. Figs 6.4(a) & (b)). Further north, where the UBB-LLB boundary lies within the Aymestry Limestone facies (eg. Perton, Woodbury), bryozoa are still very common, but less conspicuous, in the conglomeratic beds. (There are cap-shaped colonies of "F". fibrosa - ? bryozoan/stromatoporoid/coral - in these limestones, however). In the muddy siltstones between the limestone deposits of the basal LLB at May Hill, bryozoa are absent or rare. Similarly, those in the siltier beds at Perton are less frequent, and consist of more delicate, branching forms.

At Leintwardine (Lawnwell Dingle LD-), pieces of branching bryozoa are scattered among the abundant D. navicula of the basal beds. Small nodules within the irregular calcareous siltstones and limestones are frequently composed of bryozoa.

In the main part of the LLB (Map B), branching bryozoans are most common in shelf inlier sequences. The fine calcareous siltstones at Perton include planes with long bryozoan stipes, while the shell limestones usually have smaller, broken fragments. In the latter calcareous beds, gastropod shells (often C. corallii) are frequently completely enclosed by encrusting bryozoa, and "net-like" coverings are noticeable on some bivalve shells. Bryozoa are less common in the calcareous siltstones at Ludlow, although they are generally minor constituents of the fossiliferous horizons. Occasional bands rich in bryozoan-encrusted shells are found here. ~~-see photo SY/B- (encrusted Loxonema)~~. At Aymestrey, narrow, branching bryozoan fragments are associated in the shell horizons, but rare in the intervening laminated siltstones.

The distribution changes little at the top of the LLB (Map C), except that bryozoa become much more common at Shelderton. This change parallels the more frequent occurrence of shell horizons, with which

the bryozoa are associated. Higher in the same sequence, beds of worn, bryozoan-encrusted and limonitised orthocones occur at several levels, together with phosphatised fragments. The conglomeratic bed (SR/2-g) taken to represent the LLB-ULB boundary here (where N. lauensis appears) contains some bryozoan-encrusted fossils. At Aymestrey, the conglomerate AY/A-Ca, which marks the base of the channel-fill beds, includes numerous large, worn and bryozoan-encrusted orthocones.

The ULB (Map D) are reported to have fairly common bryozoa in the faunas of the calcareous siltstones and more thickly-bedded siltstone facies.

Ecology:

Bryozoa are colonial, sessile lophophorates. They are permanently attached to a hard substrate, which is selected by the free-swimming, pelagic larval stage. The range of morphological variations in bryozoa is very great, and largely ecologically controlled (Ryland '70, Stach '36). In living species, colony form relates to current activity, availability of substrates, and temperature; and hence largely to bathymetric zonation. The absence of bryozoa from areas of rapid silt accumulation indicates their intolerance of sedimentation (Lagaaij and Gautier '65). However, the environmental spectrum occupied by living bryozoa is very wide, with species known from intertidal regions down to abyssal depths. Erect branching growth forms were found by Ryland ('70) to be distributed in sub-littoral zones.

The LLB distribution, which is confined to areas of benthonic faunas, shows some environmental control of morphotypes. The bryozoa of the May Hill basal limestone conglomerates are large, thick branching forms, together with more massive colonies and encrusting types. In the overlying siltstones and thin shell limestones, less robust branching fronds are the characteristic growth form, and delicate encrusting bryozoa are found. A similar change is seen at Perton between the thick stipes in the basal conglomeratic limestones, and the thinner branching bryozoa of the interbedded silty bands. At Ludlow, branching bryozoa have smaller, lighter growth forms above the basal Aymestry Limestone facies.

The encrustation of some lithoclasts at May Hill must have taken place after their formation, and prior to further sedimentation. The enclosure of shells also reflects a break in sediment deposition. The large, strong, growth forms of many bryozoa in these beds suggests that

they were adapted to agitated environments, presumably where the lithoclasts were formed. The rarity of shelly benthos and bryozoa in the interbedded muddy siltstones indicates that the shelly conglomerates are allochthonous material, transported in from an area of active uplift and erosion.

The worn, bryozoan-encrusted fossils of the hLLB at Leintwardine and Aymestrey must also result from stand-stills in deposition of sediment. Limonitisation, and the presence of phosphatised nodules, are consistent with this.

A vertical change in the bryozoan fauna is seen at Ludlow. Here, the large, conspicuous branching types of the basal calcareous facies are replaced by smaller forms in the calcareous siltstones. In the higher silty LLB of the western section NF/A, light, delicate branching bryozoa are found among the shell assemblages, but encrusting forms are more typical.

Conclusions:

Bryozoa are morphologically-variable, benthonic animals, requiring a hard substrate for attachment. Their growth form is environmentally adapted, relating to current action, availability of substrate, sedimentation rate, temperature and depth. Stronger larger forms are found in the basal conglomeratic beds, and in the Aymestry Limestone facies. The former deposits are thought to represent turbulent conditions. The generally larger size in calcareous facies may indicate that less turbid conditions were preferable. The decreased abundance and size of branching colonies towards the shelf edge could result from intolerance for silty, soft-bottom conditions.

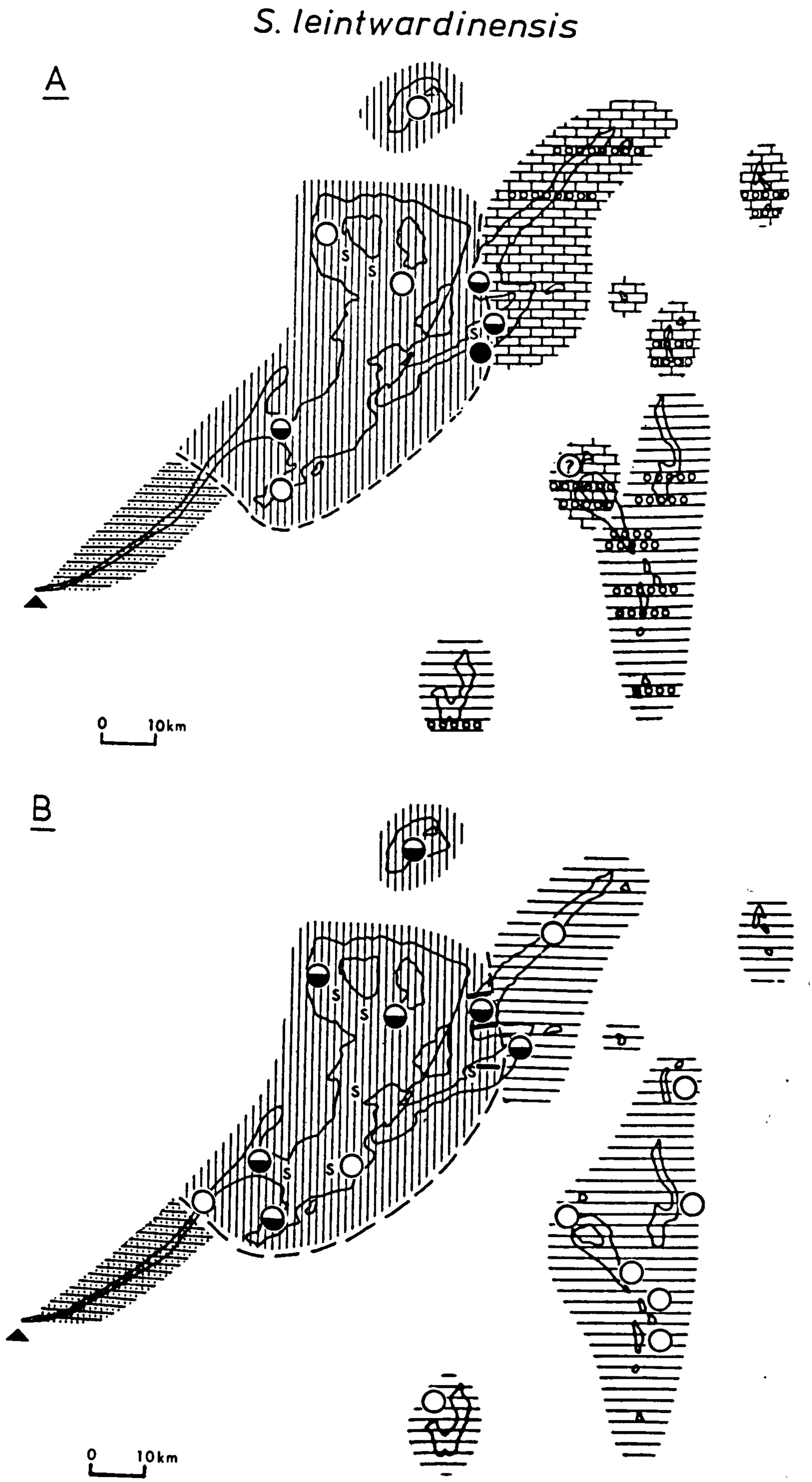


Fig. 5.6 : S. leintwardinensis

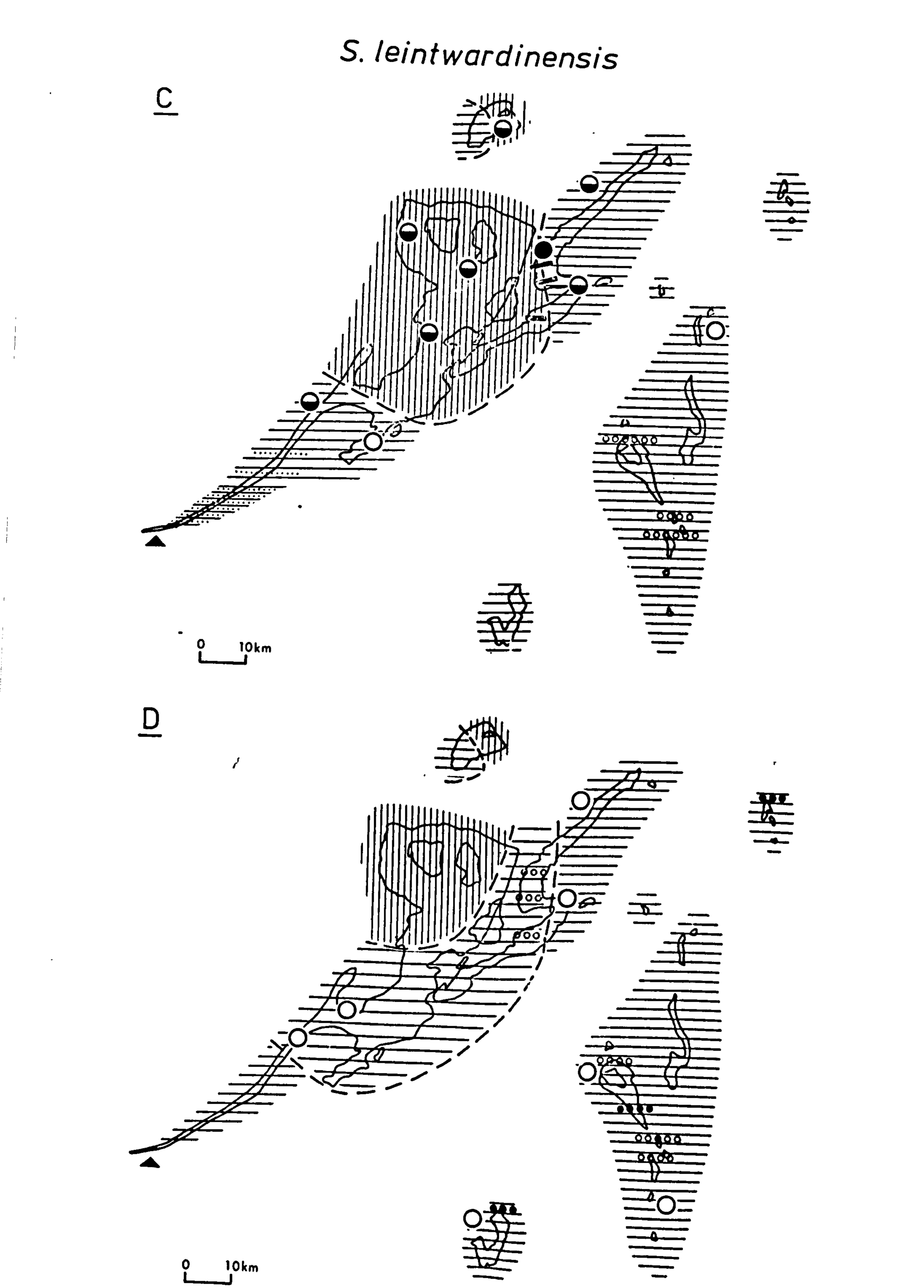


Fig. 5.6 : S. leintwardinensis

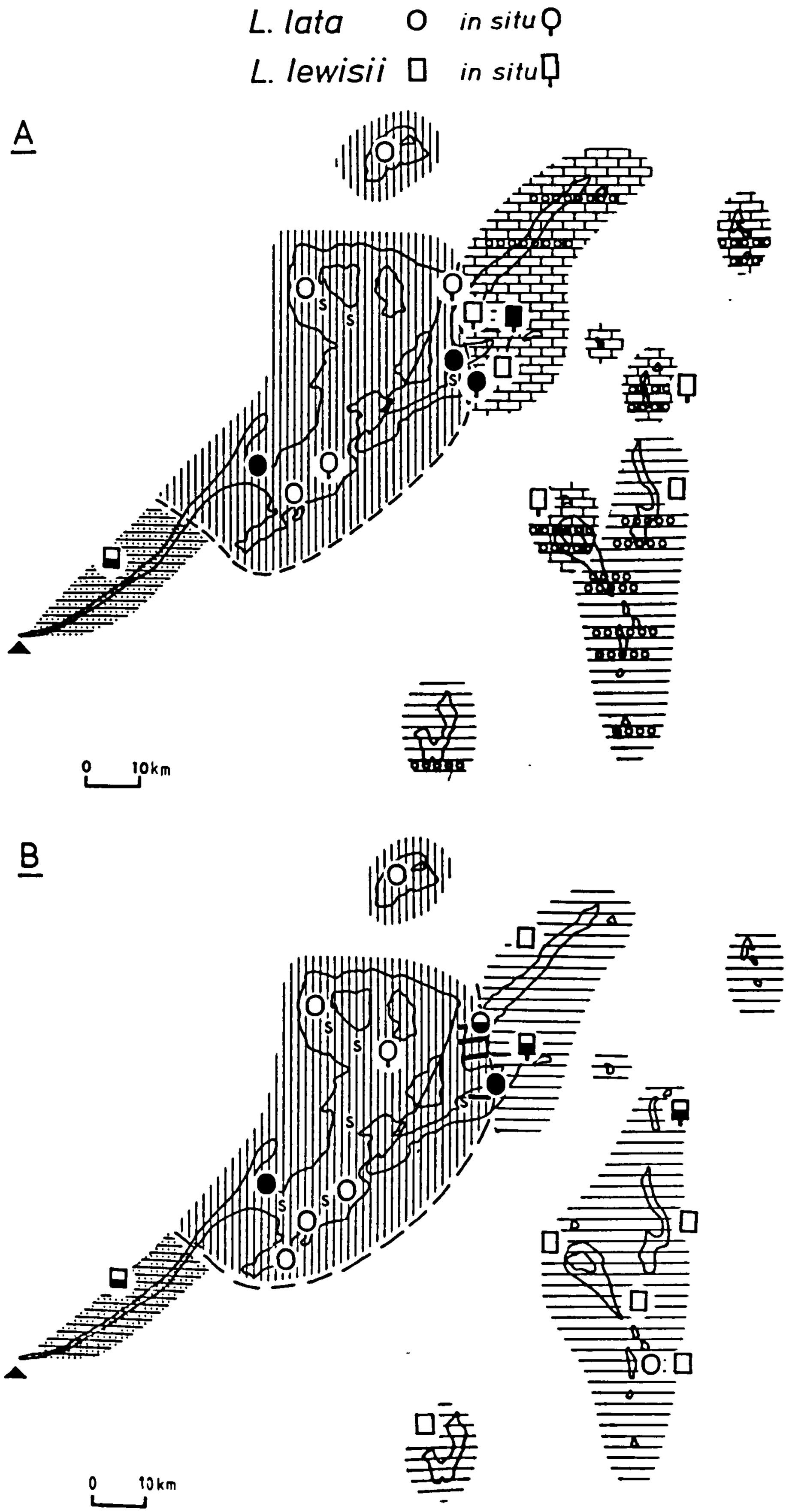


Fig. 5.8 : Lingula spp.

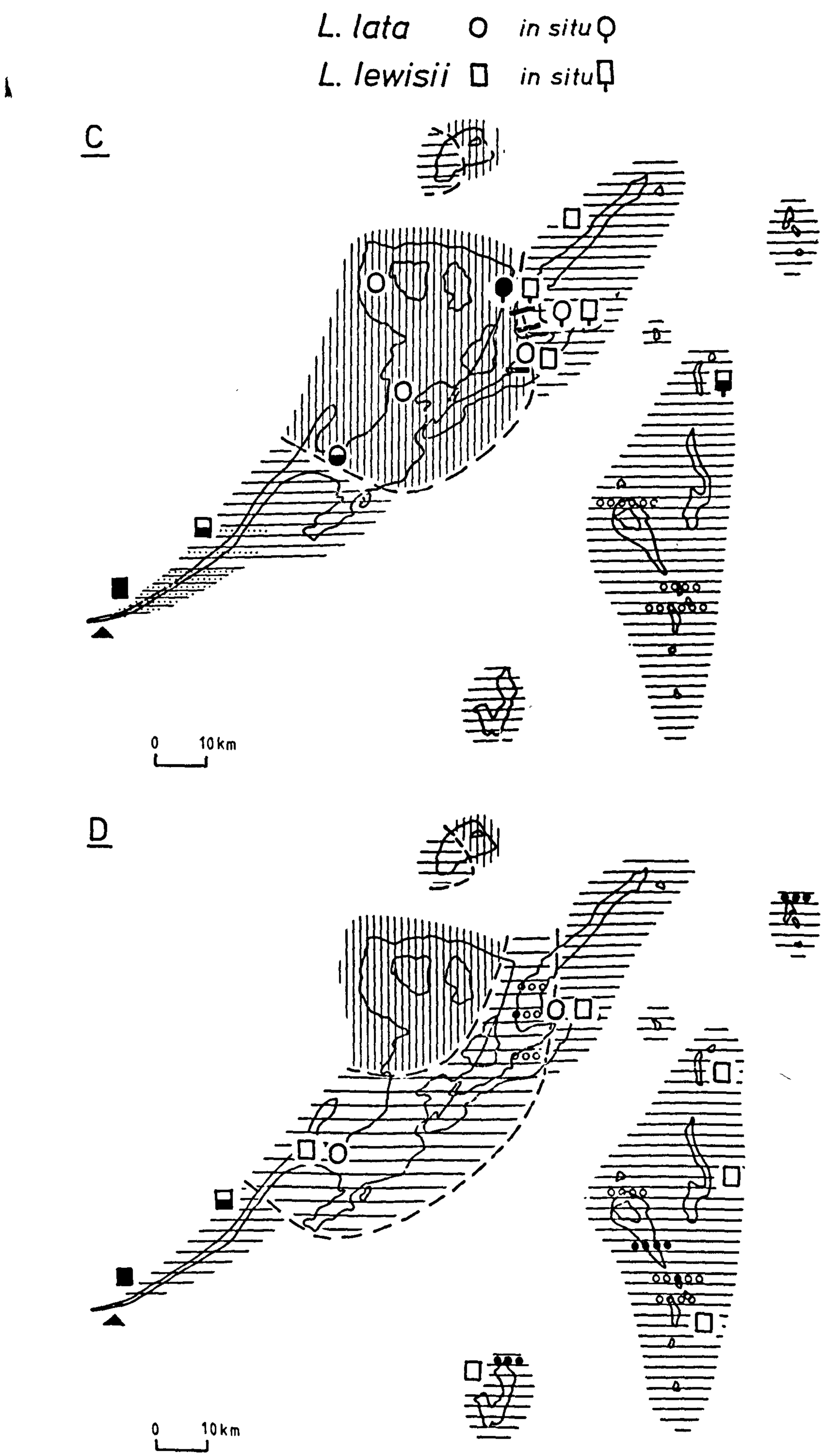


Fig. 5.8 : Lingula spp.

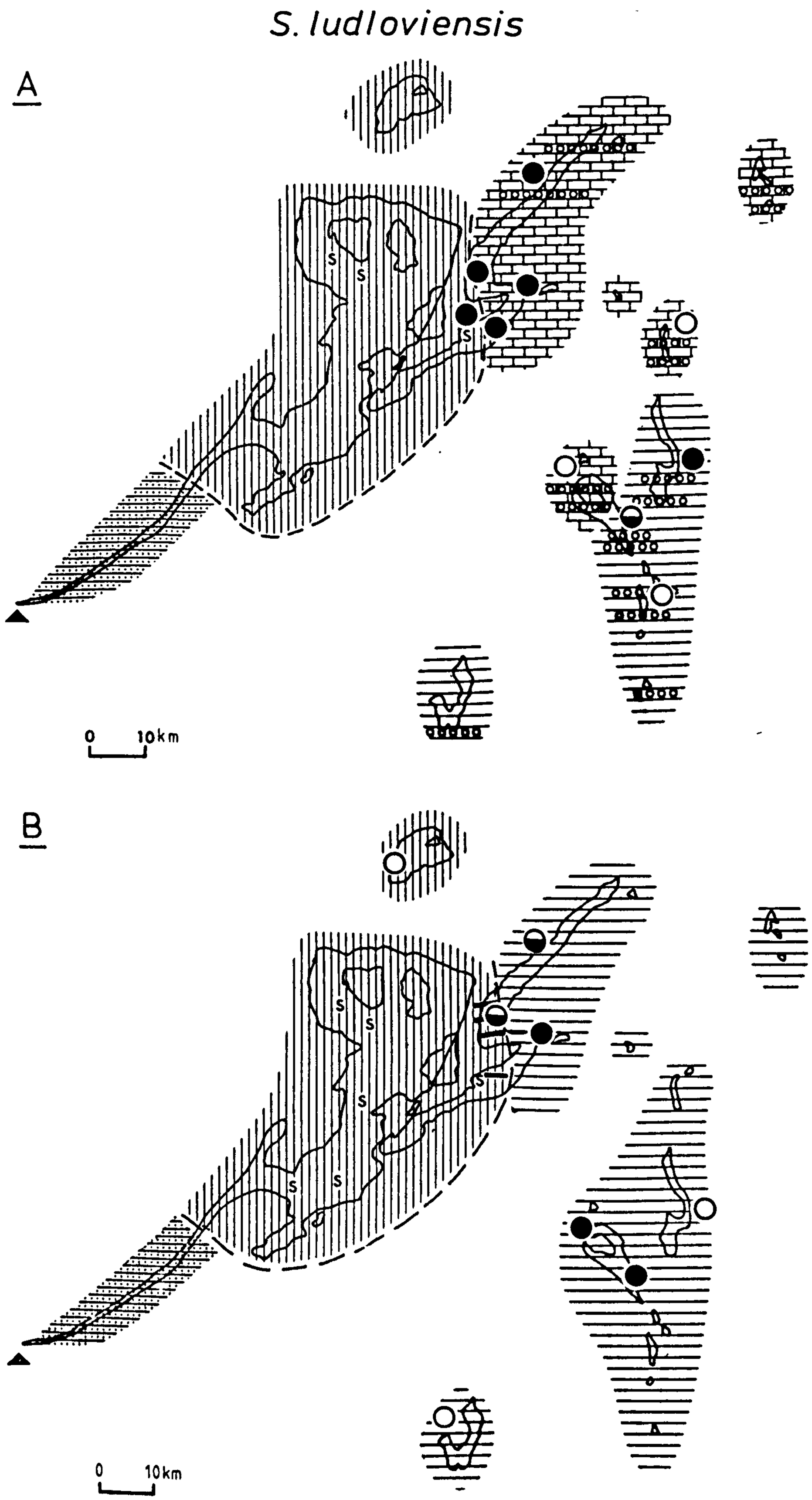


Fig. 5.10 : S. ludloviensis

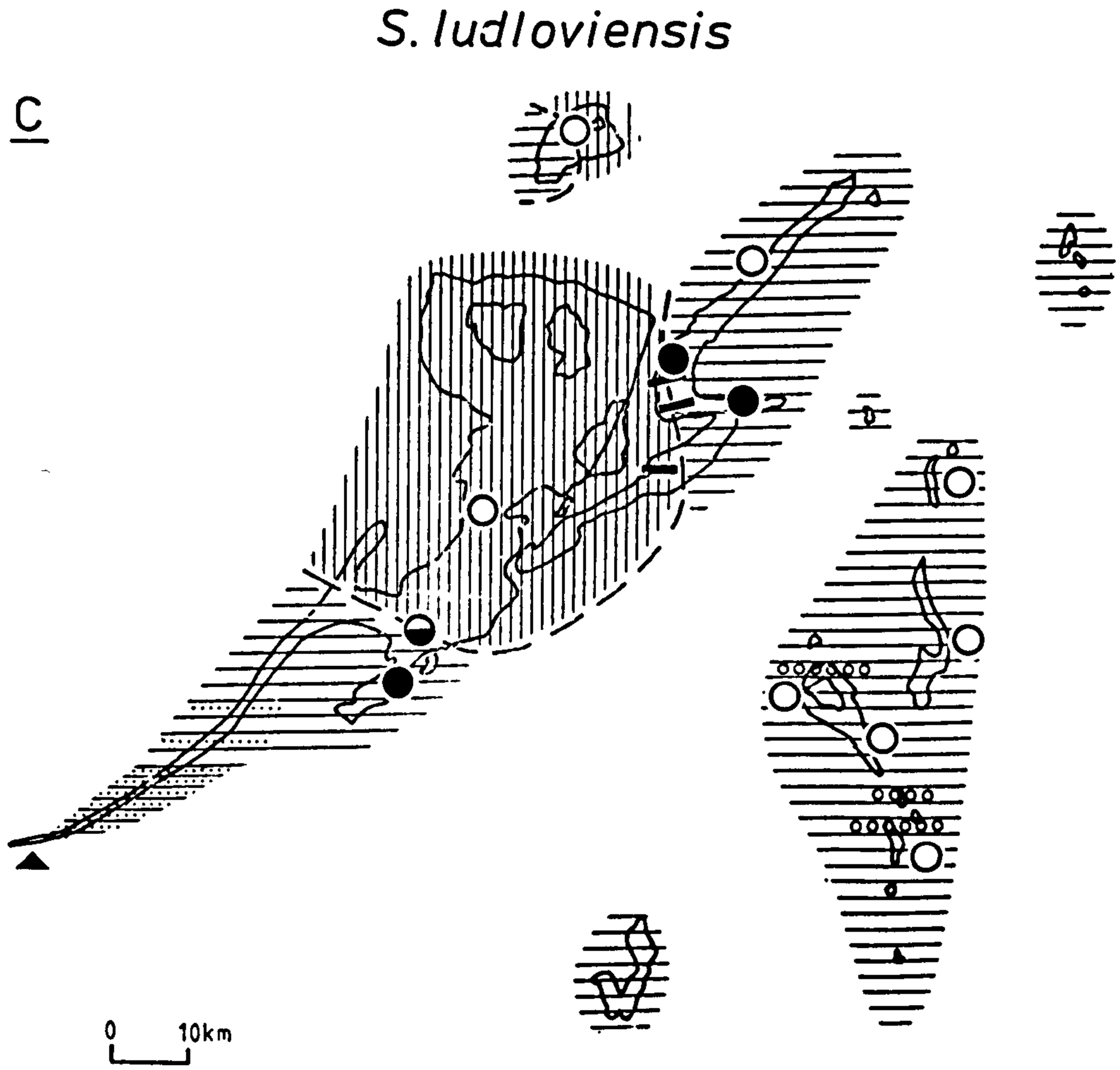
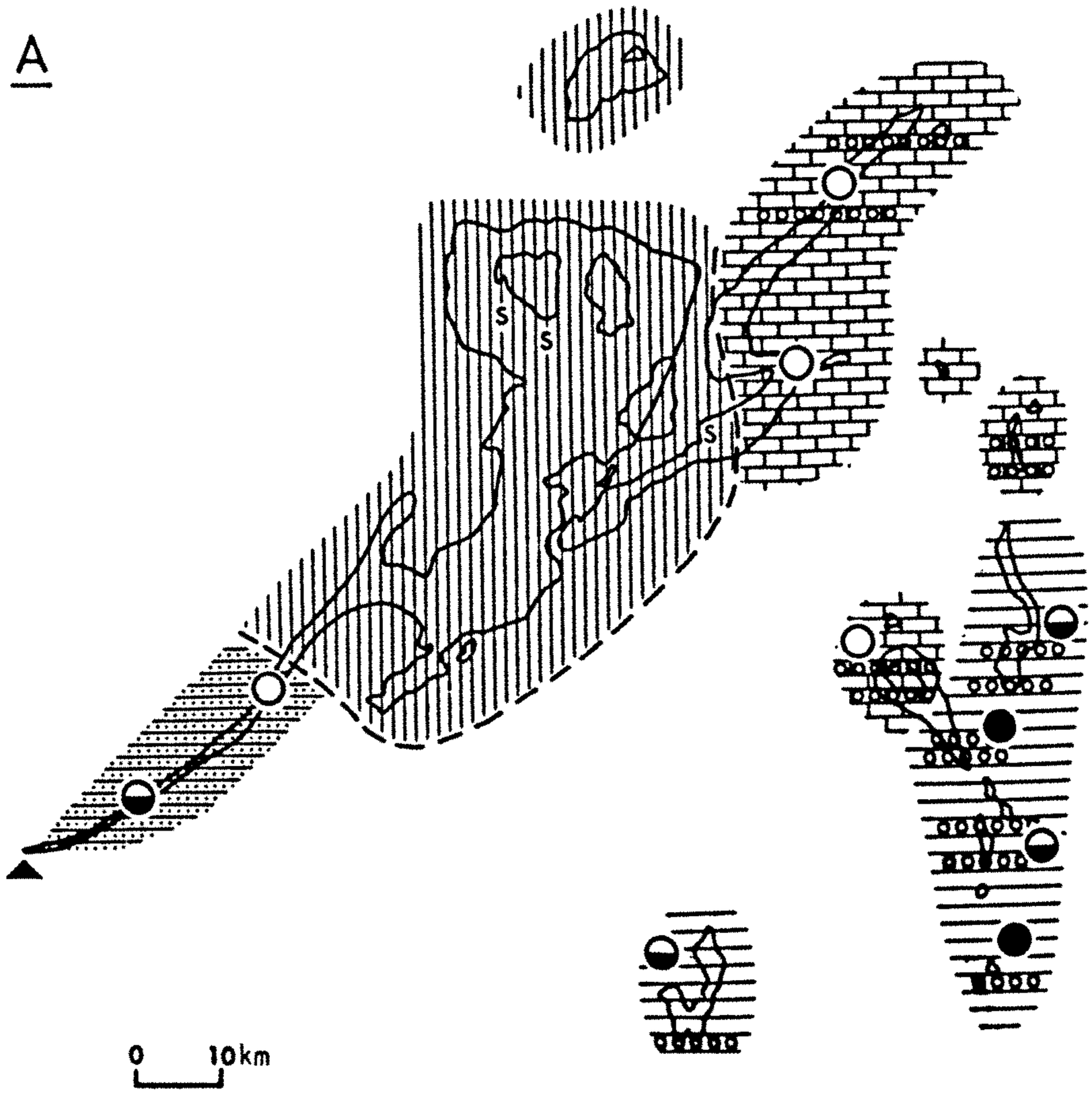


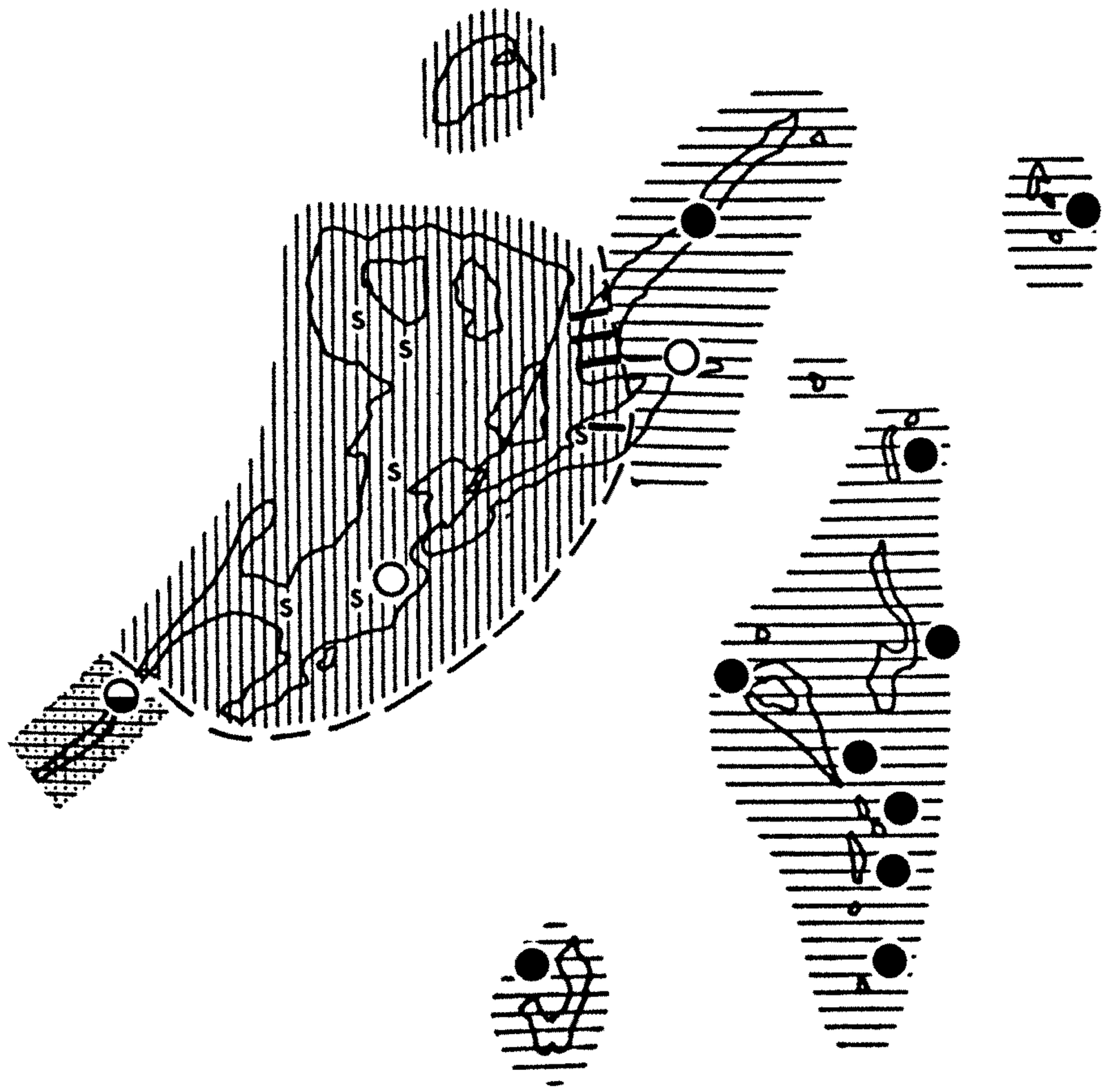
Fig. 5.10 : S. ludloviensis

P. ludloviensis

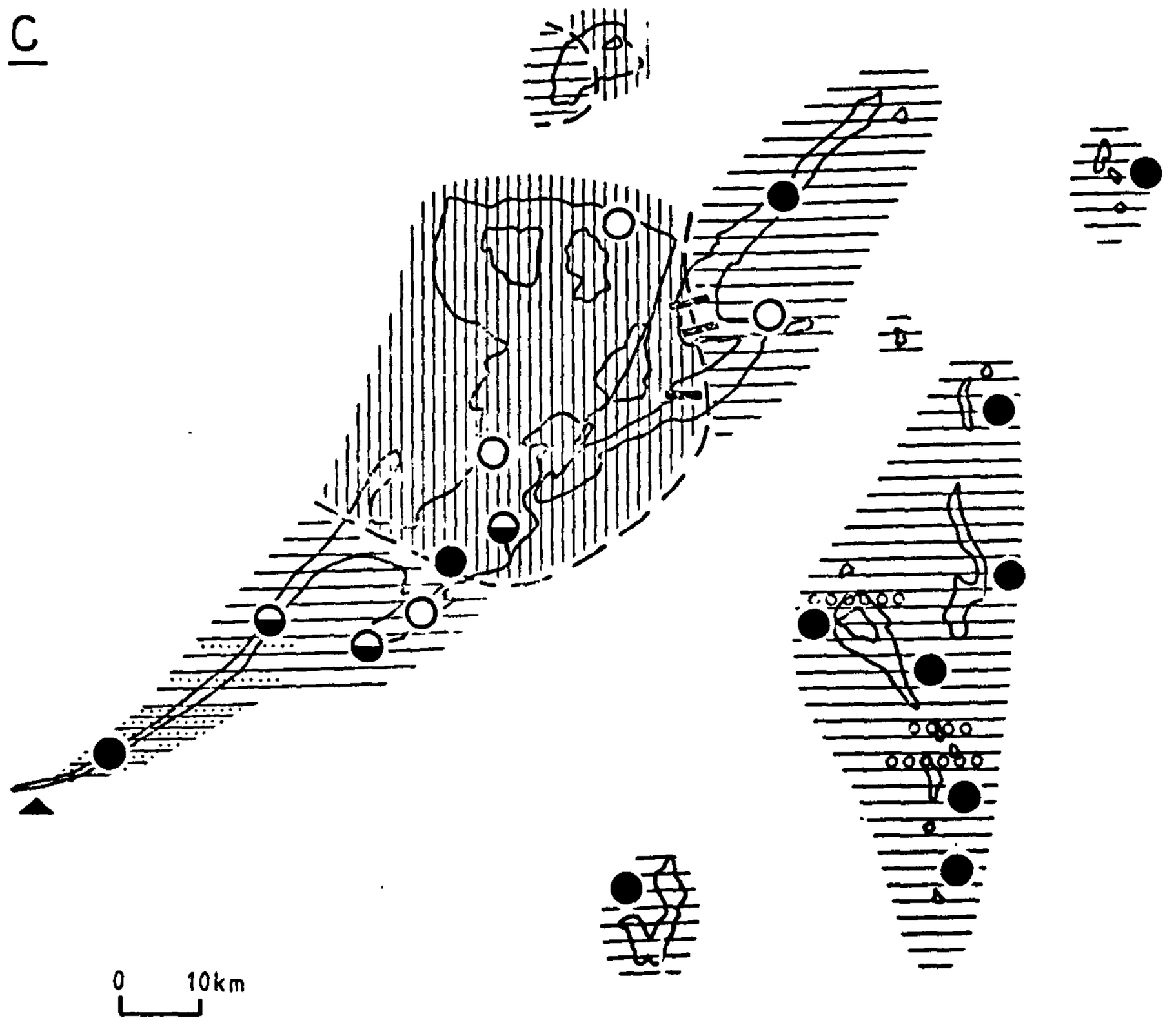
A



B



ludloviensis



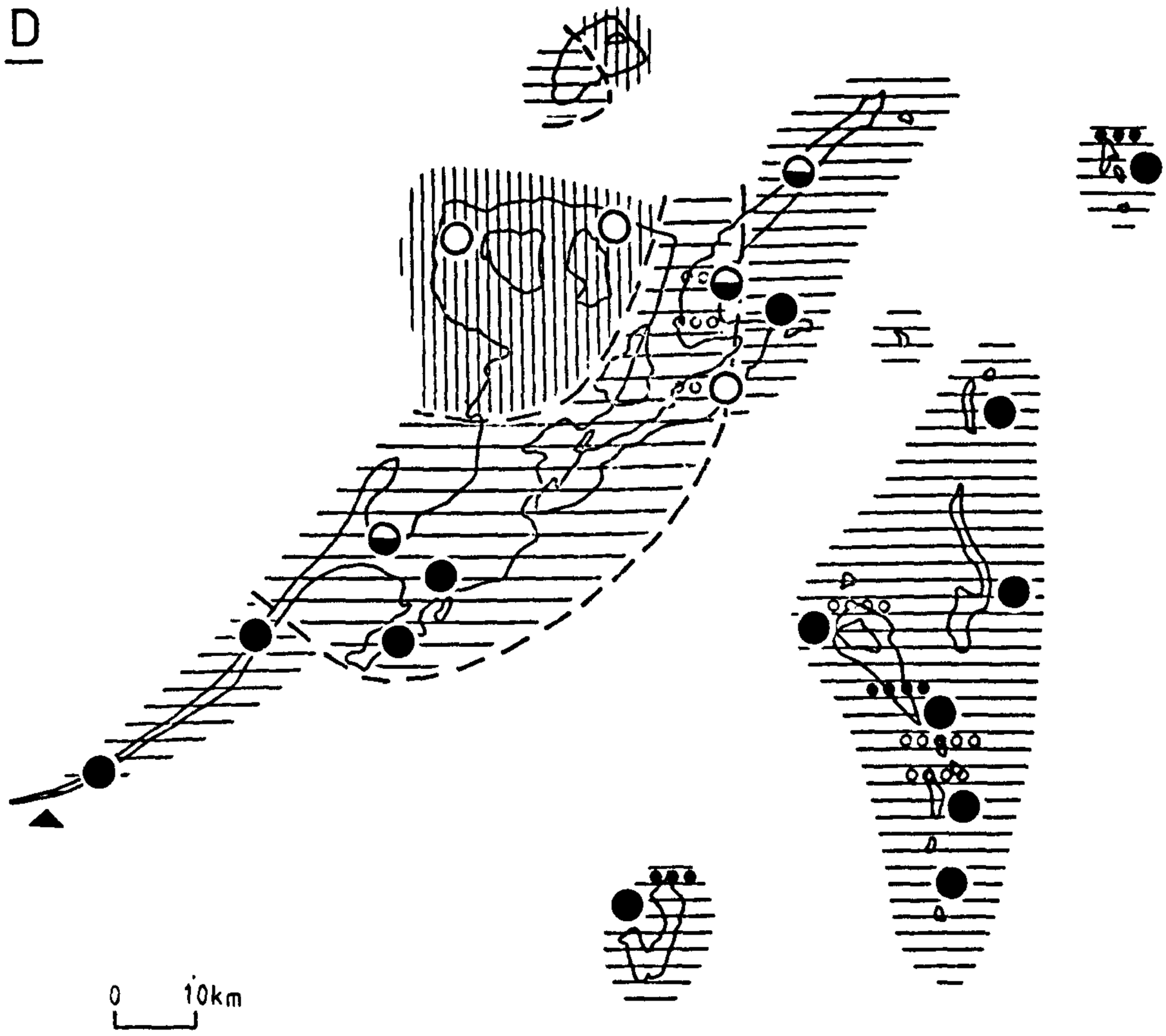
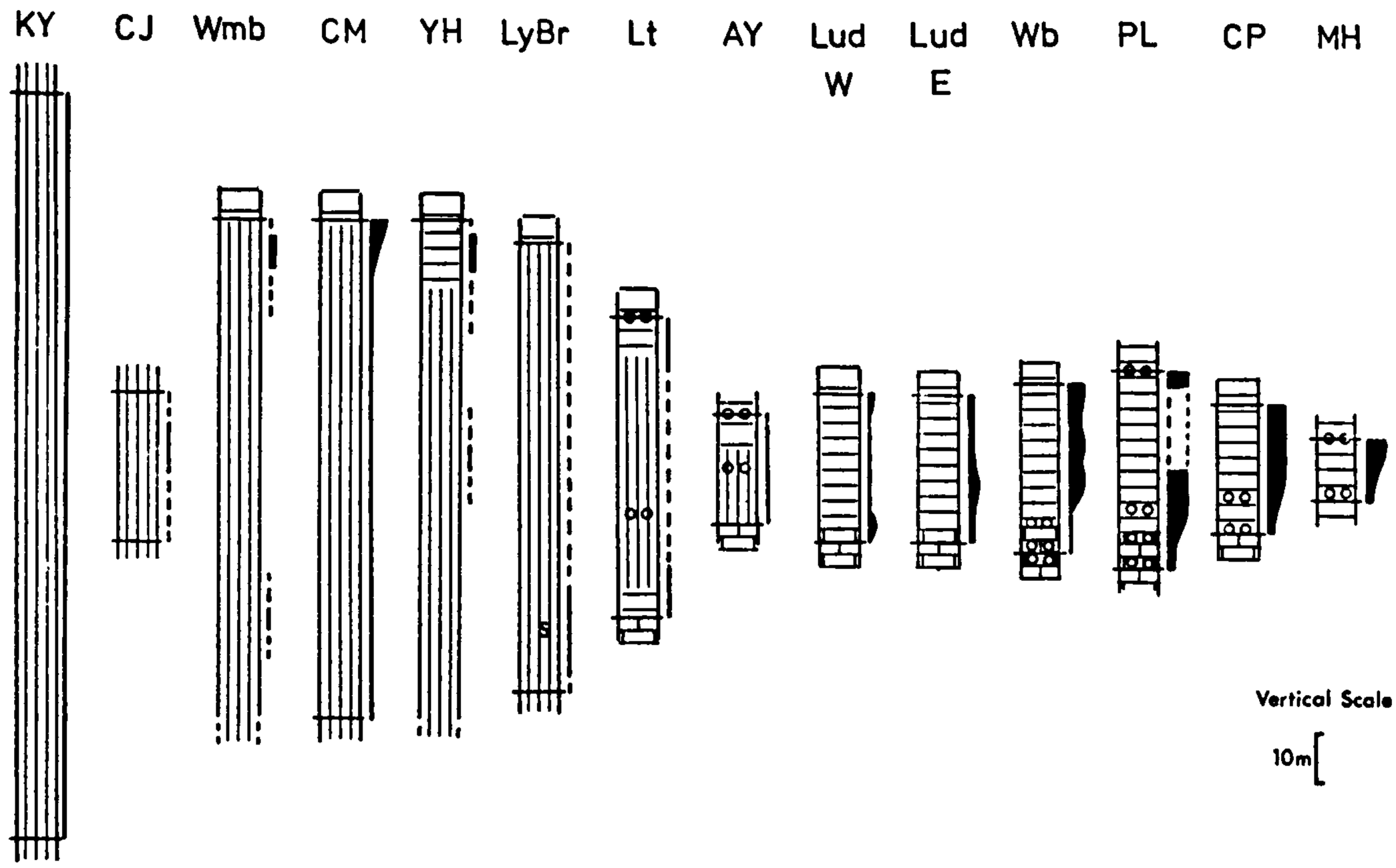


Fig. 5.11 : P. ludloviensis

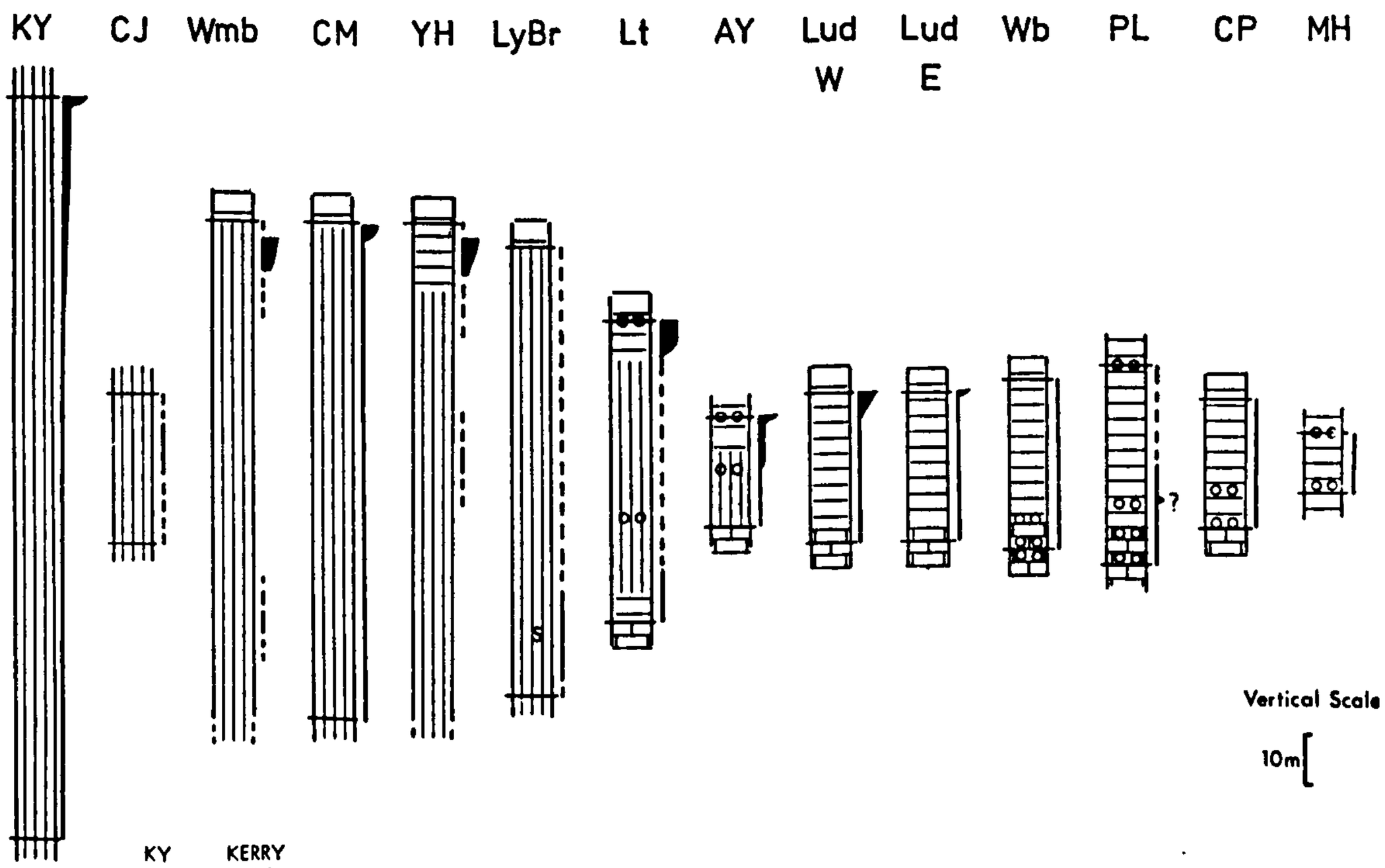
P. ludloviensis

Fig. 5.12



A. grayi

Fig. 5.13



KY	KERRY
CJ	Knighton
Wmb	Whimble
CM	Crickadarn Mill
YH	Ysgwydd Hwch
LyBr	Lyepole Bridge
Lt	LEINTWARDINE
AY	AYMESTREY
Lud	LUDLOW
Wb	WOODBURY
PL	PERTON
CP	CHANCES PITCH
MH	MAY HILL

Fig. 5.12 : P. ludloviensis
Fig. 5.13 : A. grayi

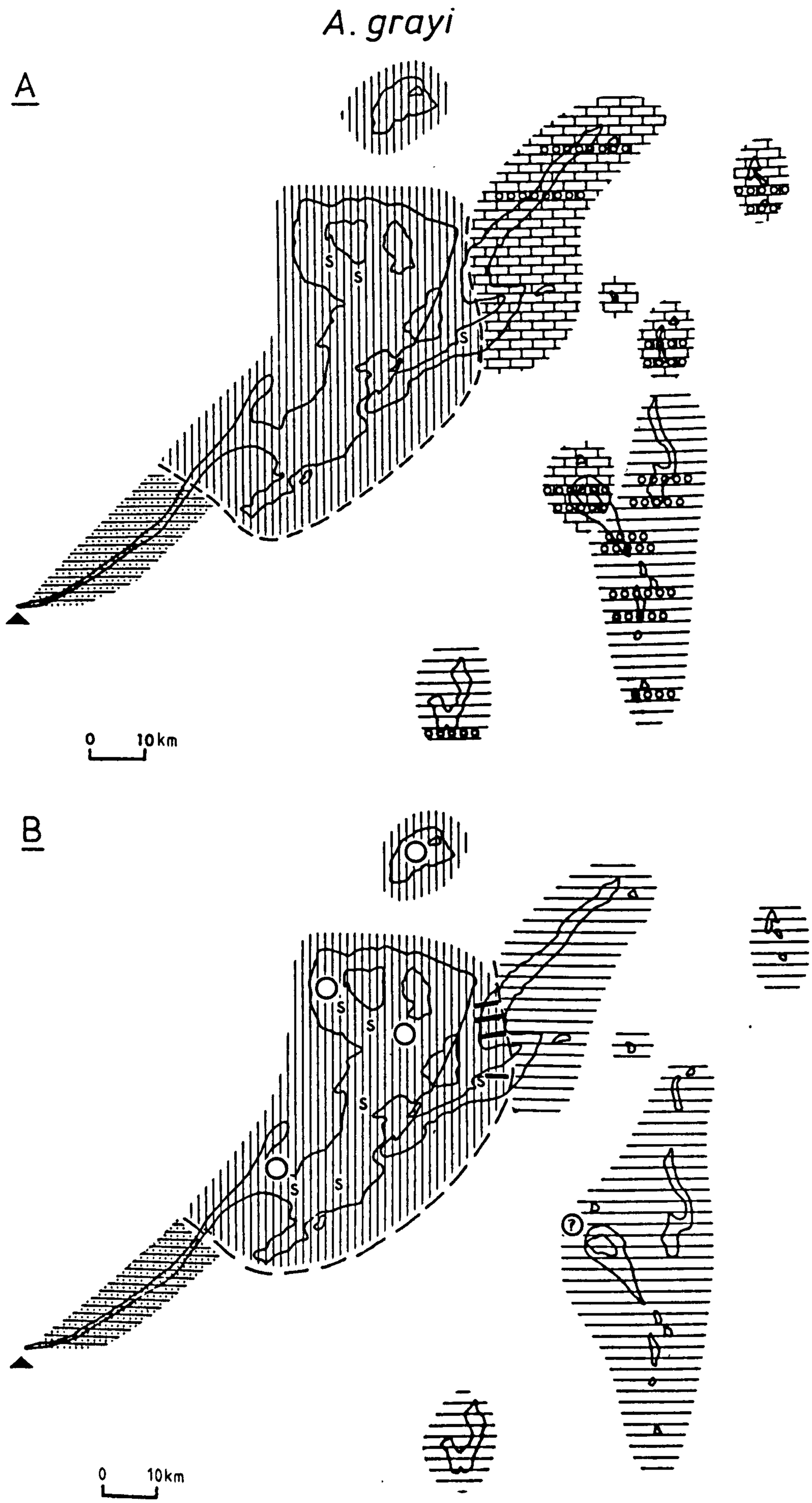


Fig. 5.14 : A. grayi

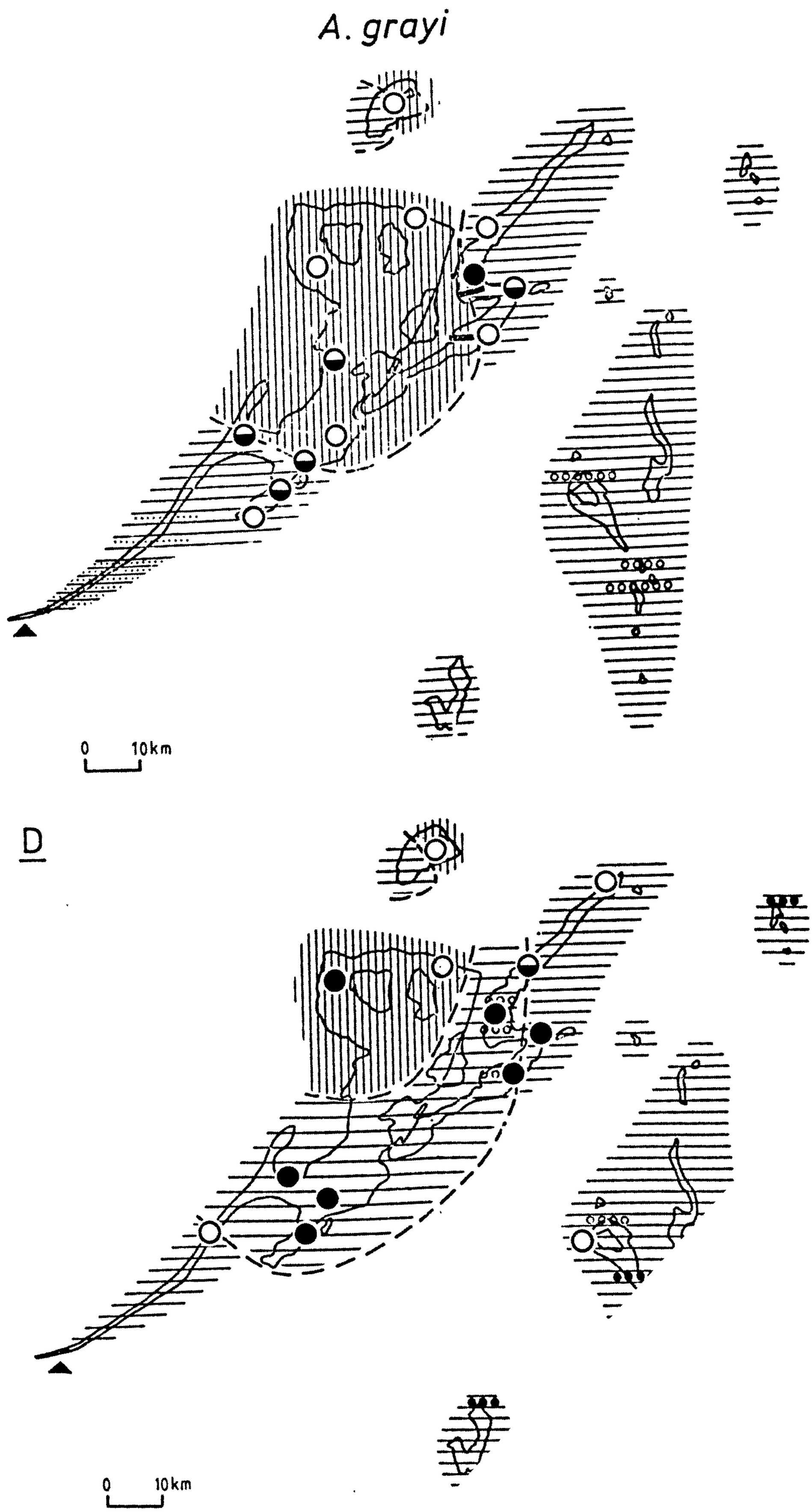


Fig. 5.14 : A. grayi

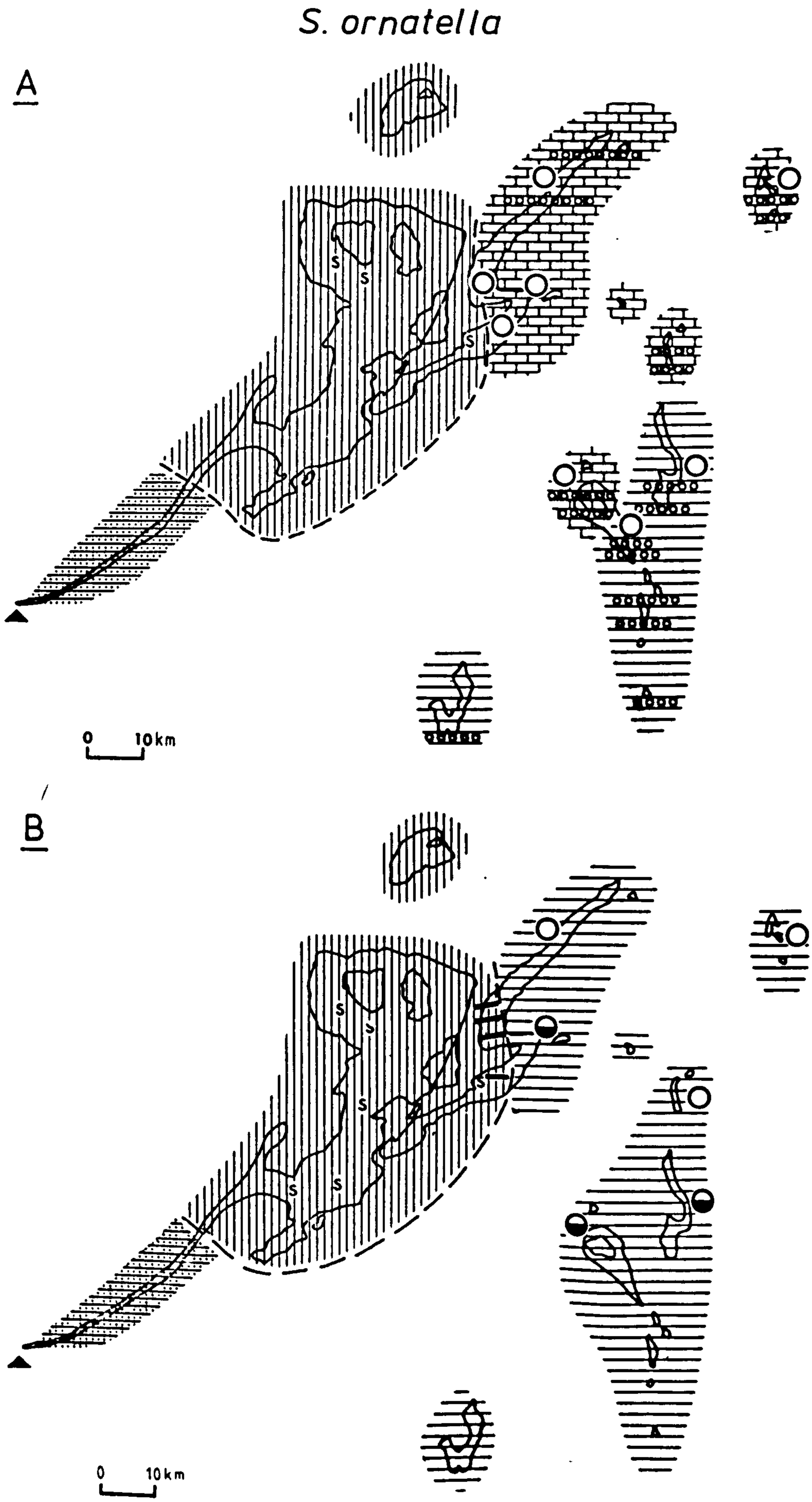


Fig. 5.15 : S. ornatella

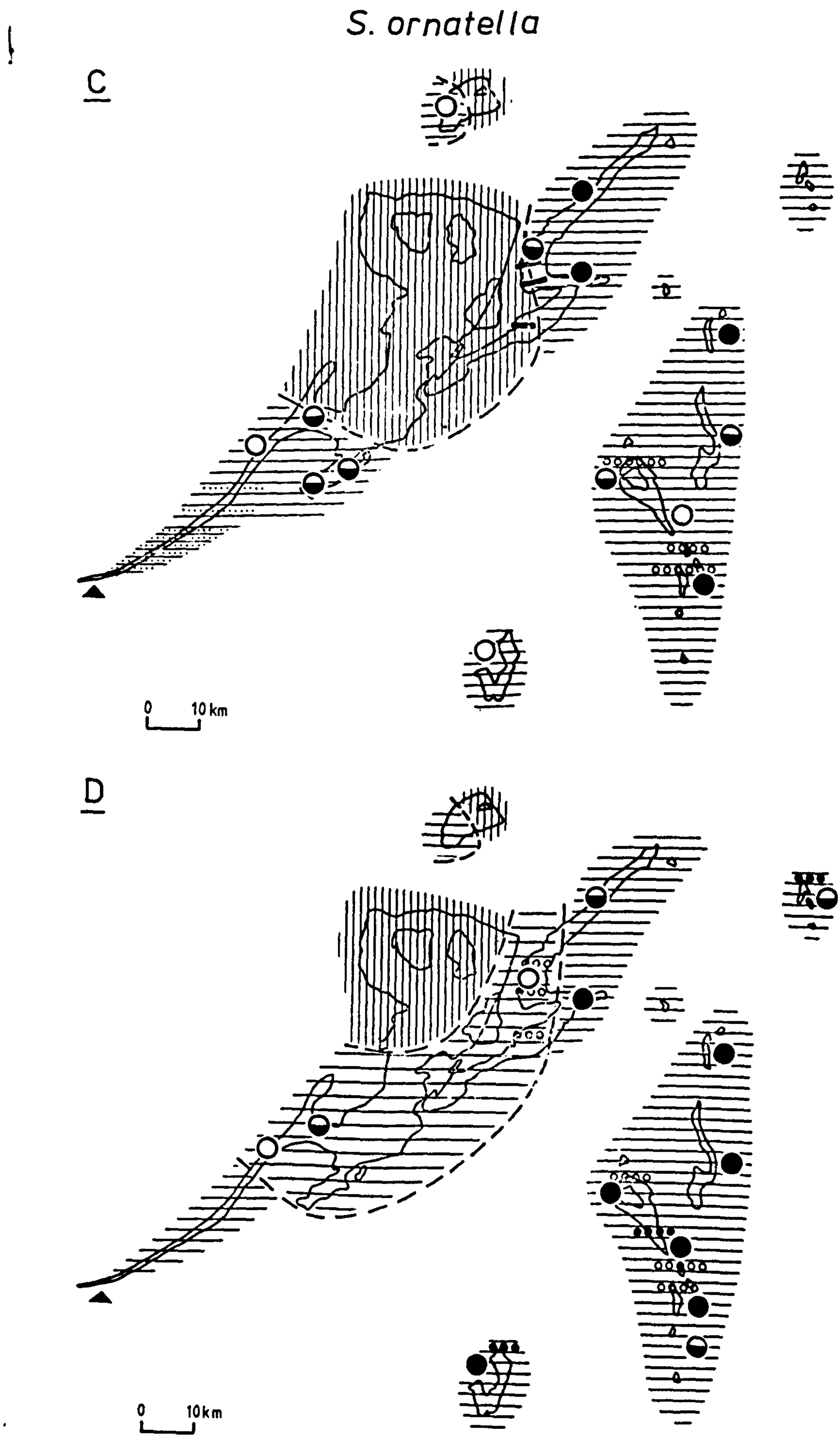
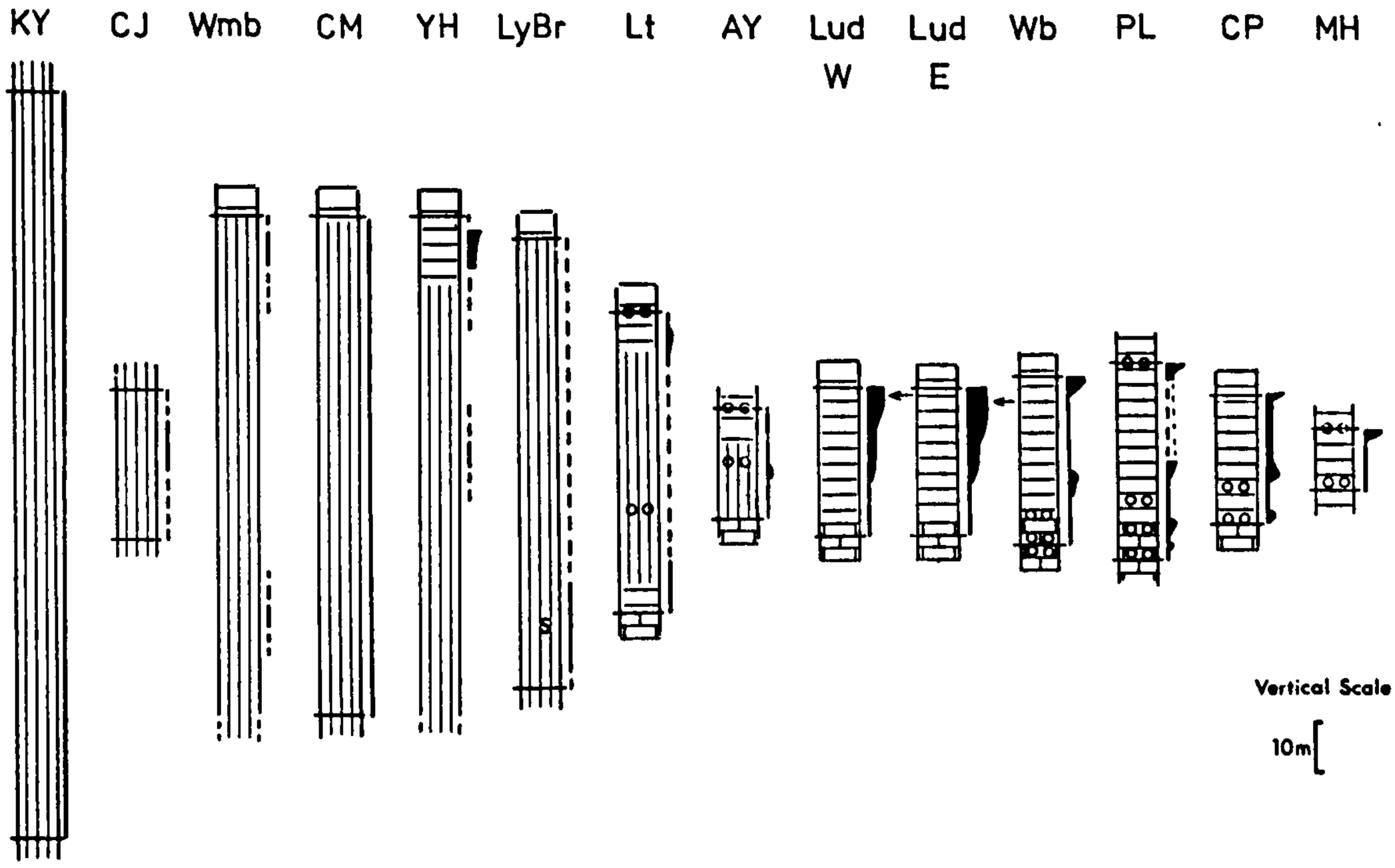
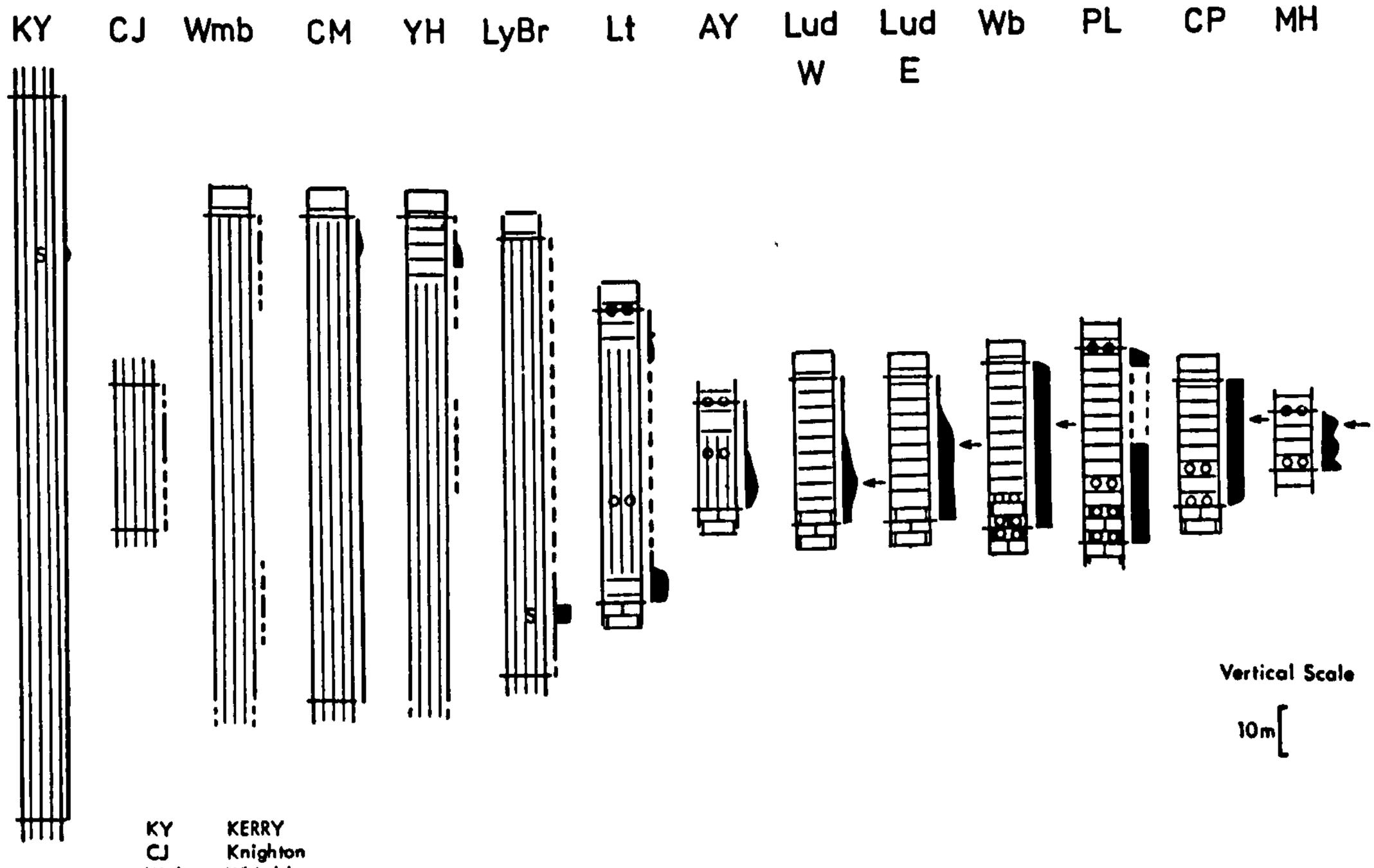


Fig. 5.15 : S. ornatella

S. ornatella Fig. 5.16



S. wilsoni Fig. 5.17



KY	KERRY
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Lud	LUDLOW
Wb	WOODBURY
PL	PERTON
CP	CHANCES PITCH
MH	MAY HILL

Fig. 5.16 : S. ornatella
Fig. 5.17 : S. wilsoni

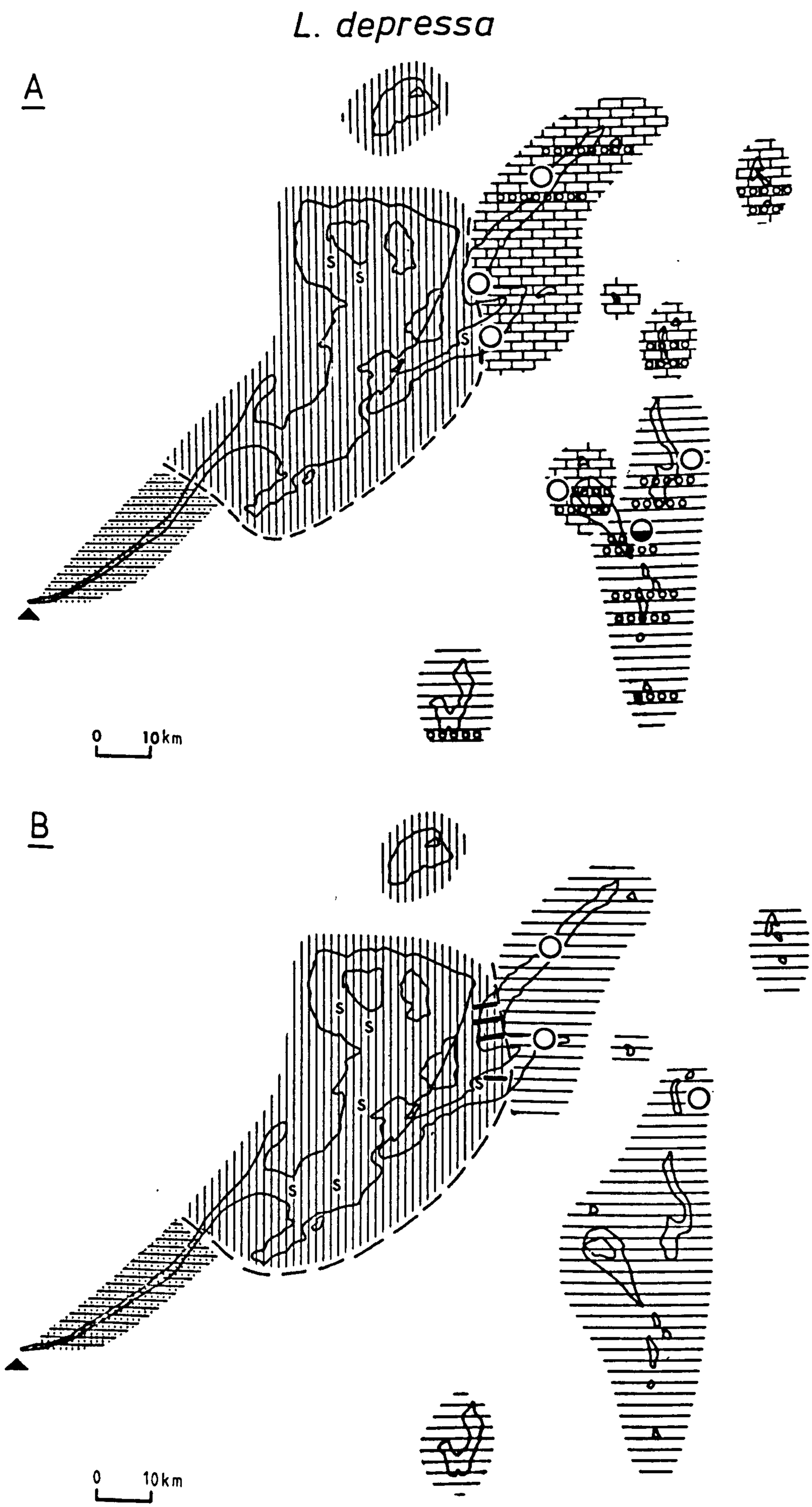


Fig. 5.18 : L. depressa

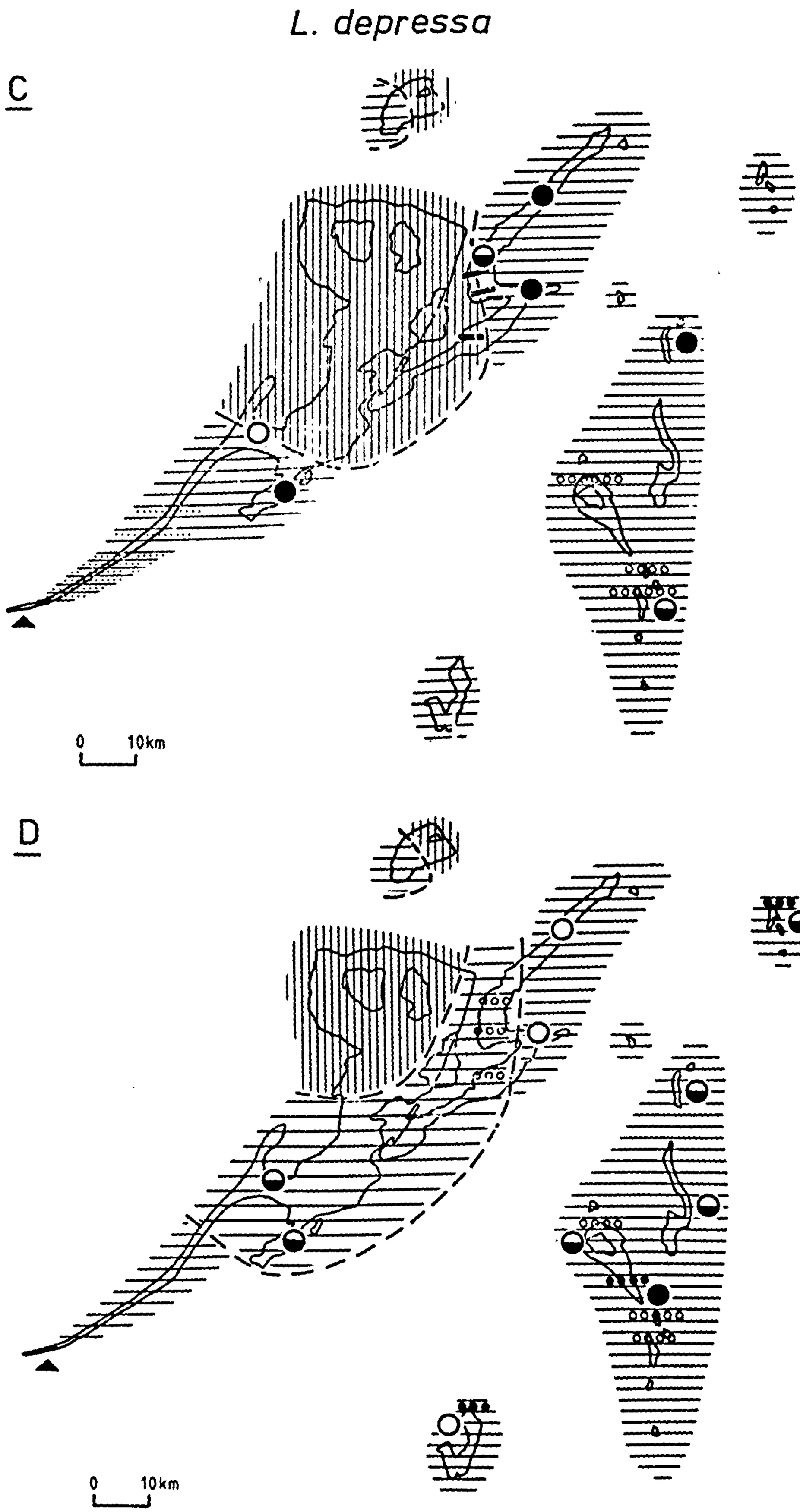
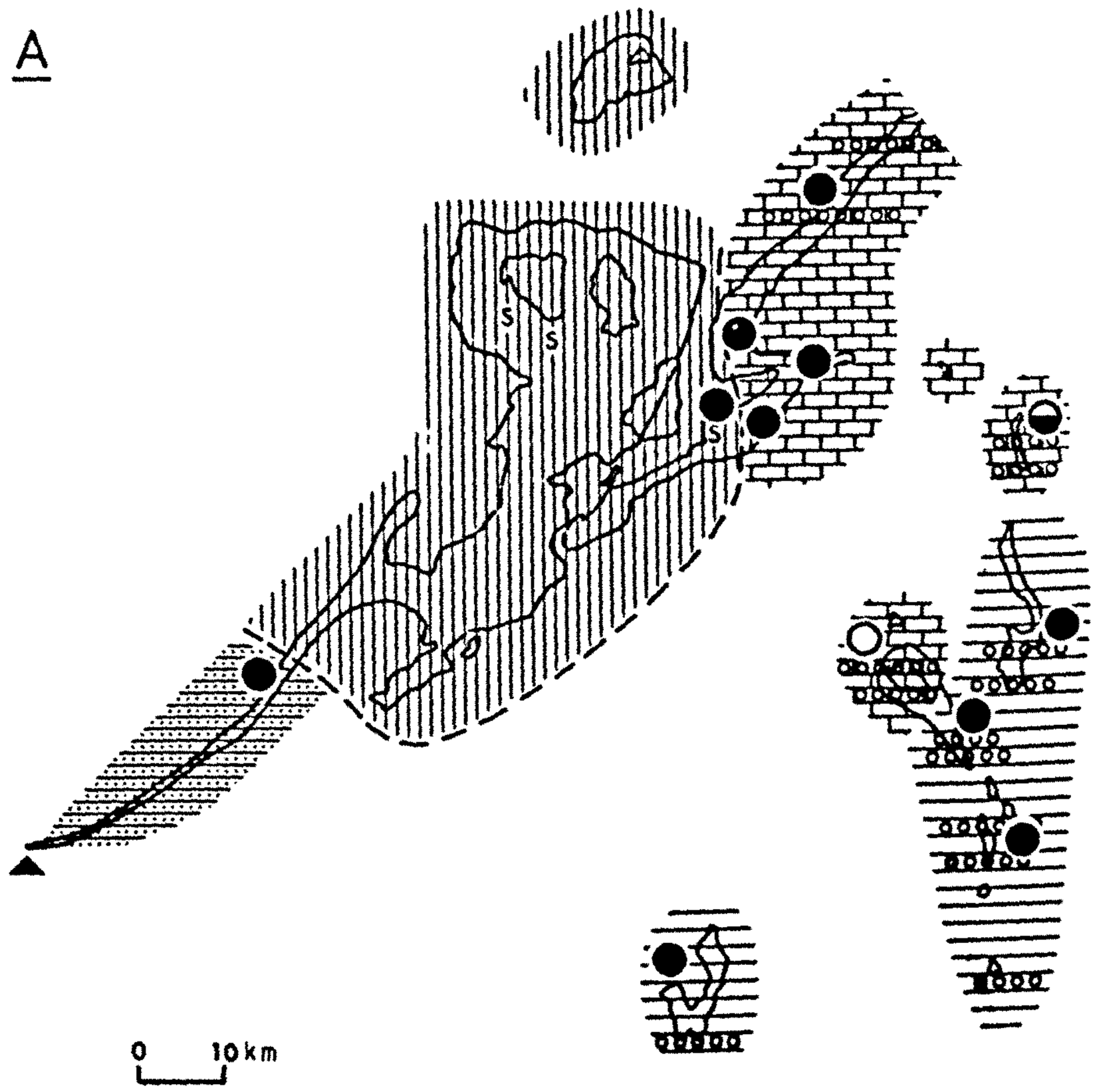


Fig. 18 : L. depressa

I. orbicularis

A



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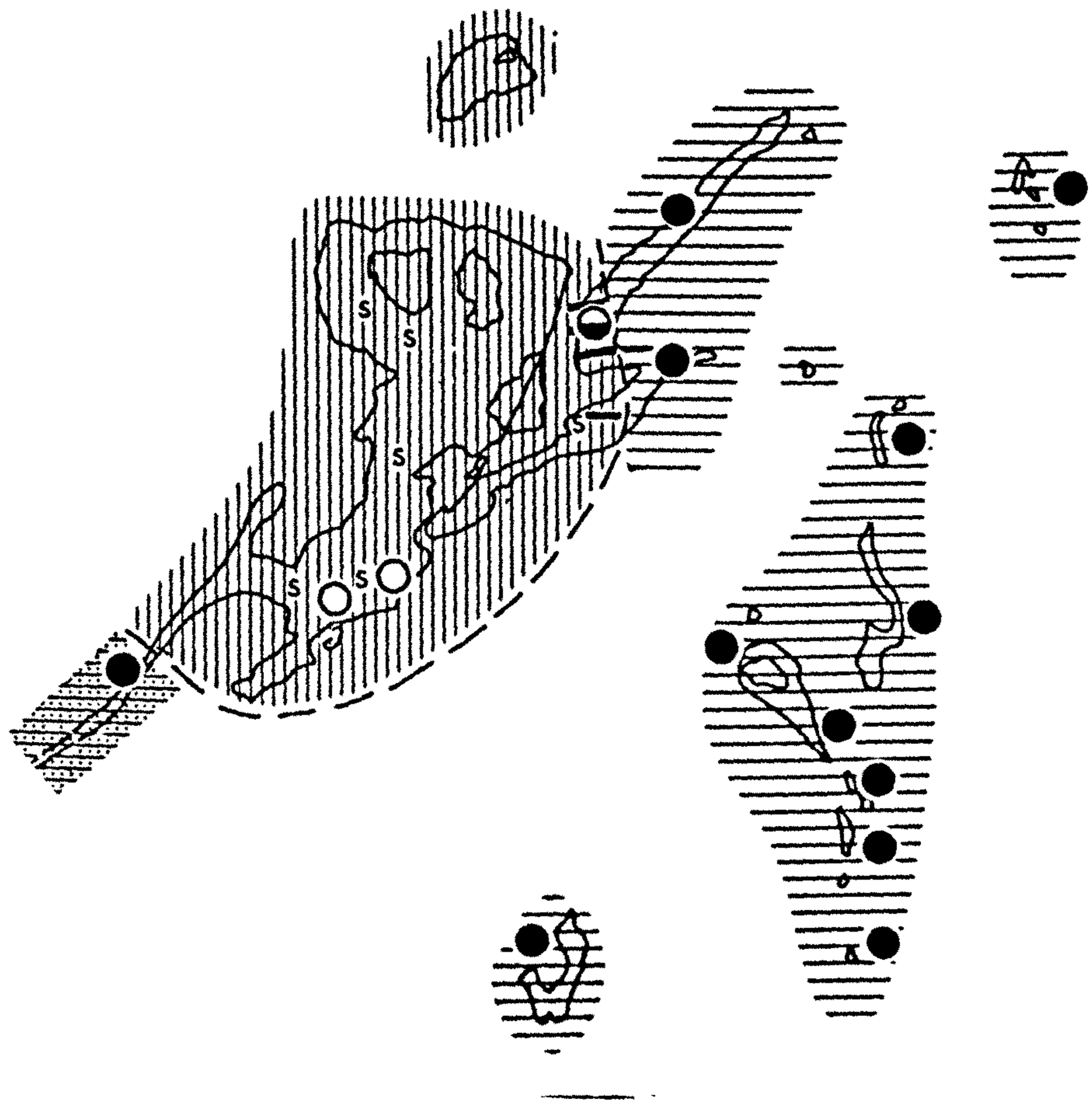


icularis

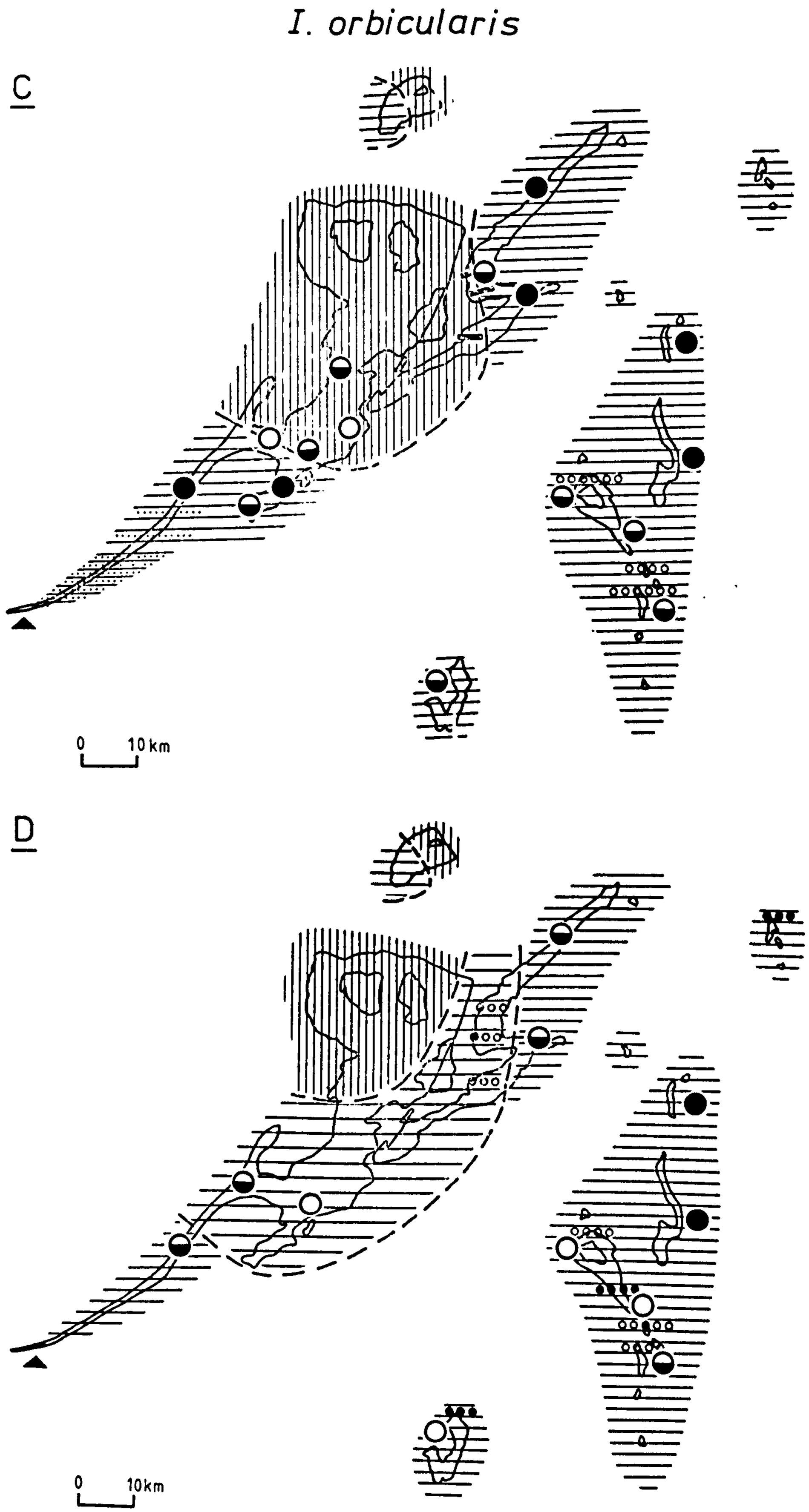
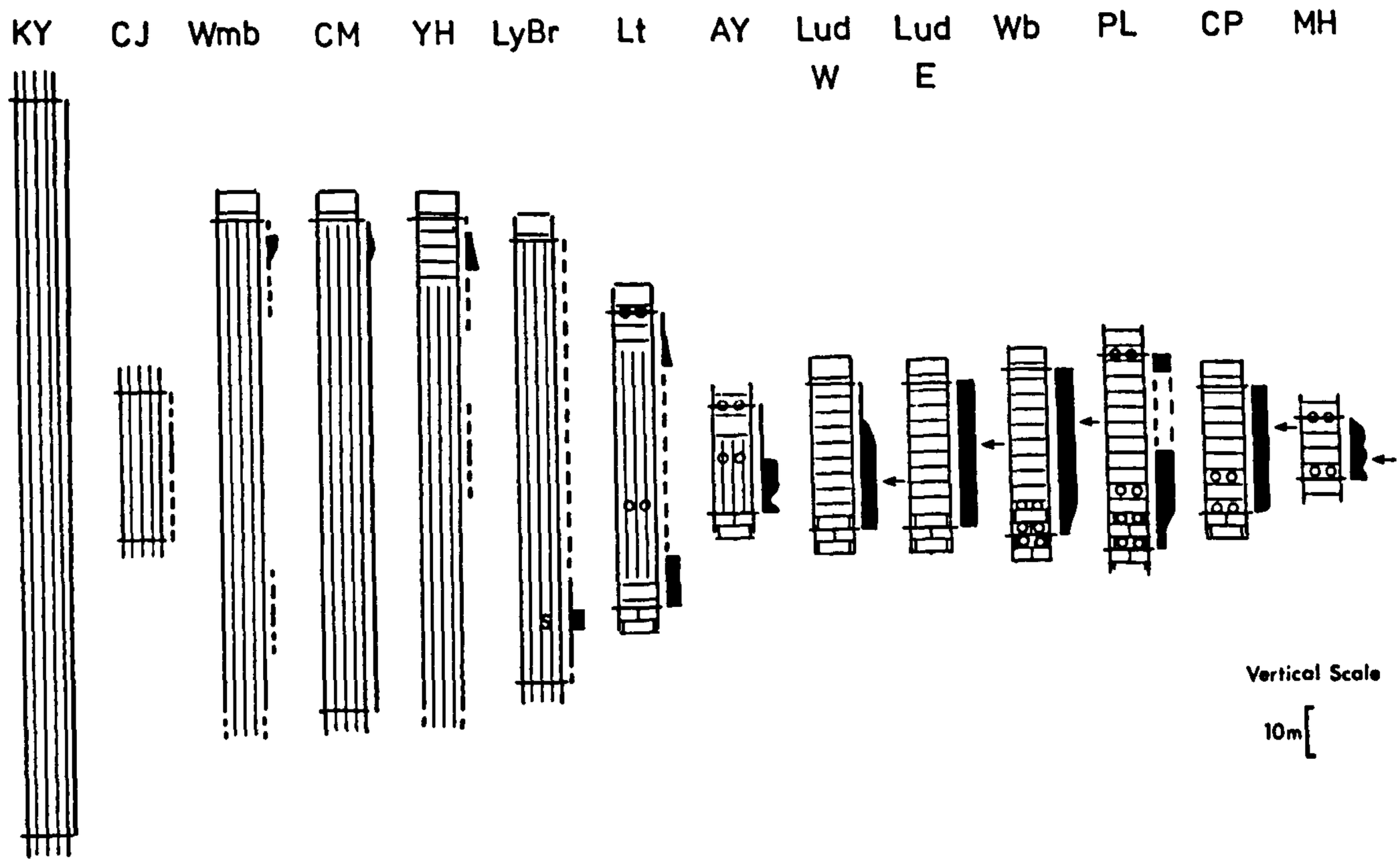
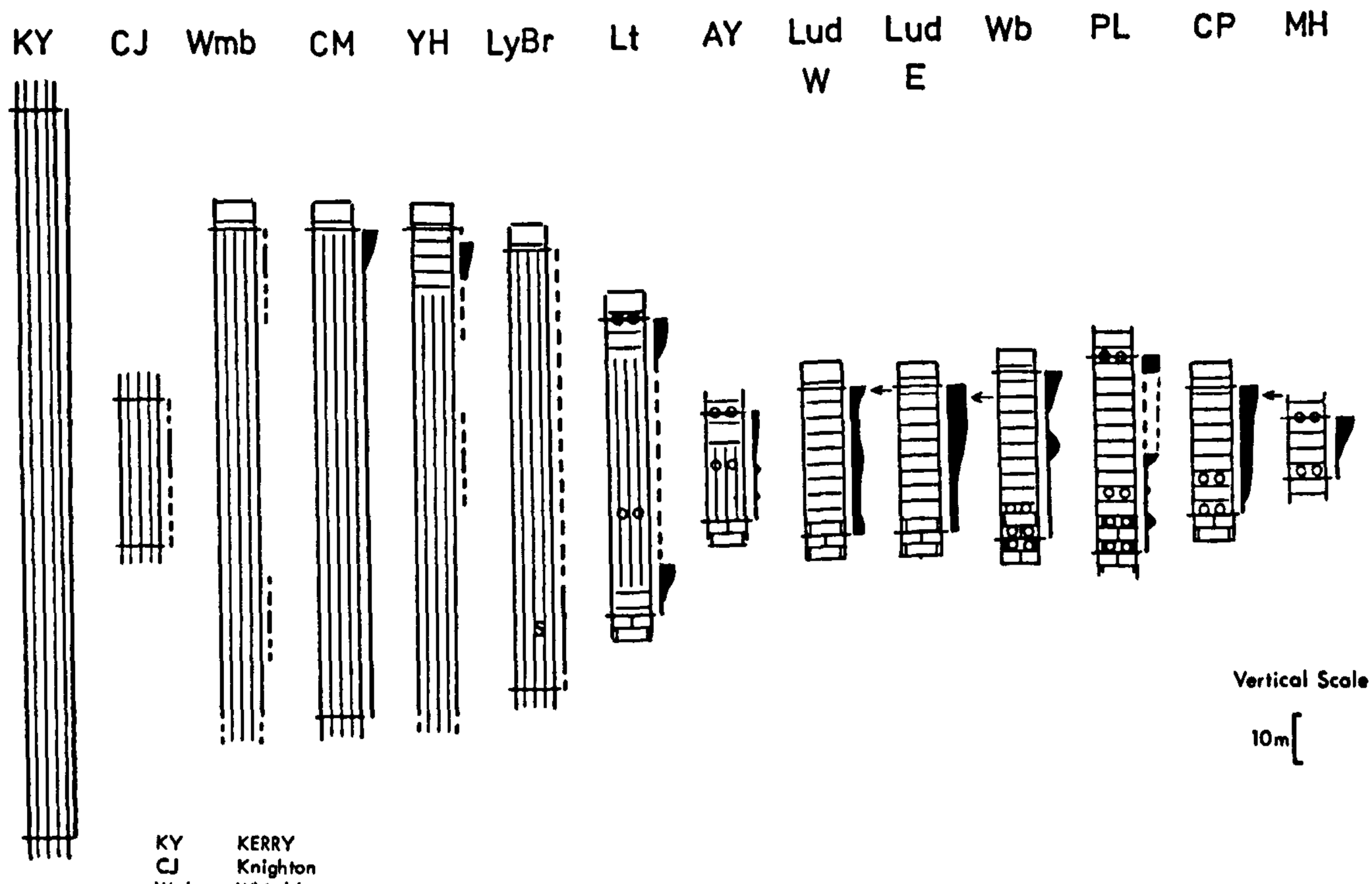


Fig. 5.19 : I. orbicularis

I. orbicularis Fig. 5.20



S. lunata Fig. 5.21



KY	KERRY
CJ	Knighton
Wmb	Whimble
CM	Crickadarn Mill
YH	Ysgwydd Hwch
LyBr	Lyepole Bridge
Lt	LEINTWARDINE
AY	AYMESTREY
Lud	LUDLOW
Wb	WOODBURY
PL	PERTON
CP	CHANCES PITCH
MH	MAY HILL

Fig. 5.20 : I. orbicularis
Fig. 5.21 : S. lunata

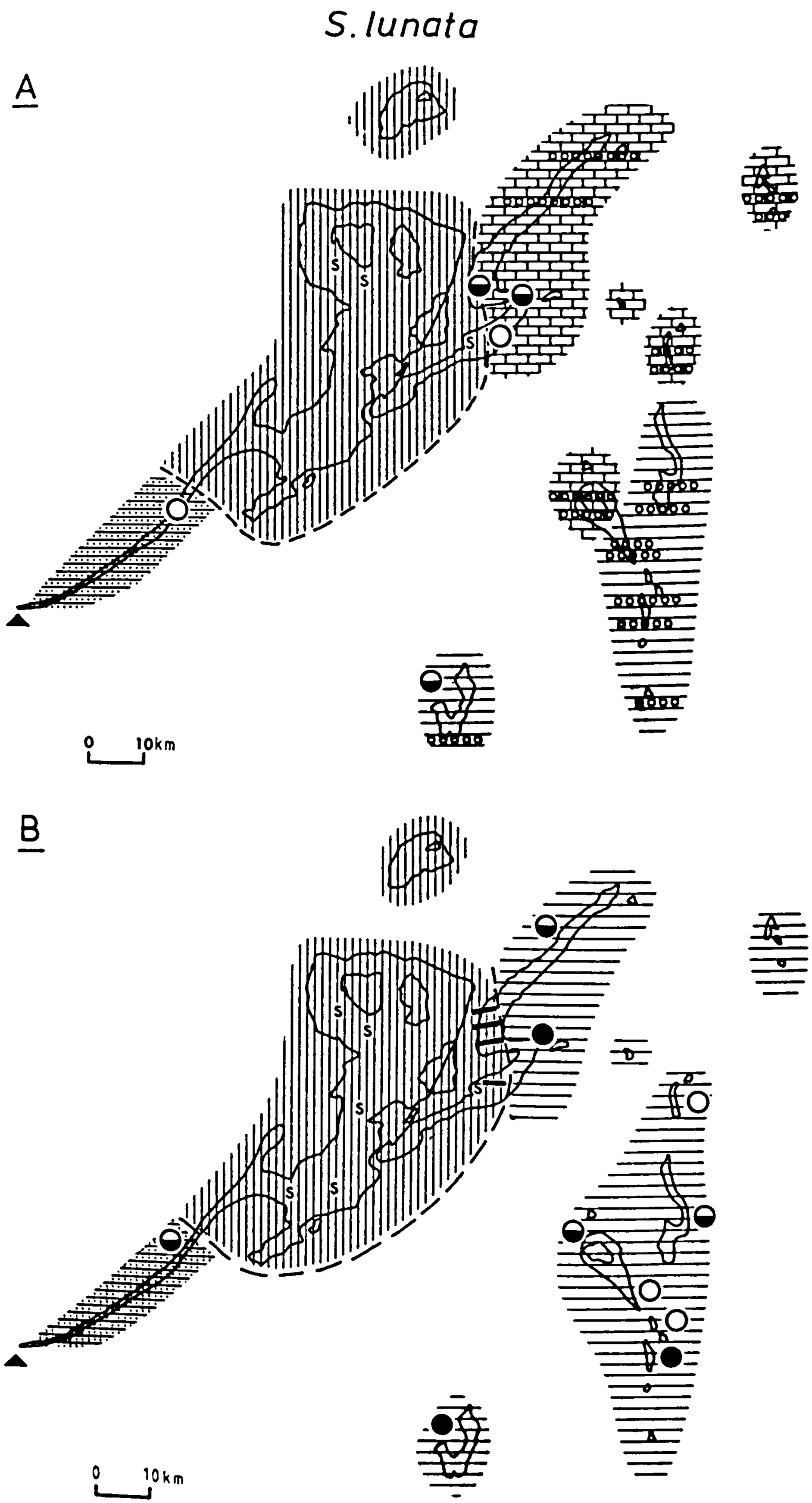
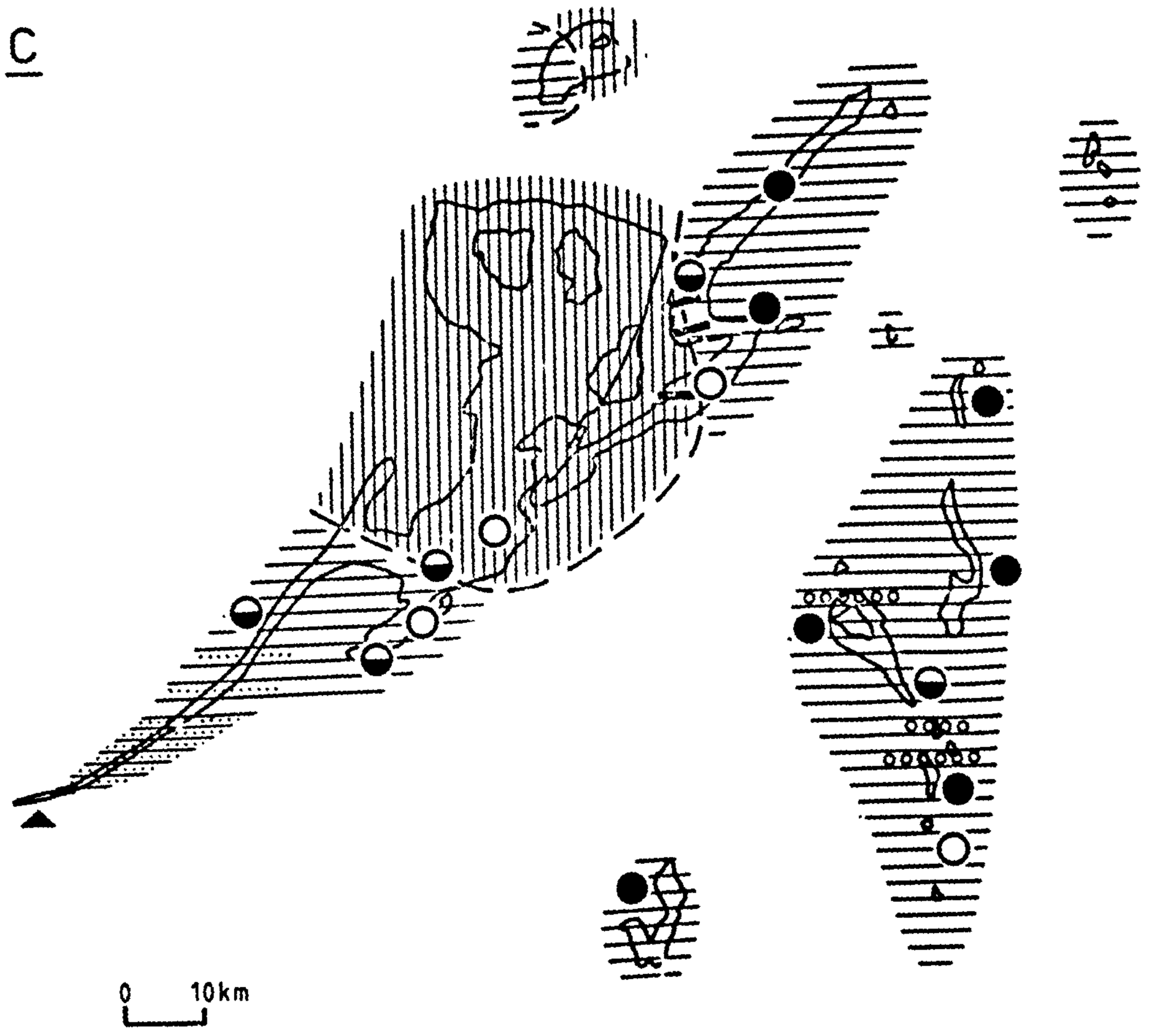


Fig. 5.22 : S. lunata



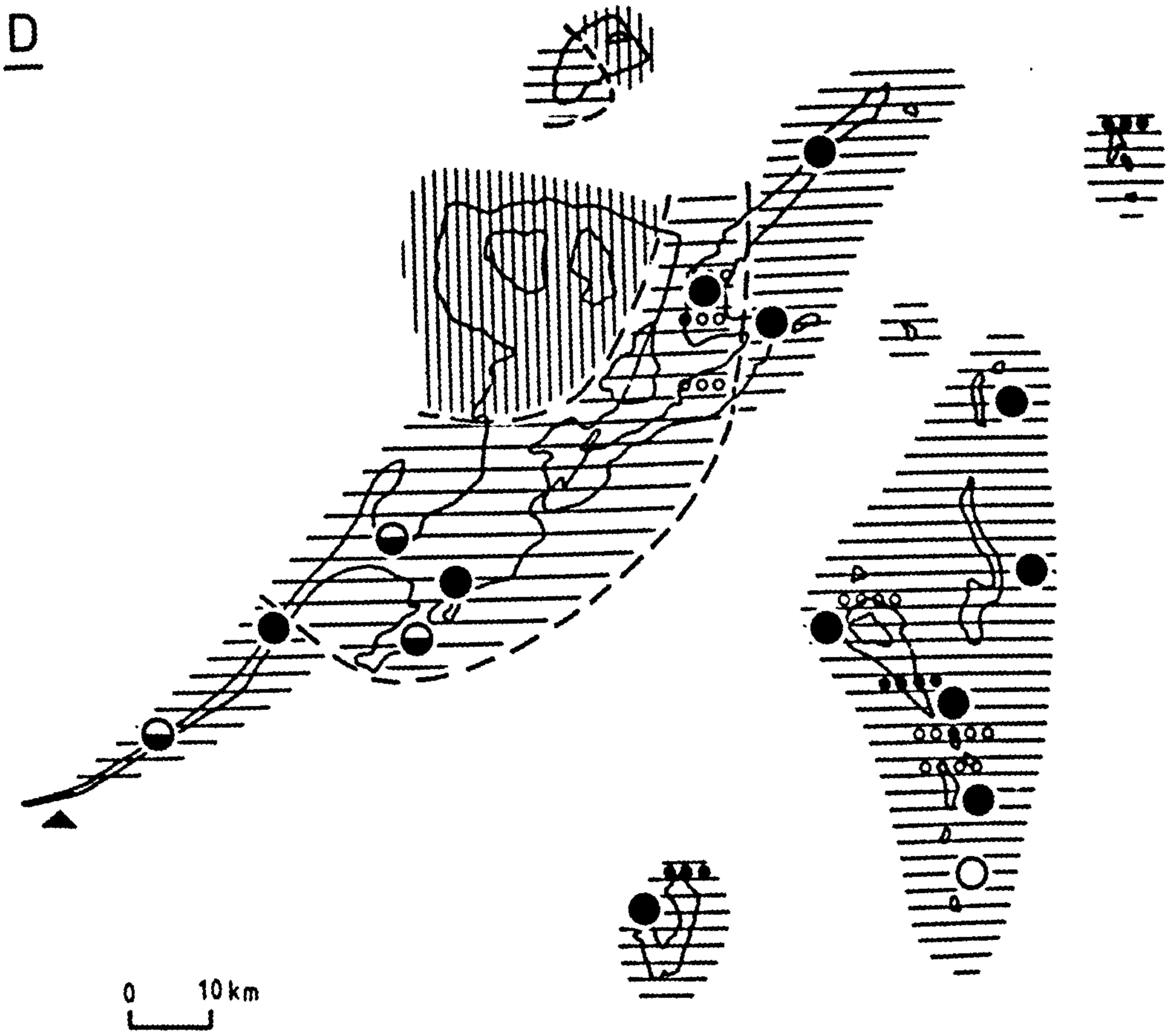
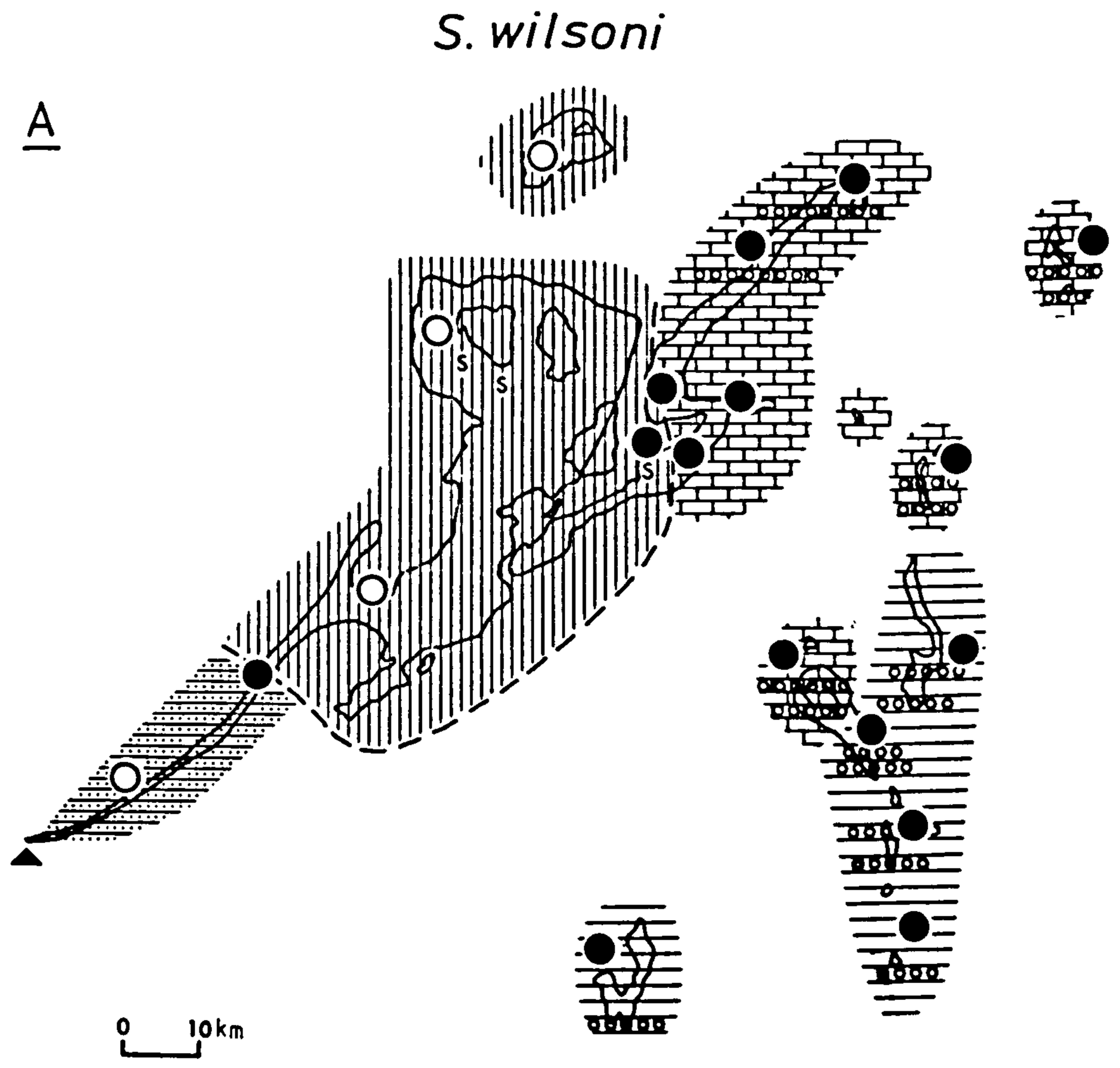


Fig. 5.22 : S. lunata



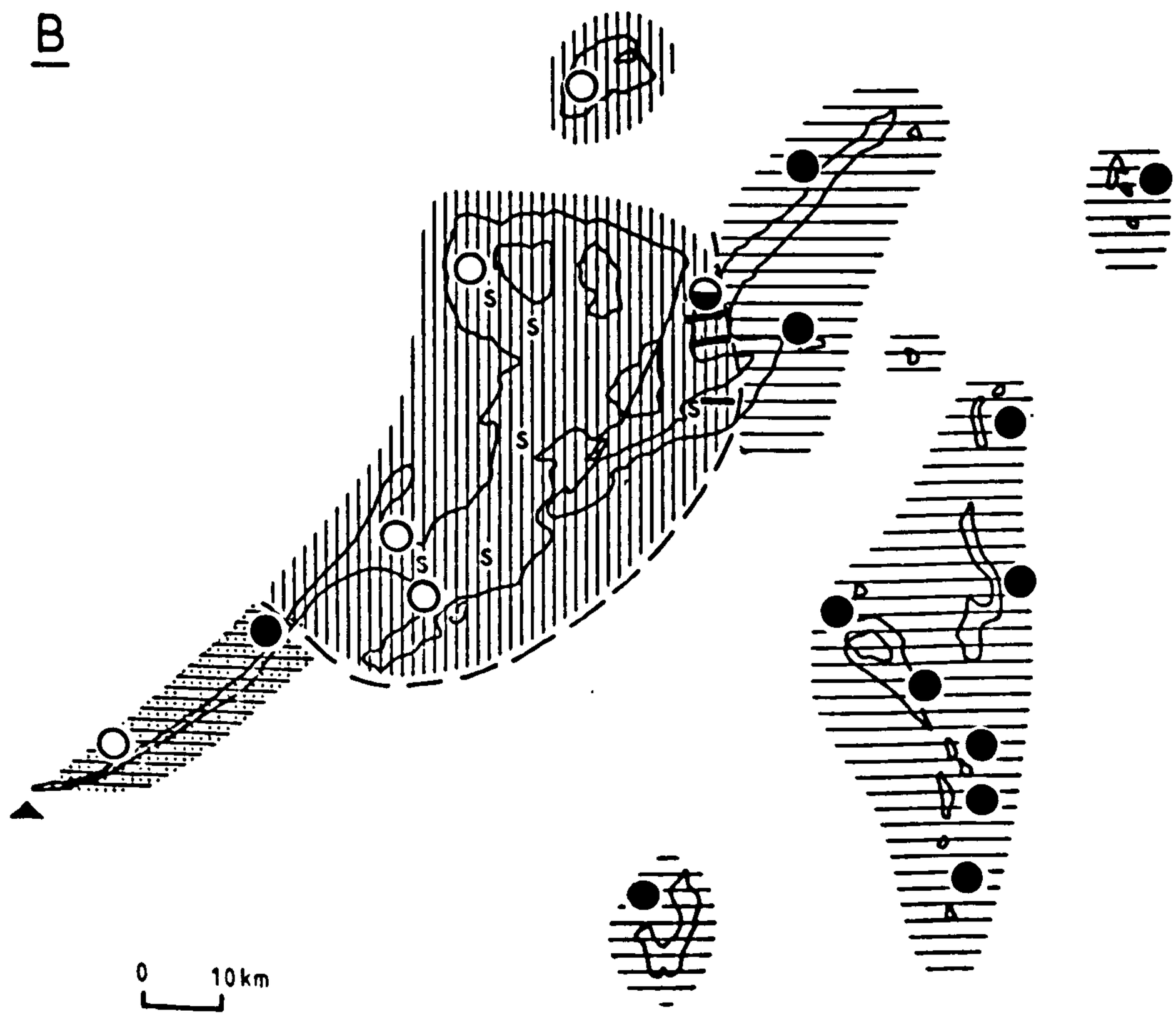


Fig. 5.23 : S. wilsoni

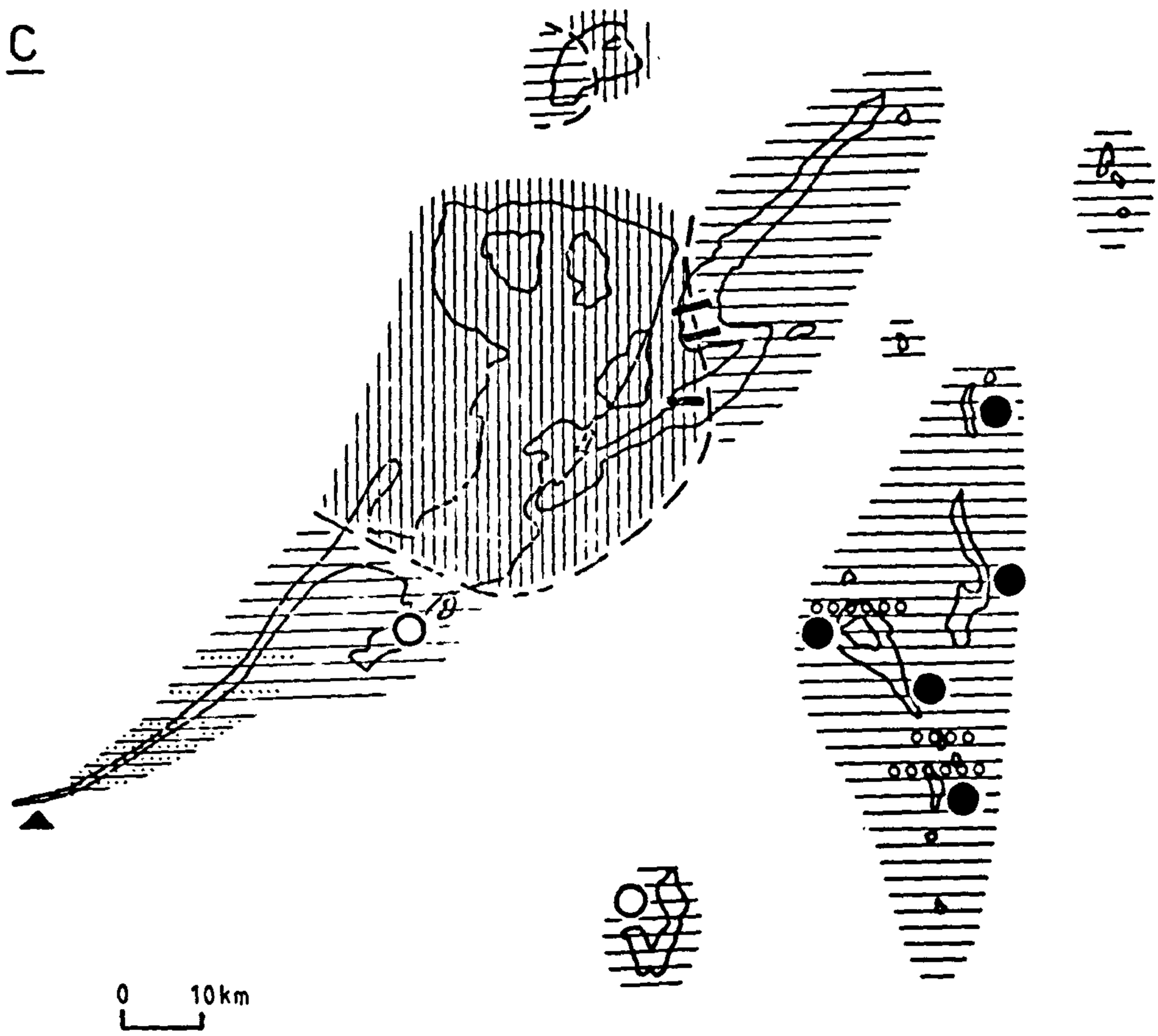


Fig. 5.23 : S. wilsoni

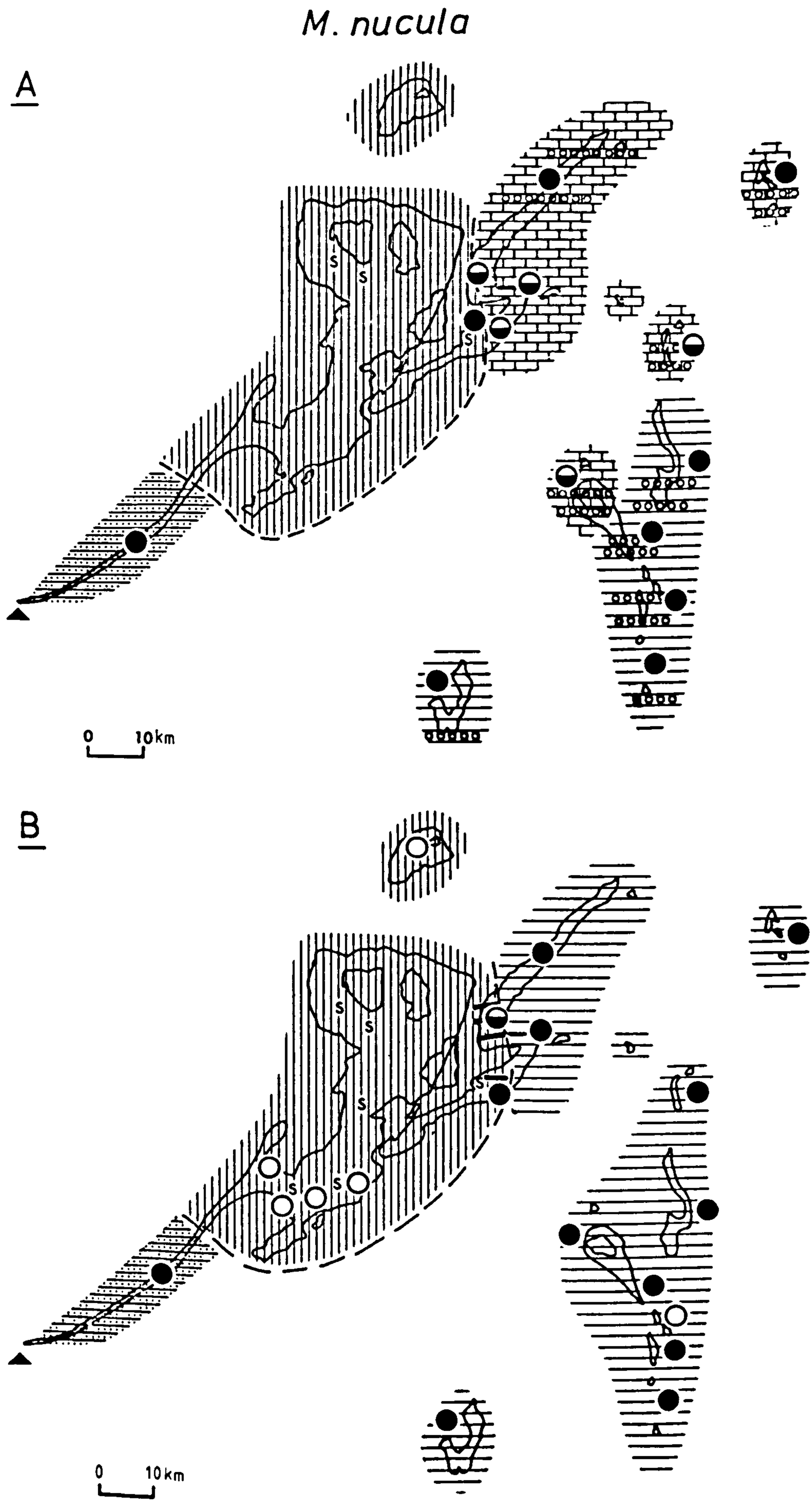


Fig. 5.24 : M. nucula

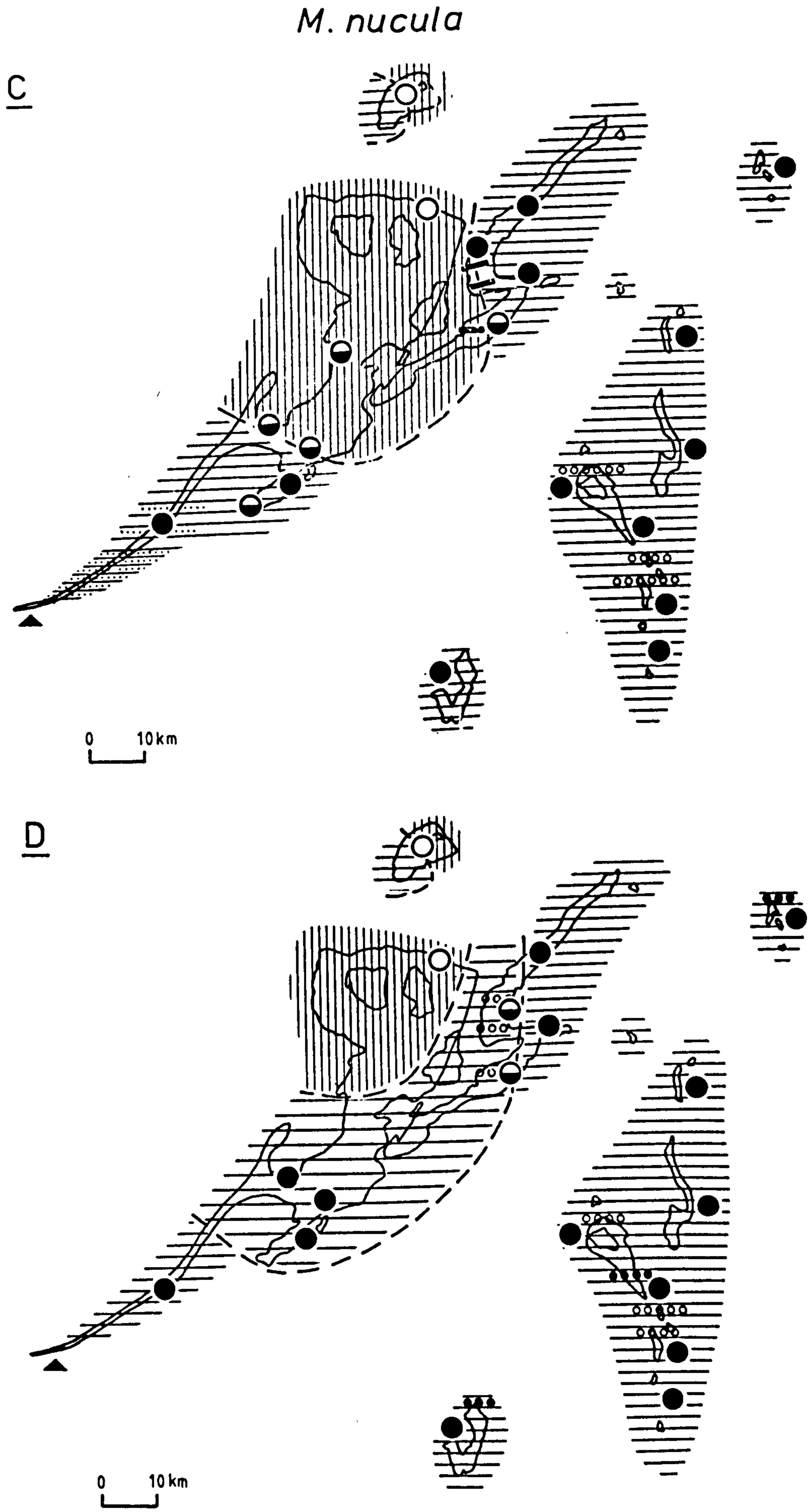


Fig. 5.24 : M. nucula

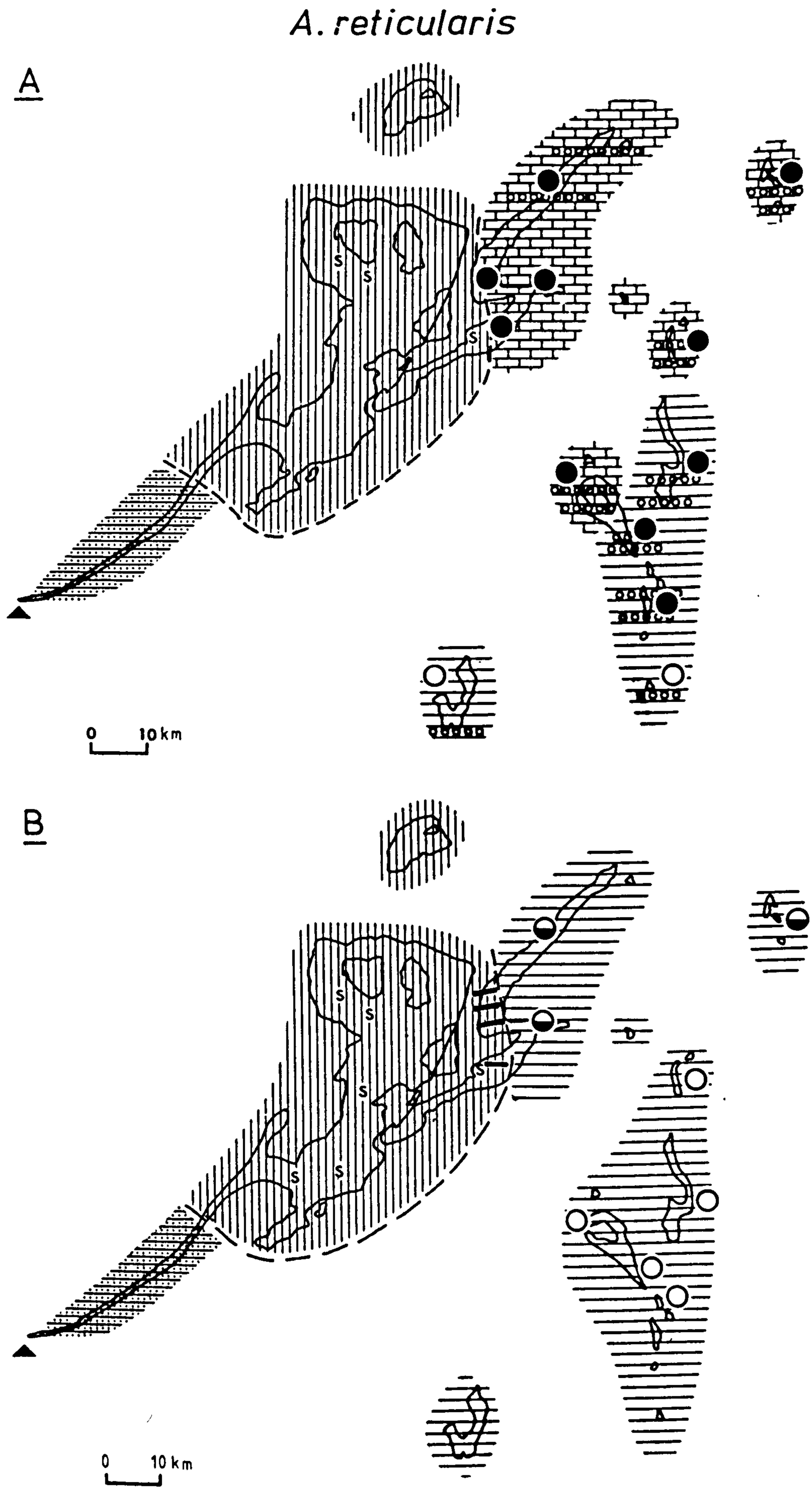


Fig. 5.25 : A. reticularis

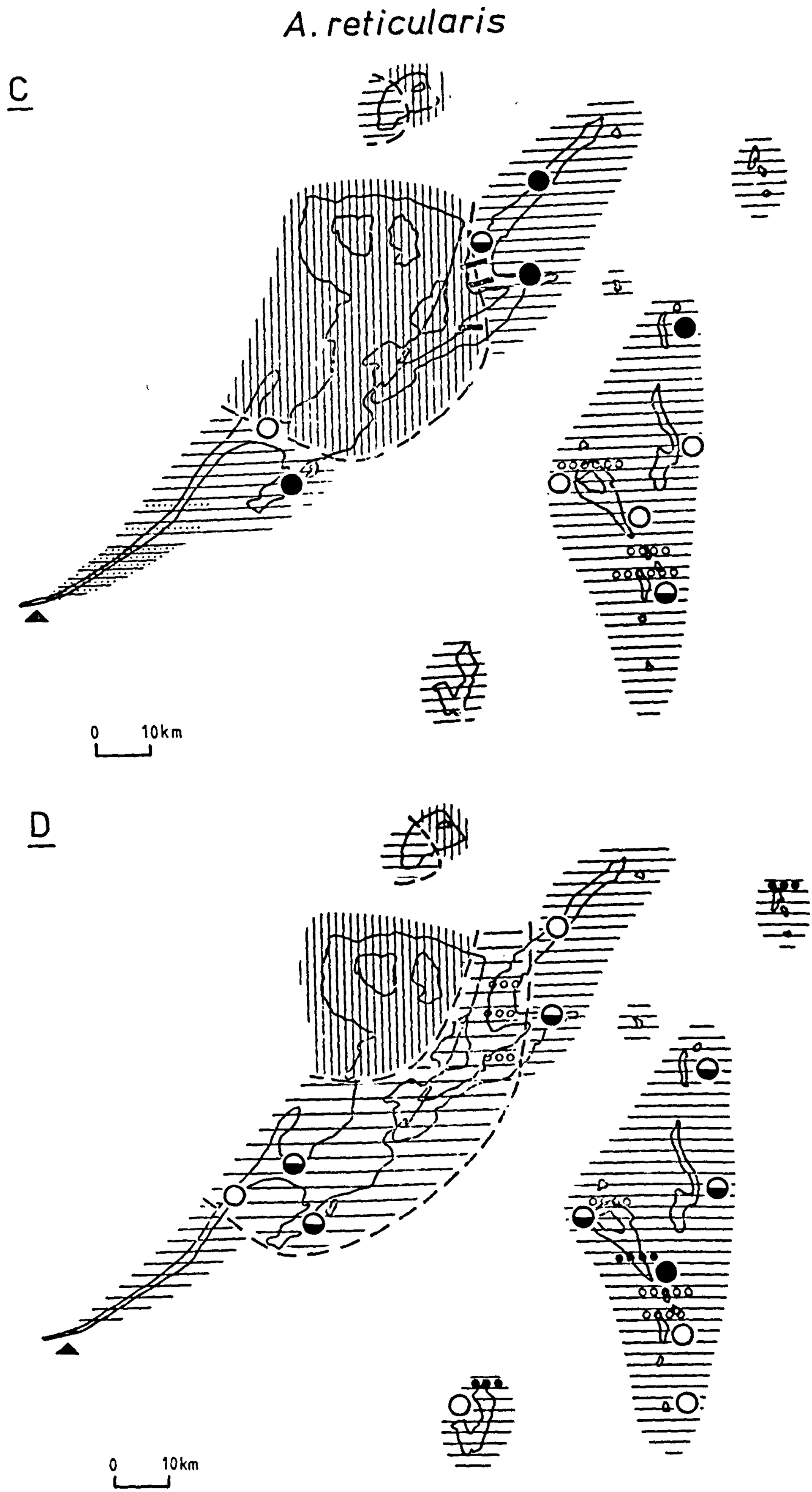
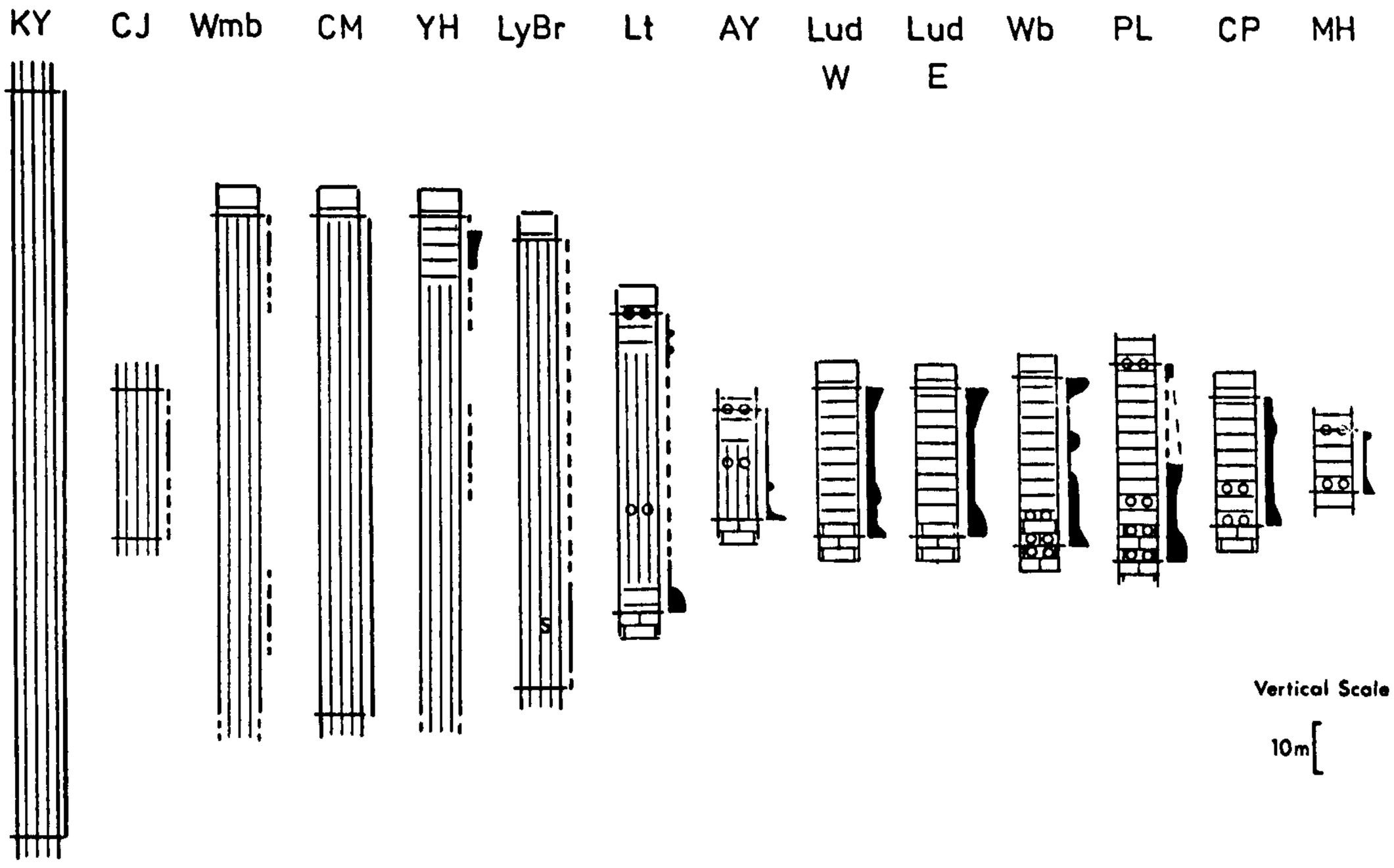
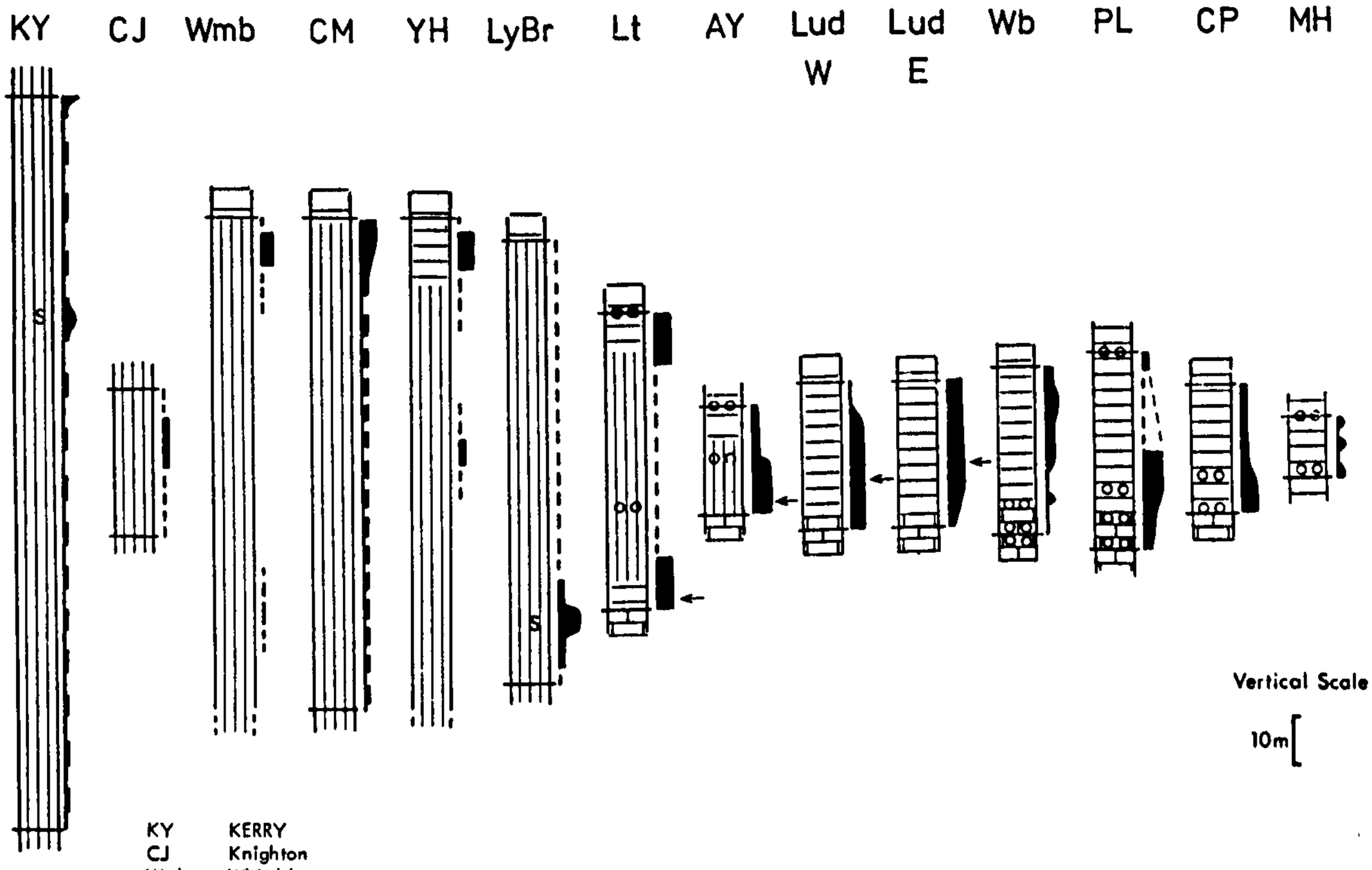


Fig. 5.25 : A. reticularis

A. reticularis Fig. 5.26



D. navicula Fig. 5.27



KY	KERRY
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Lud	LUDLOW
Wb	WOODBURY
PL	PERTON
CP	CHANCES PITCH
MH	MAY HILL

Fig. 5.26 : A. reticularis
Fig. 5.27 : D. navicula

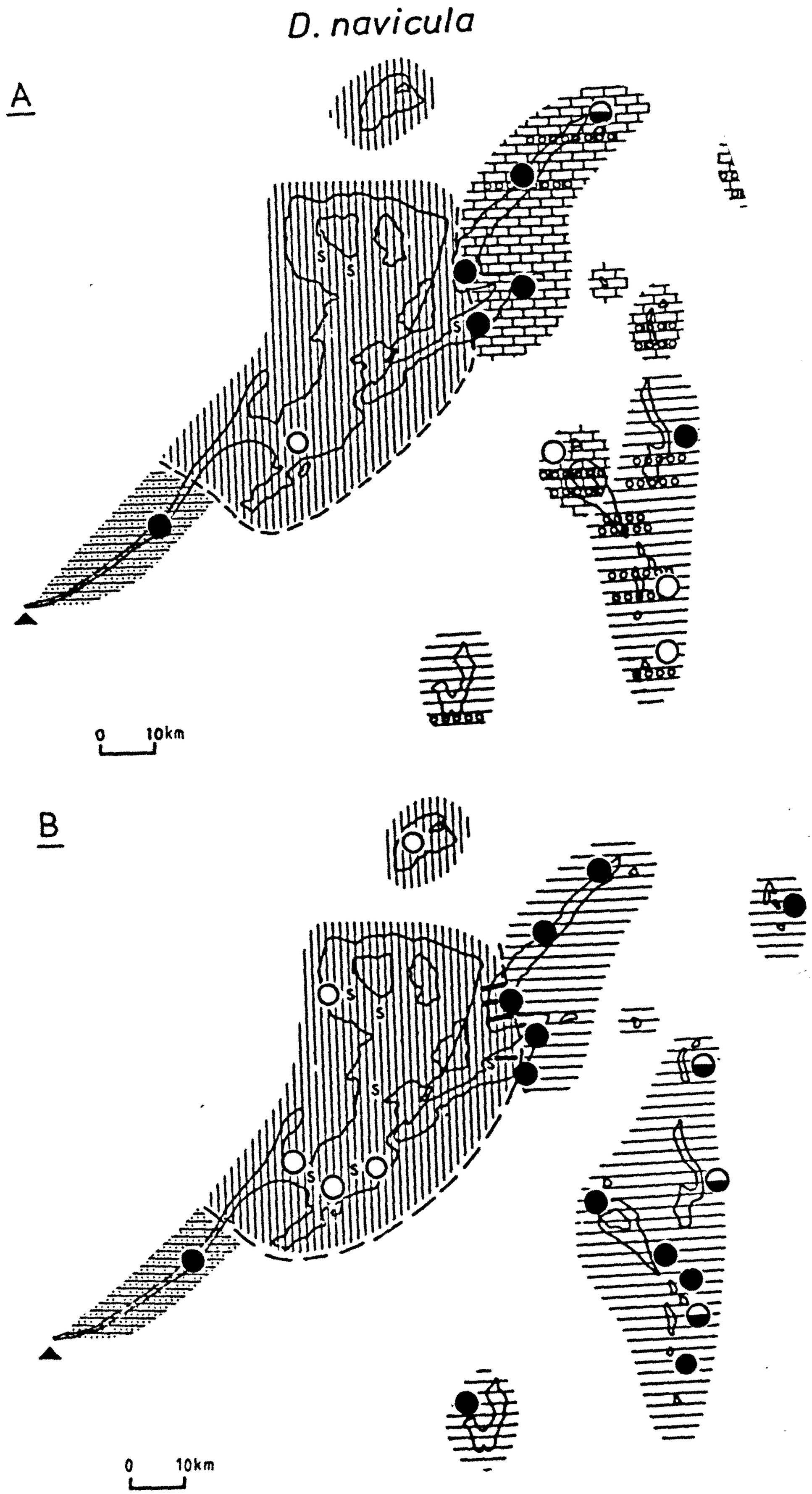
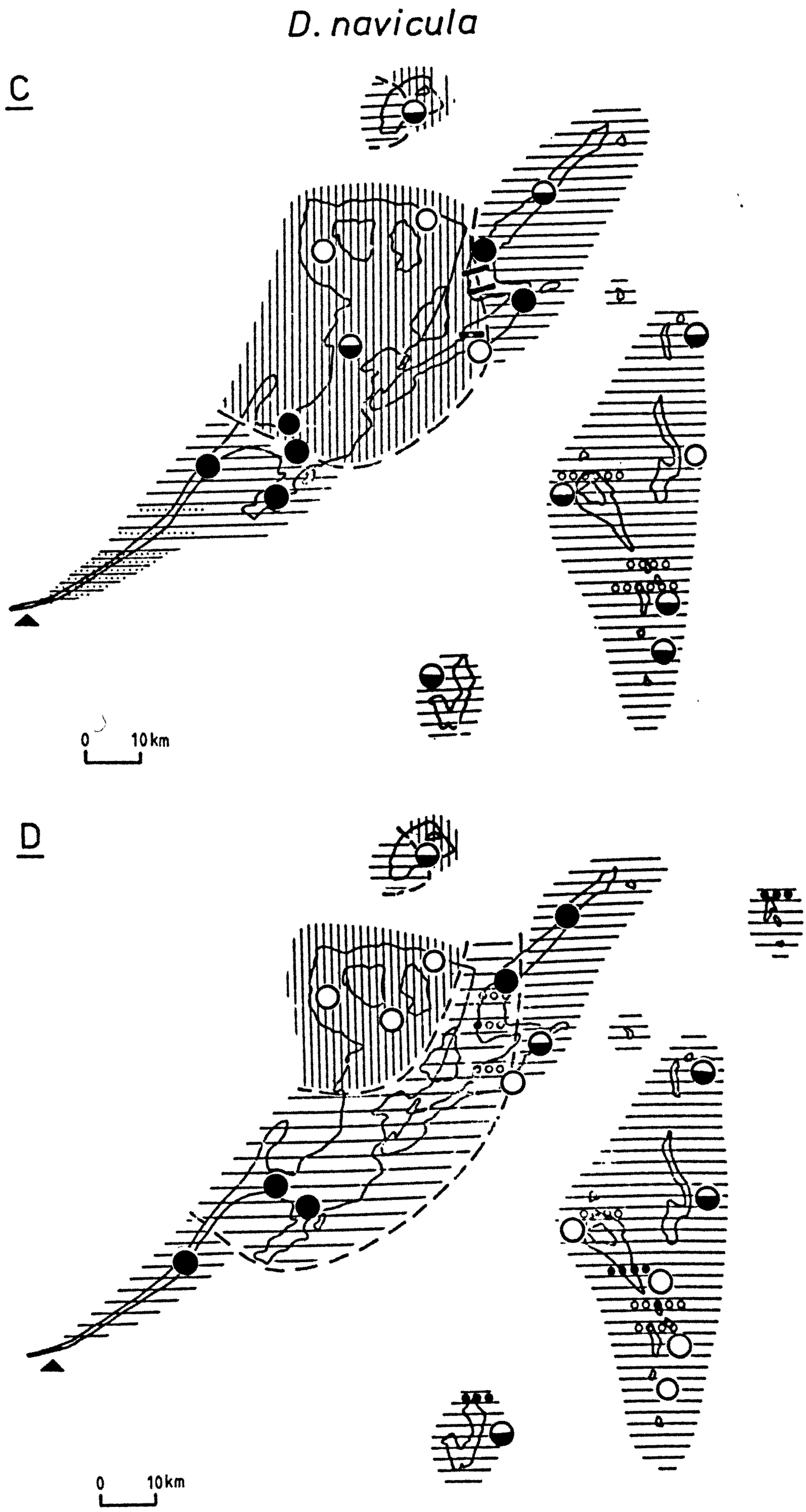


Fig. 5.28 : D. navicula



28 : D. navicula

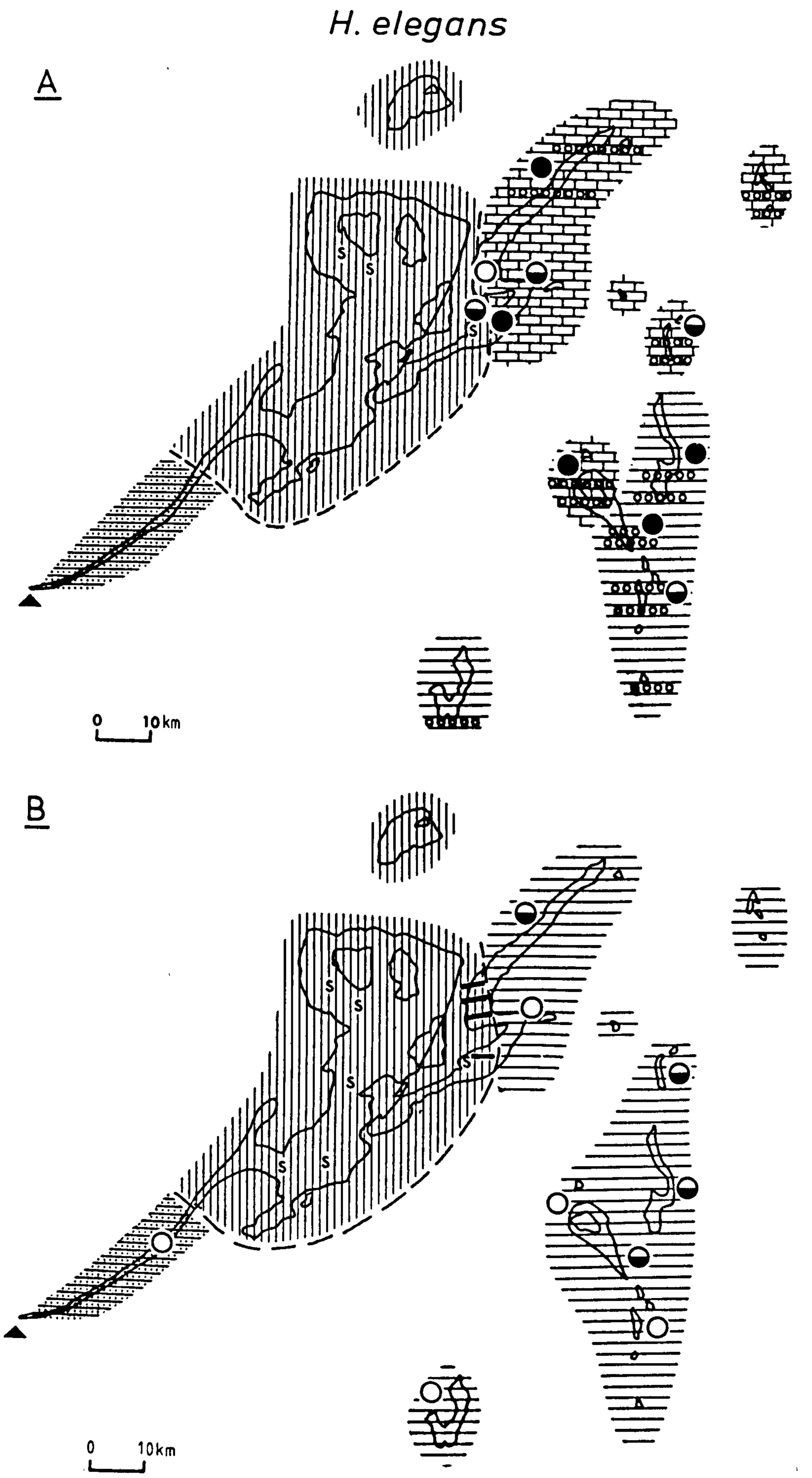
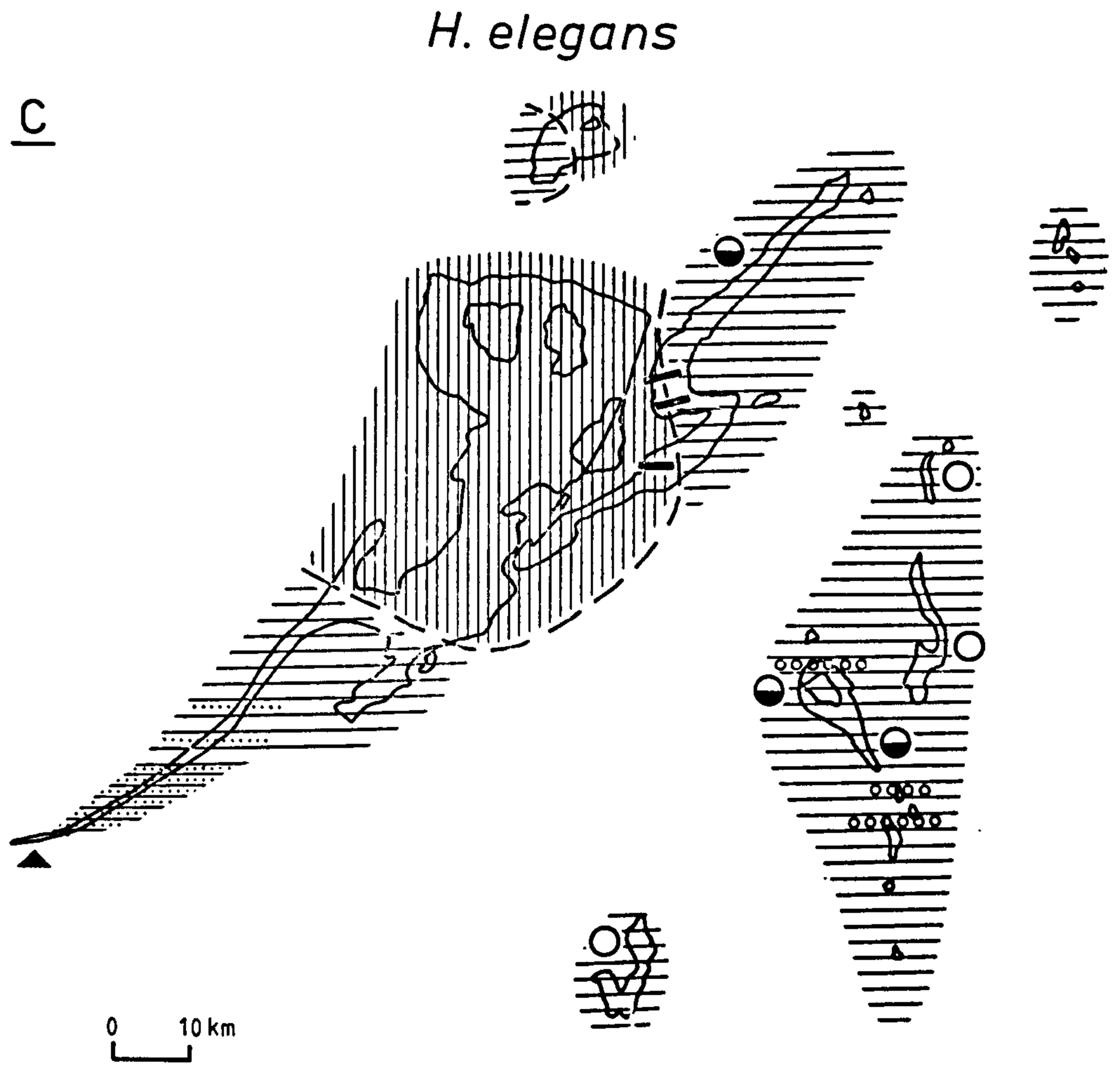


Fig. 5.29 : H. elegans



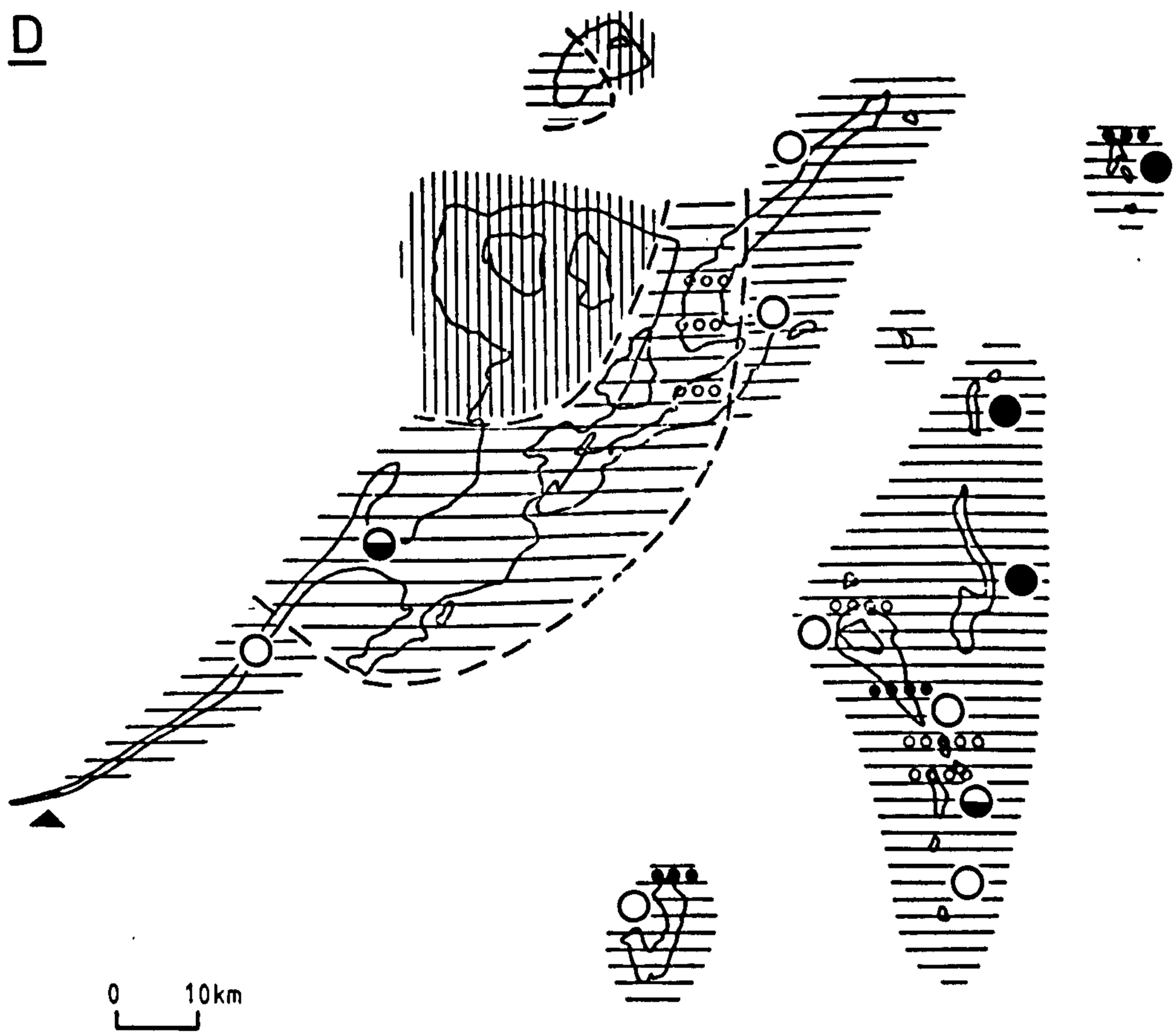


Fig. 5.29 : H. elegans

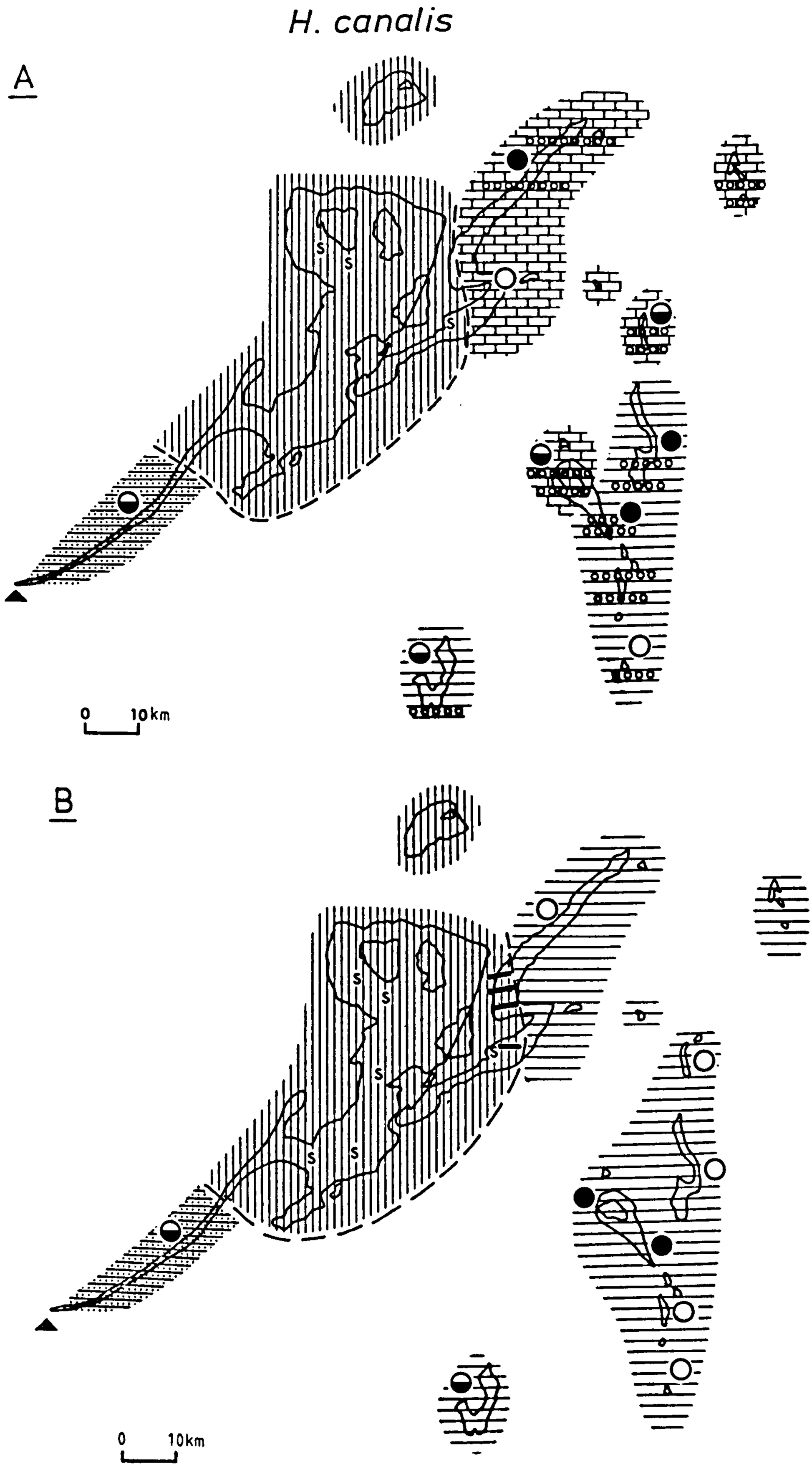


Fig. 5.30 : H. canalis

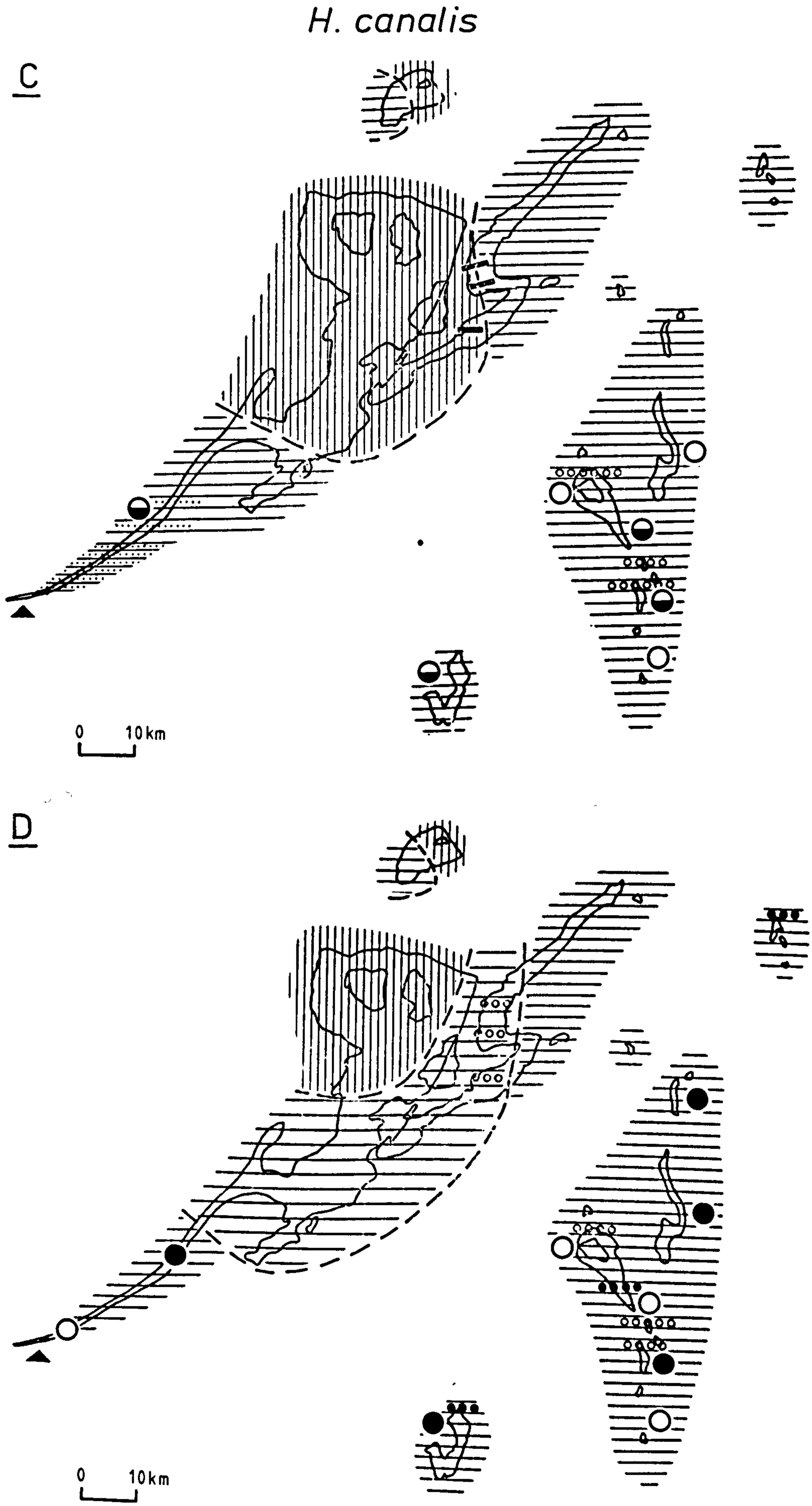


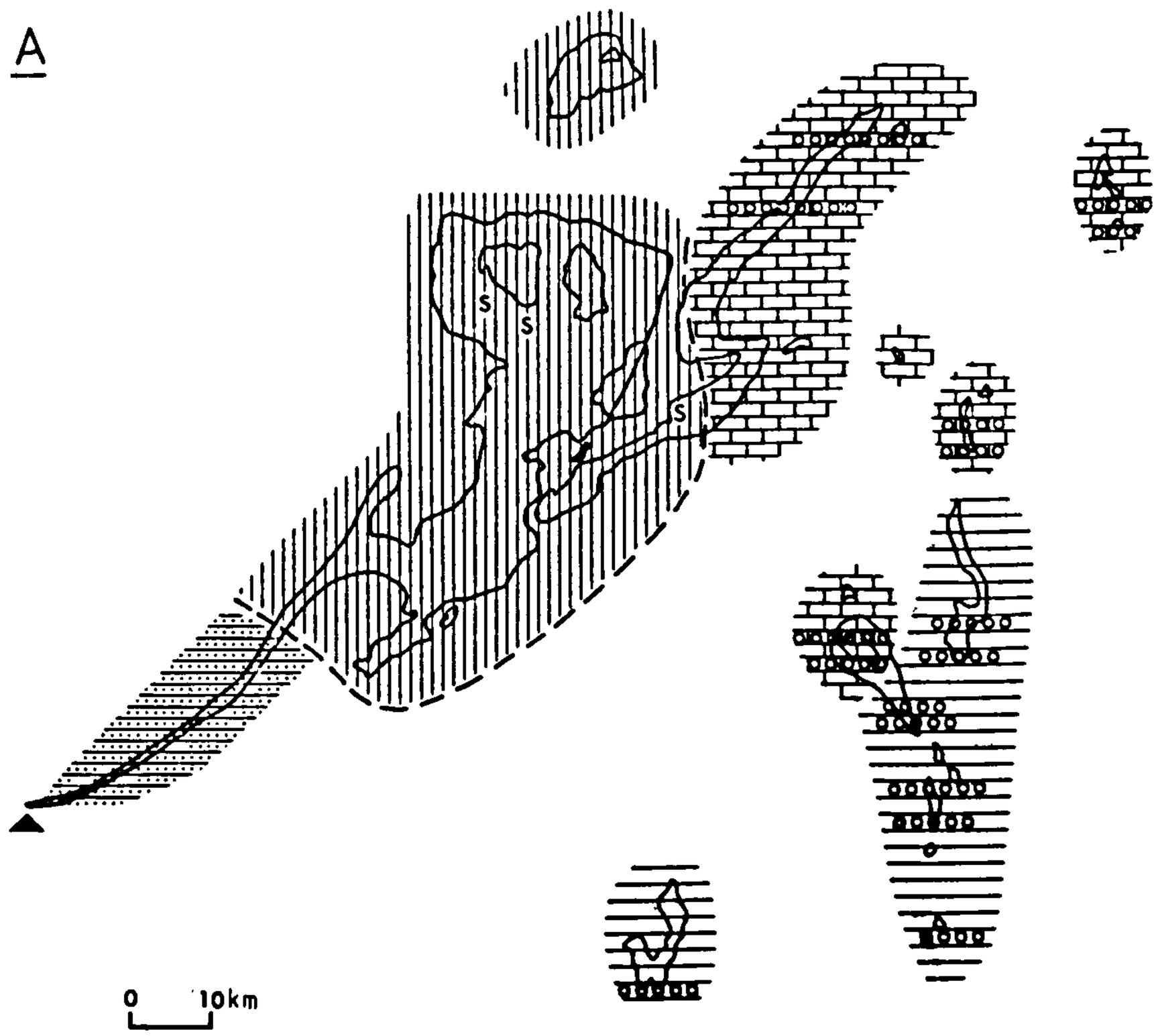
Fig. 5.30 : H. canalis

Calymenids - *C. lawsoni* □

C. puellaris ○

Calymene sp. △

A



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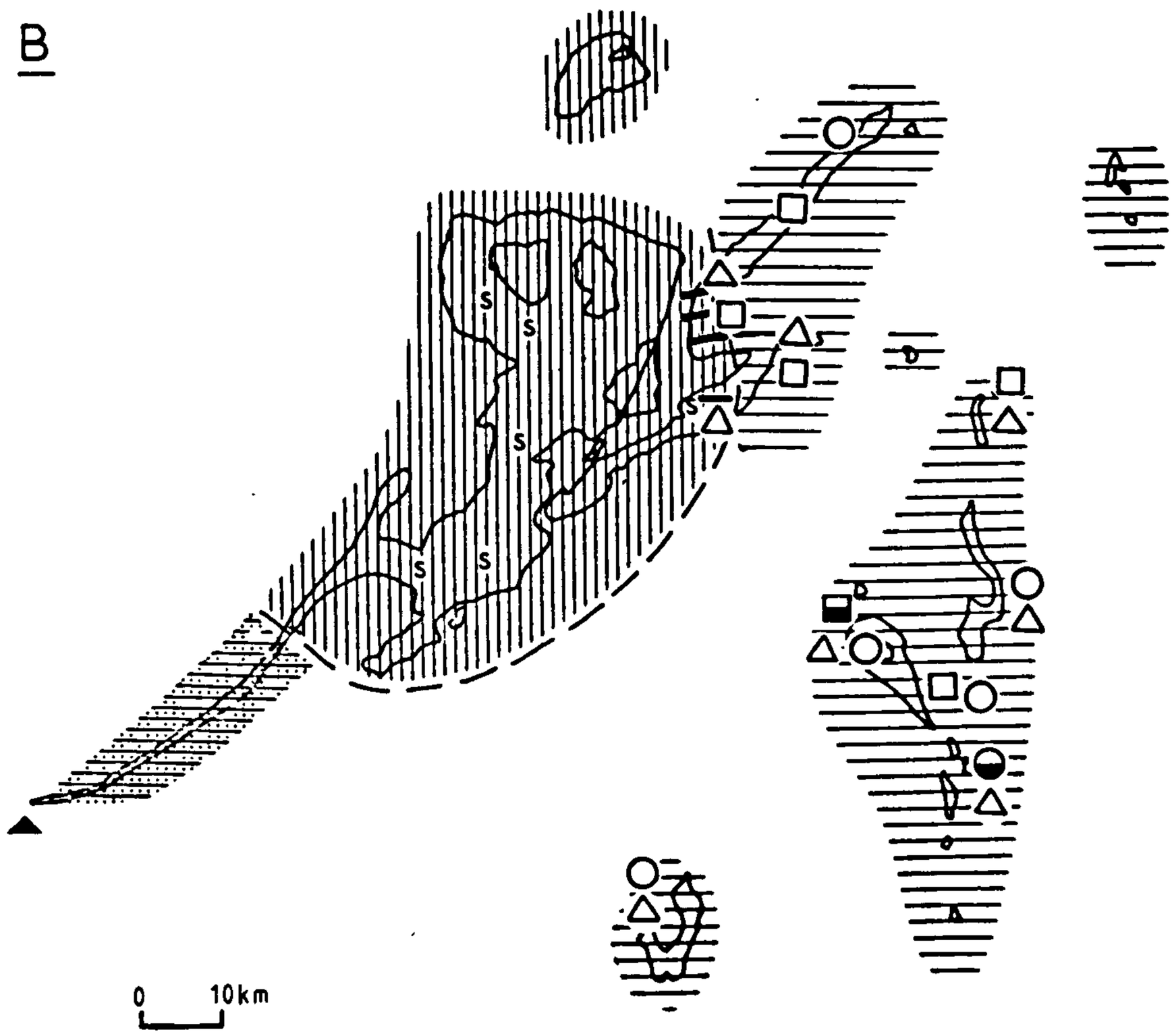


Fig. 5.33 : Calymenids

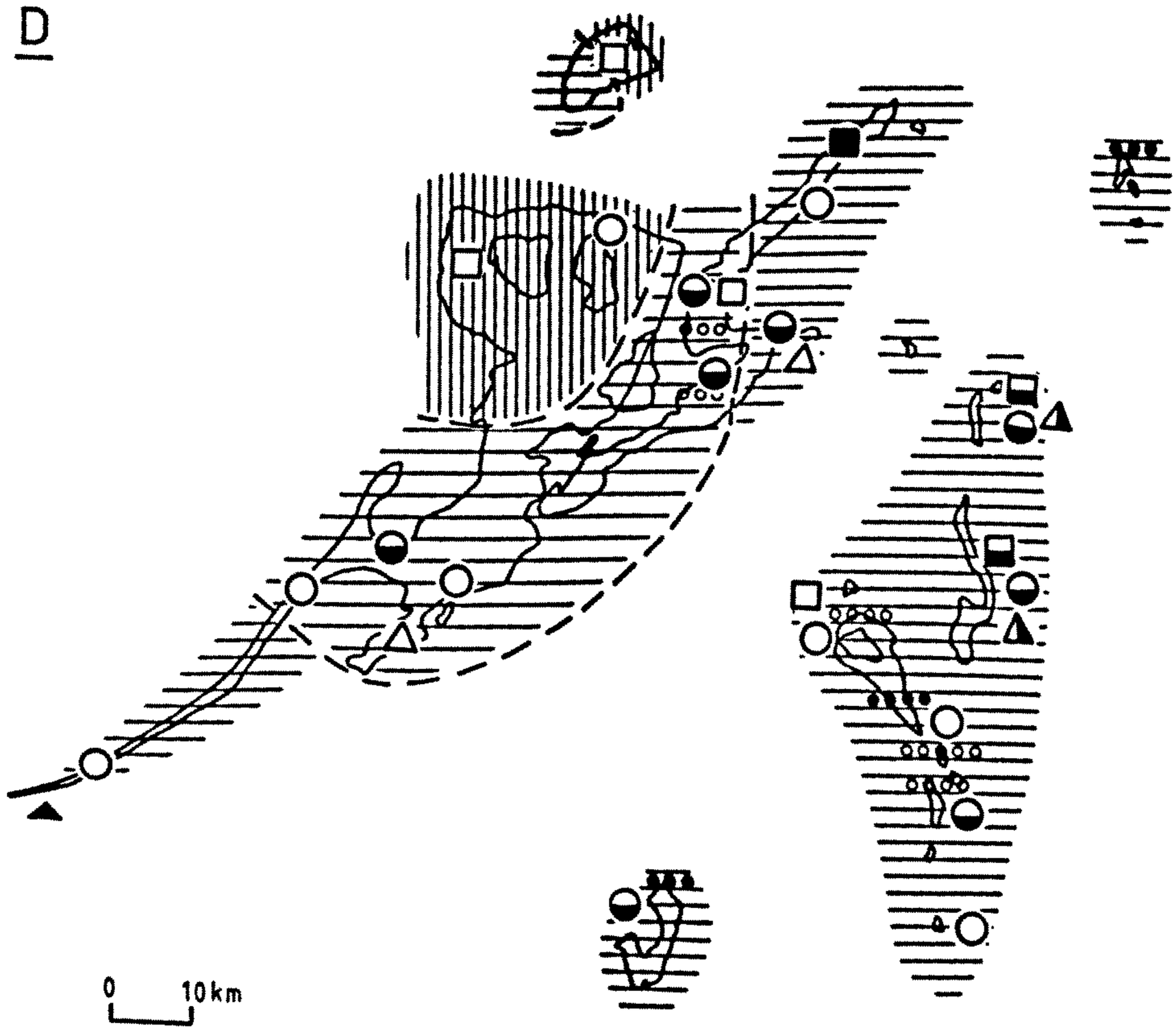
Calymenids - *C. lawsoni* □

C. puellaris ○

Calymene sp. △

C

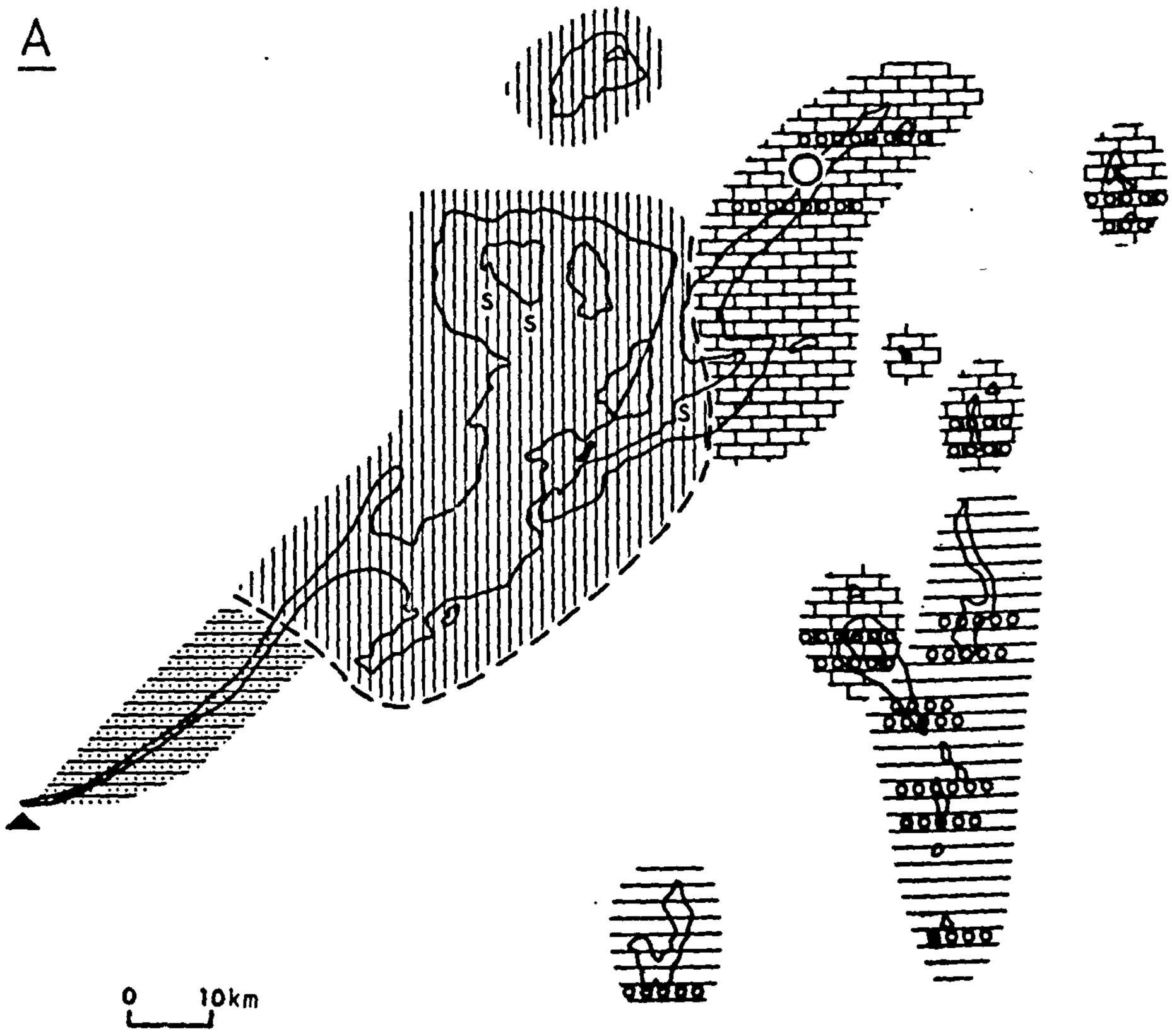
D



.33 : Calymenids

Encrinurus spp.

A



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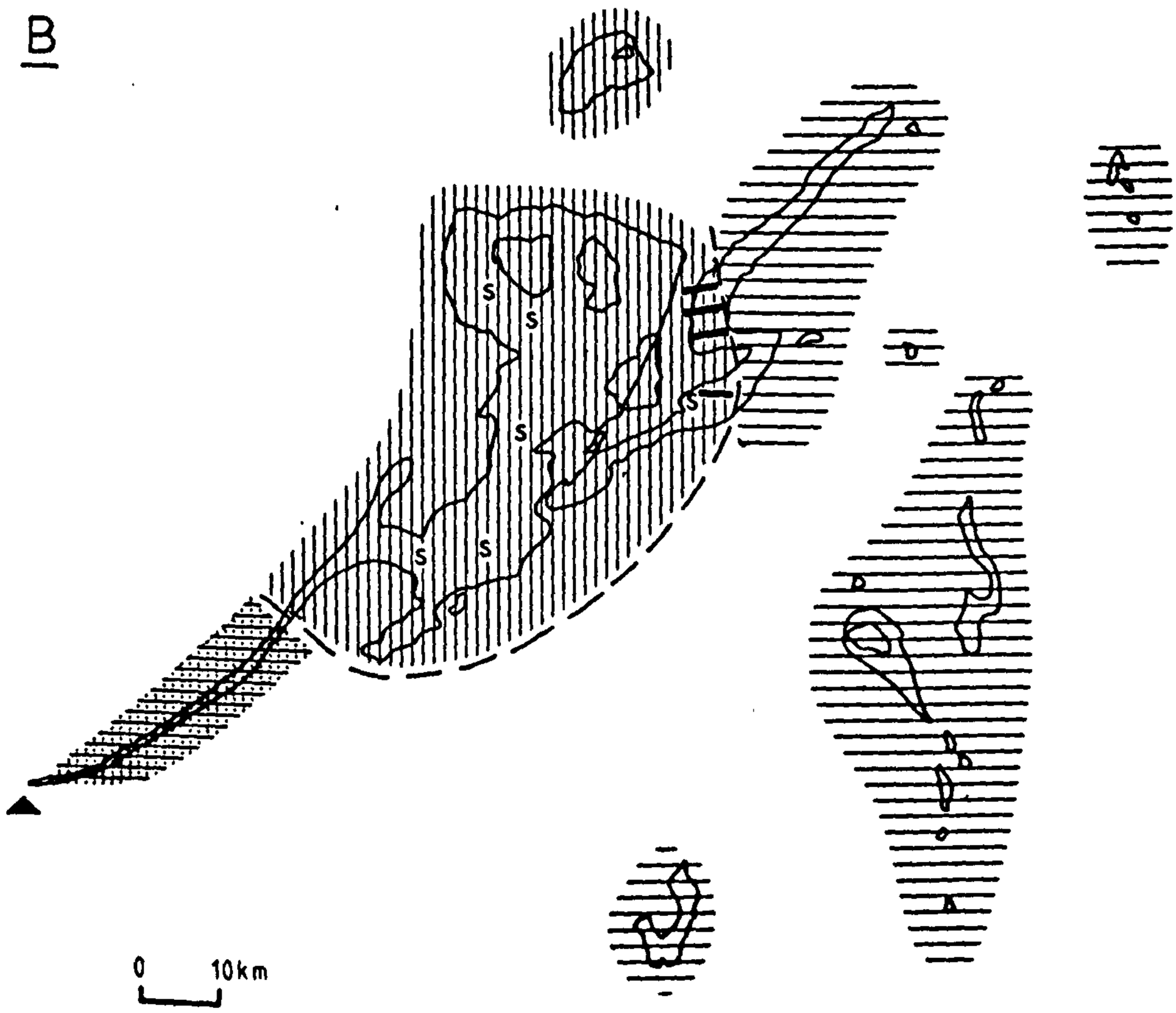


Fig. 5.34 : Encrinurus spp.

Encrinurus spp.

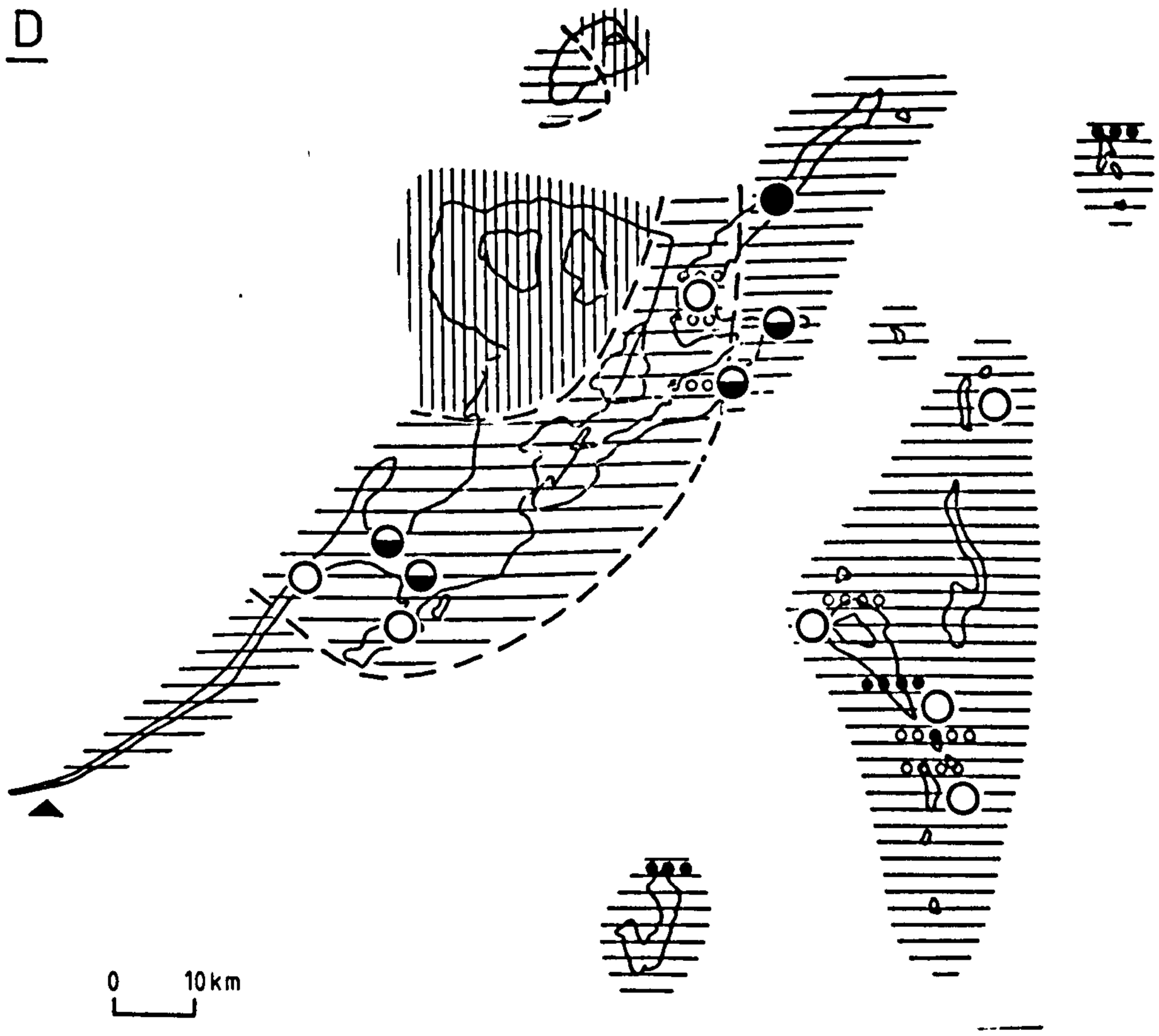
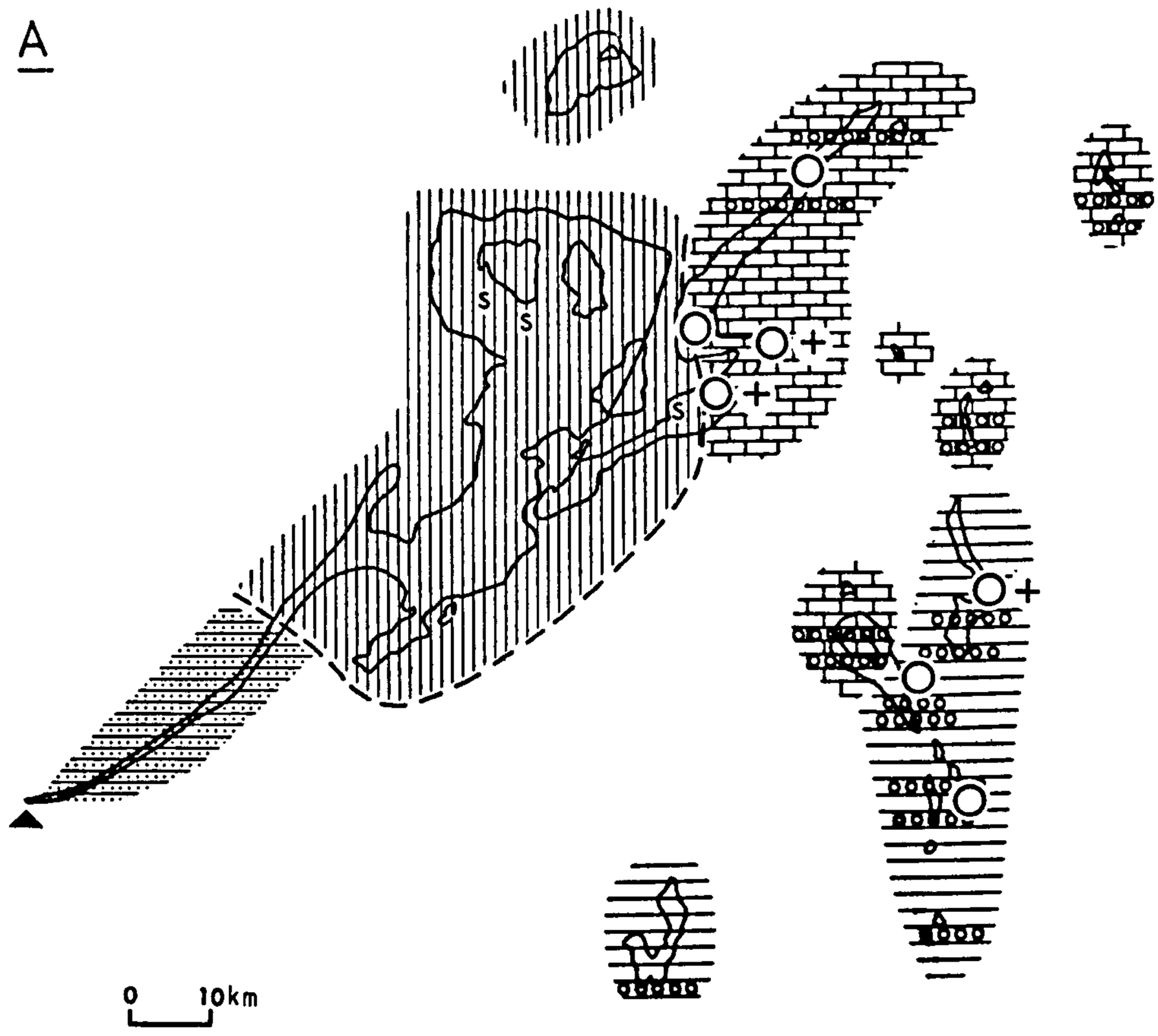


Fig. 5.34 : Encrinurus spp.

Proetids - *P. obconicus* O

W. ludlowensis +

A



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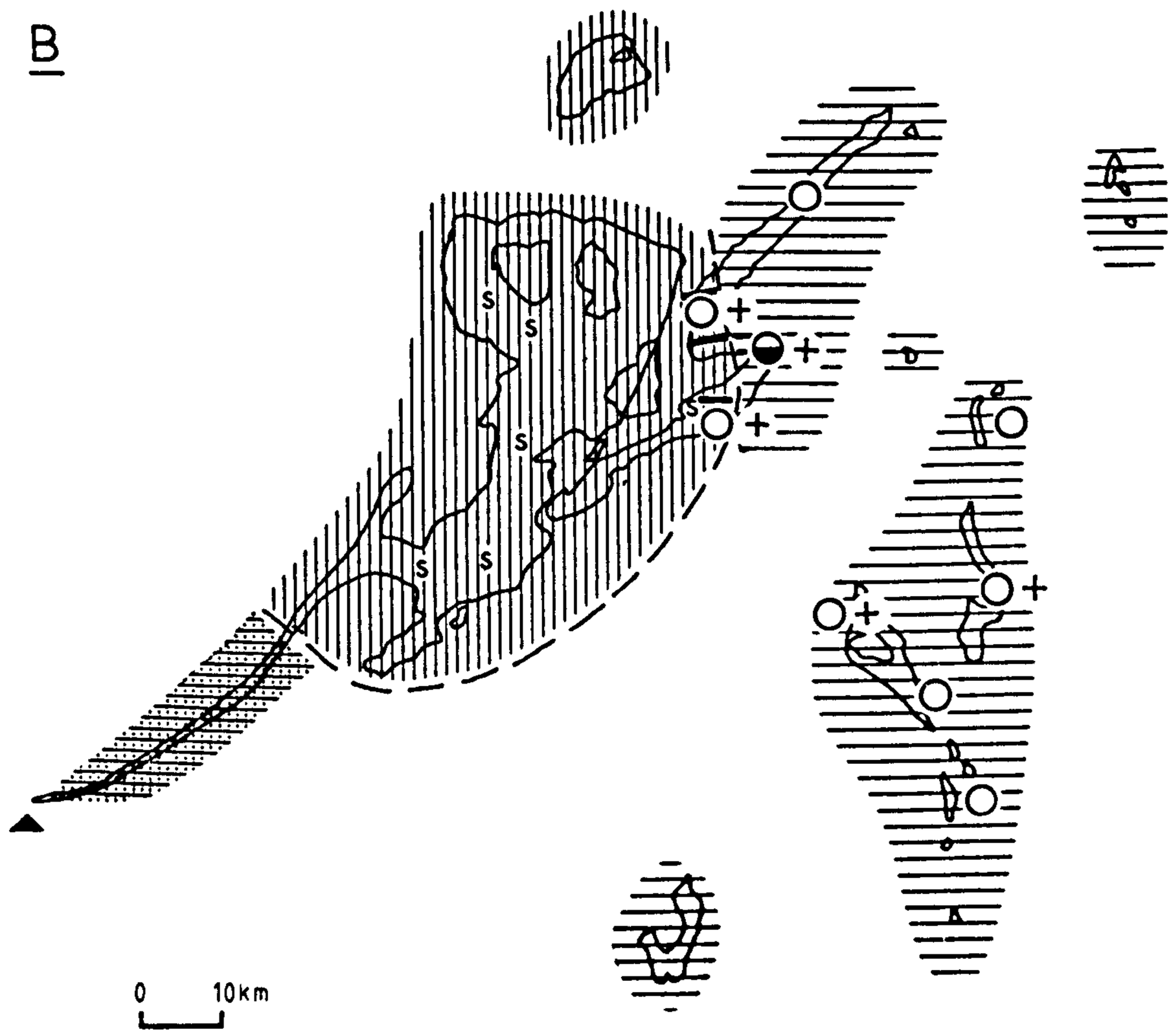


Fig. 5.35 : Proetids

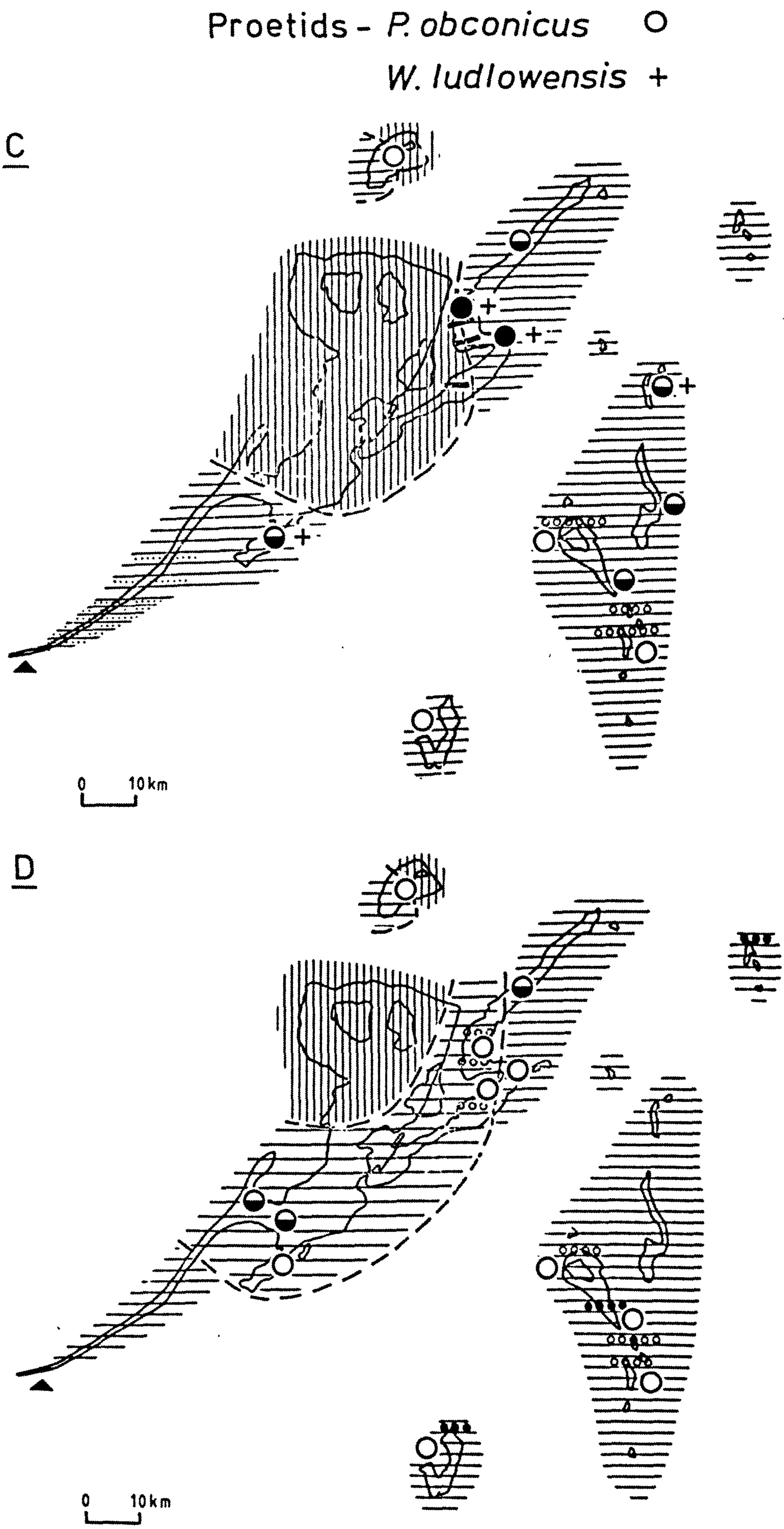
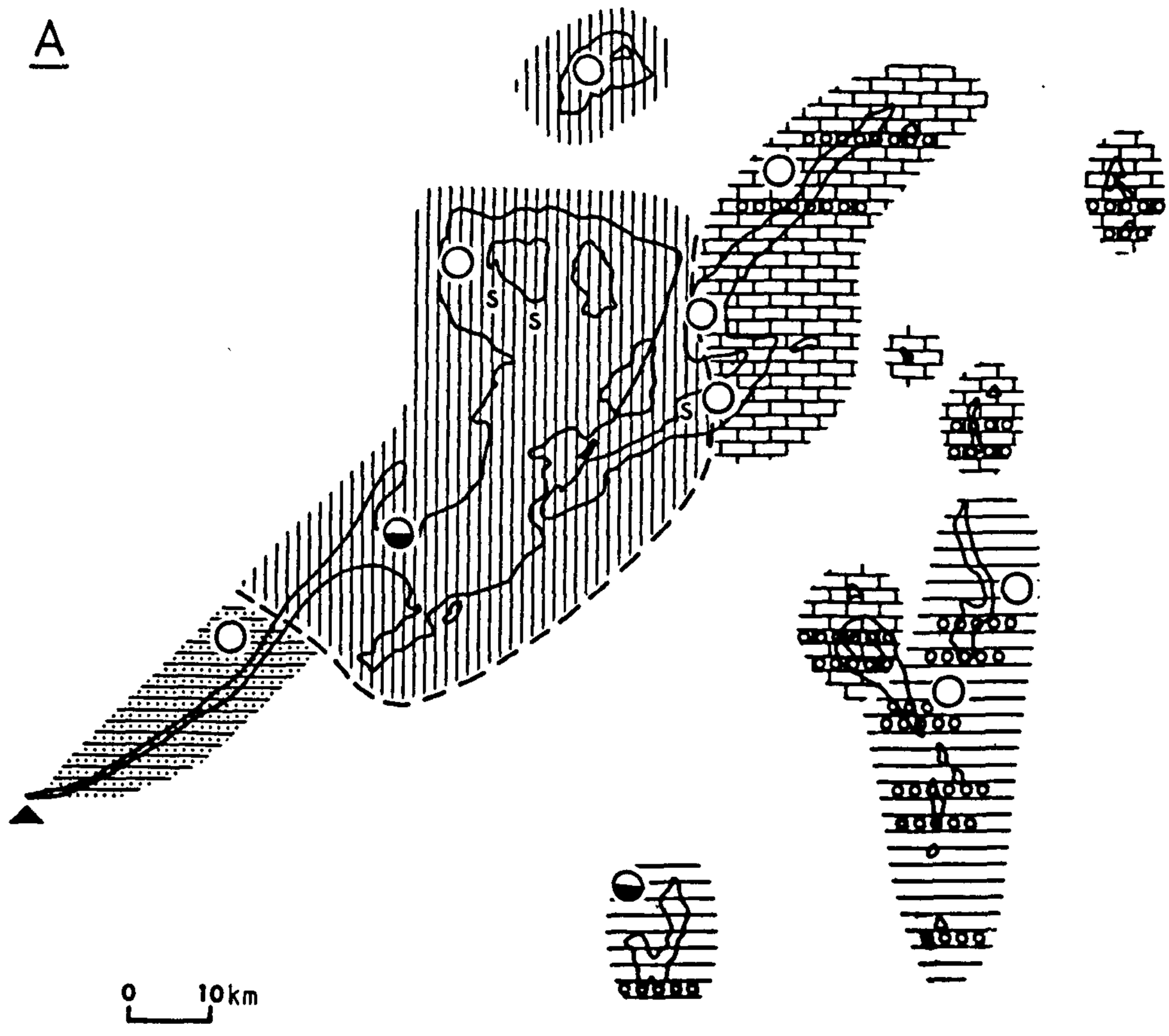


Fig. 5.35 : Proetids

Beyrichiaceans

-excluding Neobeyrichiids

A



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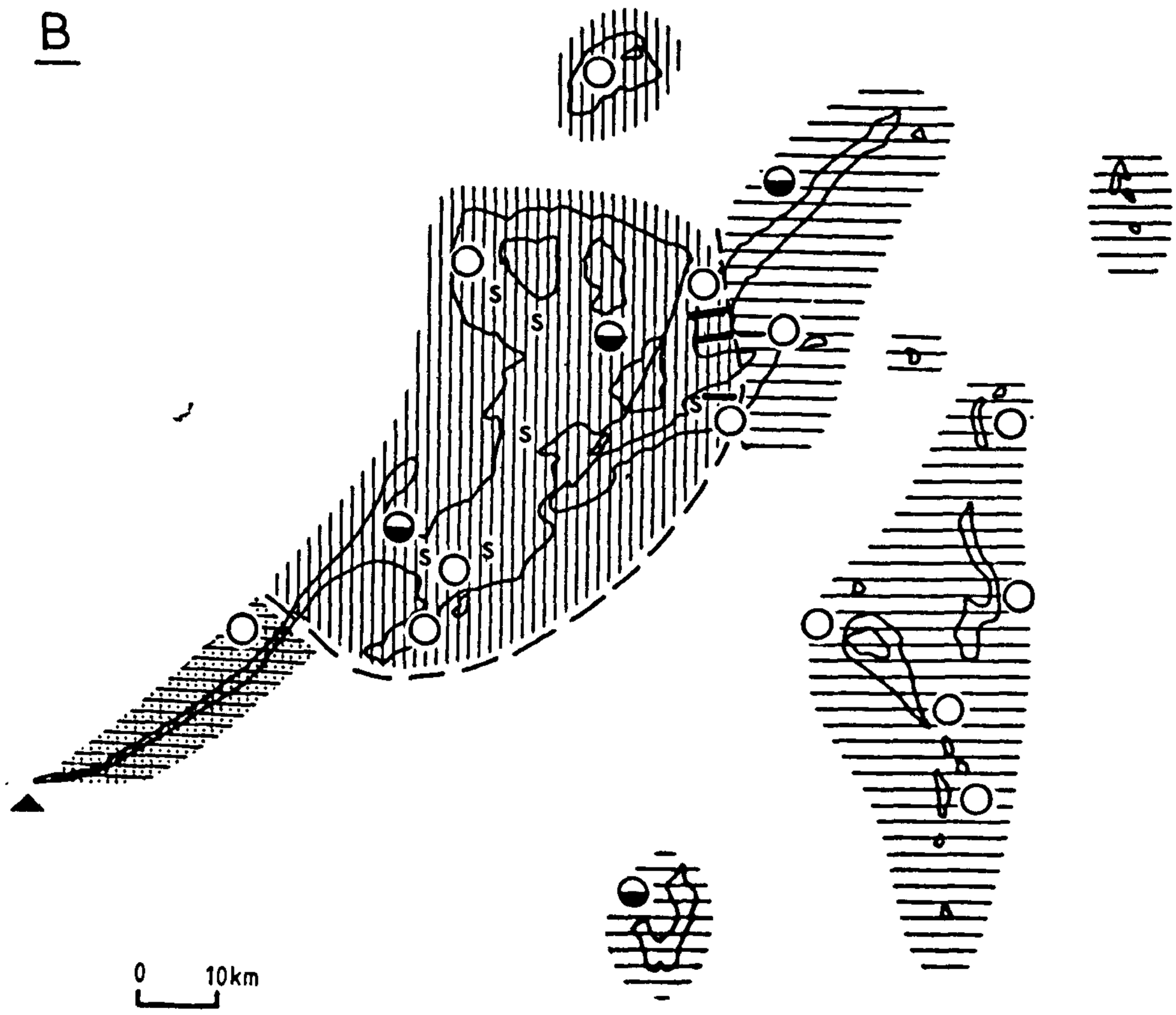
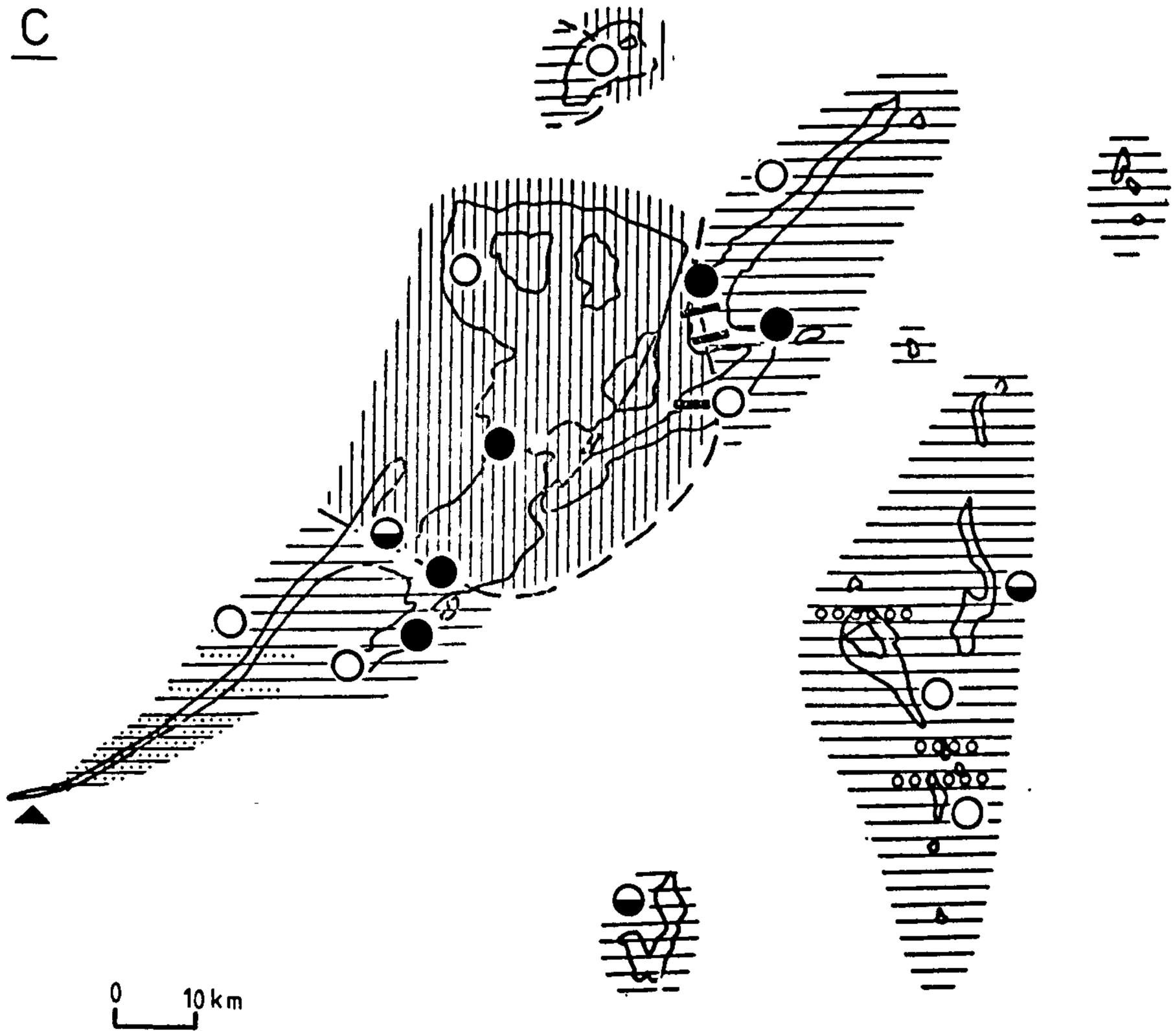


Fig. 5.36 : Beyrichiaceans - excluding Neobeyrichiids

Beyrichiaceans

-excluding Neobeyrichiids

C



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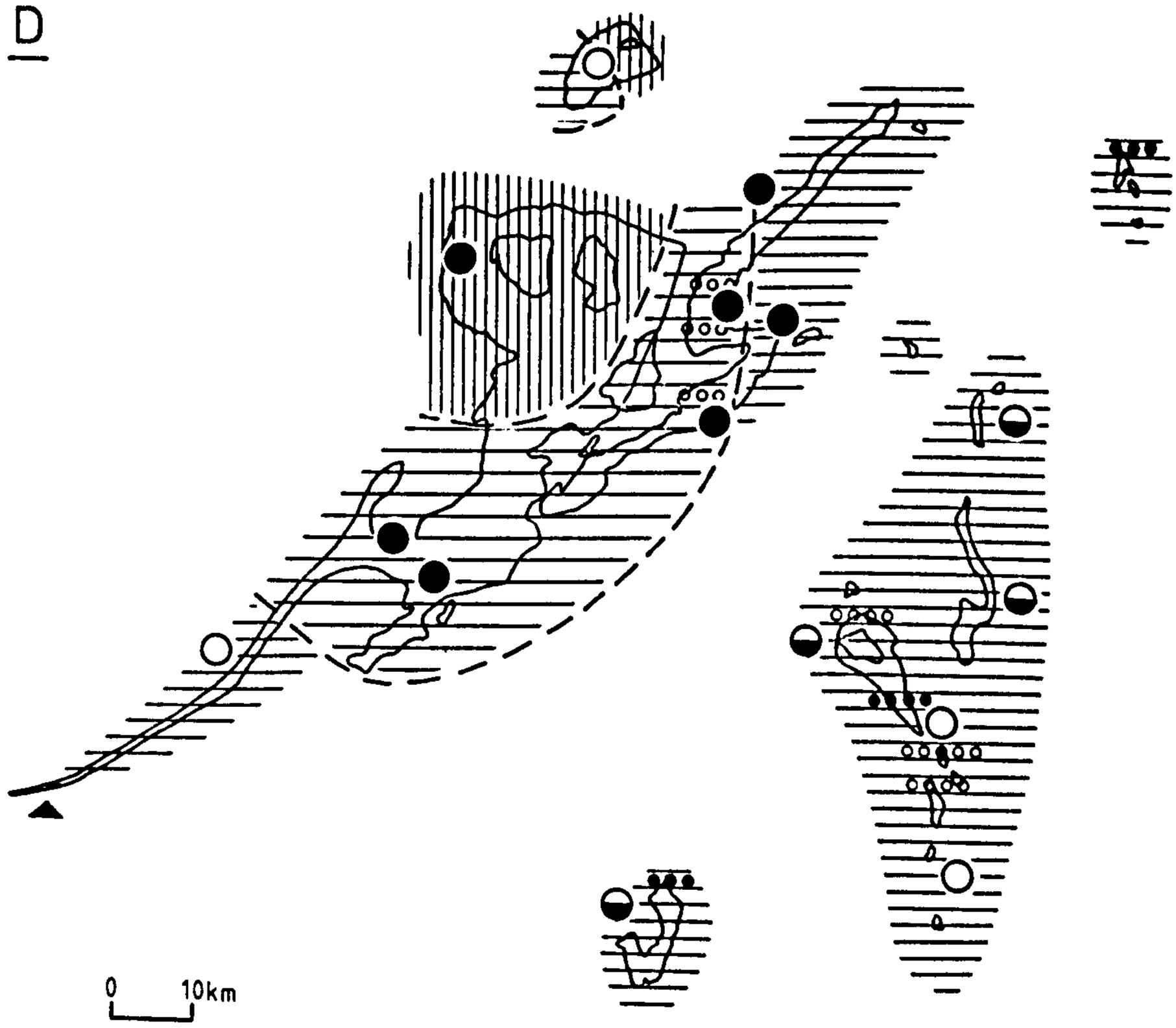


Fig. 5.36 : Beyrichiaceans - excluding Neobeyrichiids

Neobeyrichiids

A

B

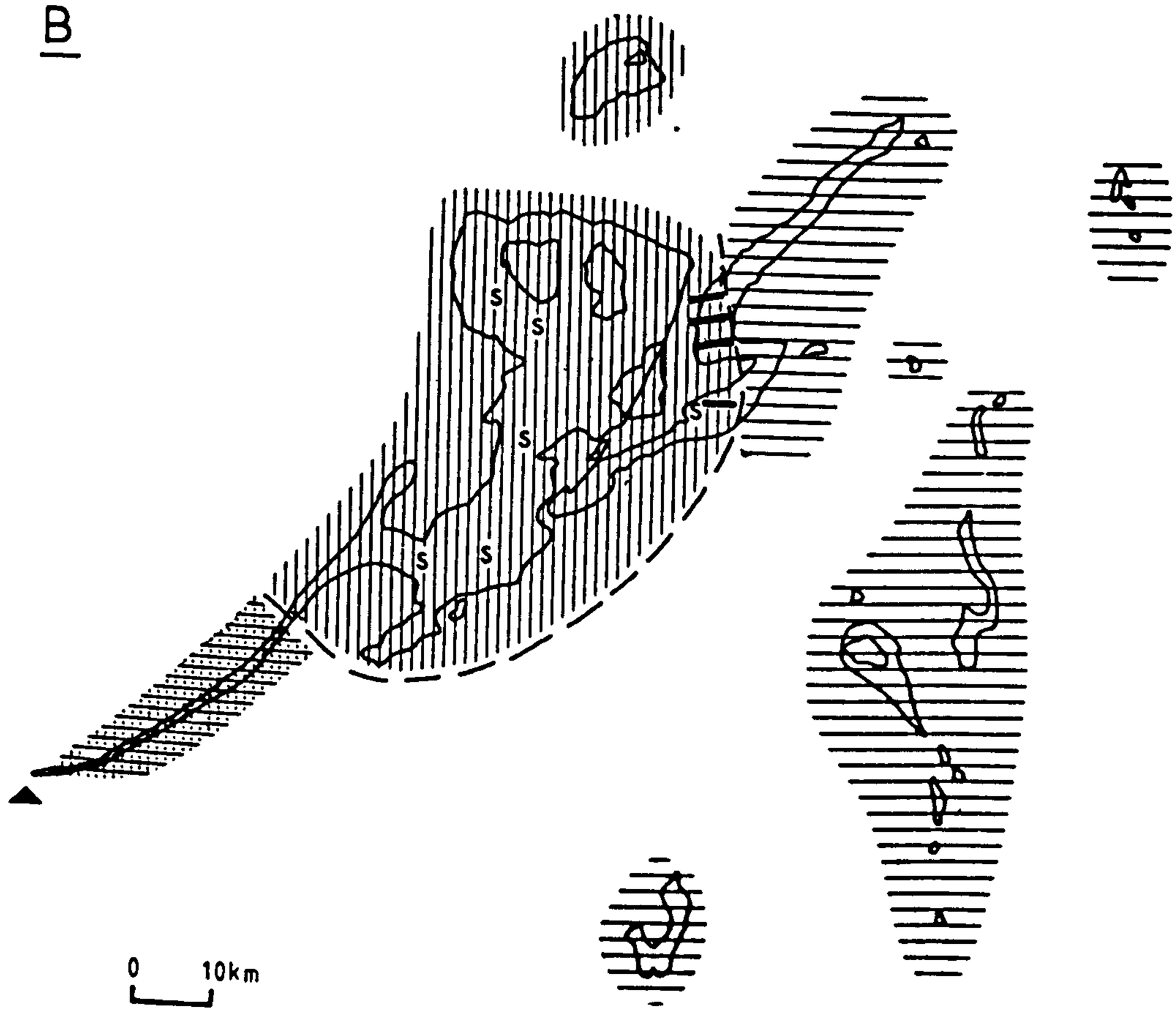
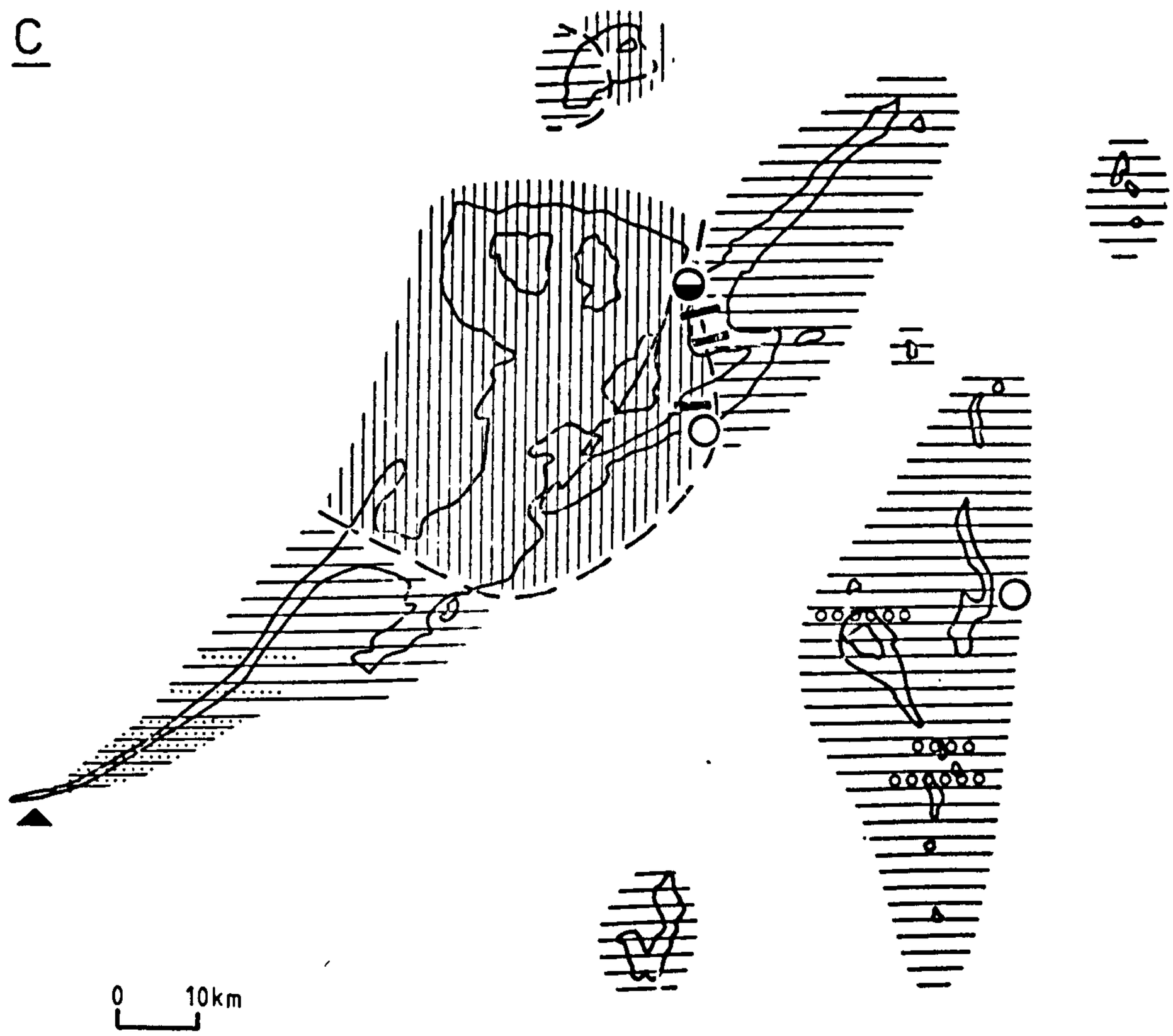


Fig. 5.37 : Neobeyrichiids

Neobeyrichiids



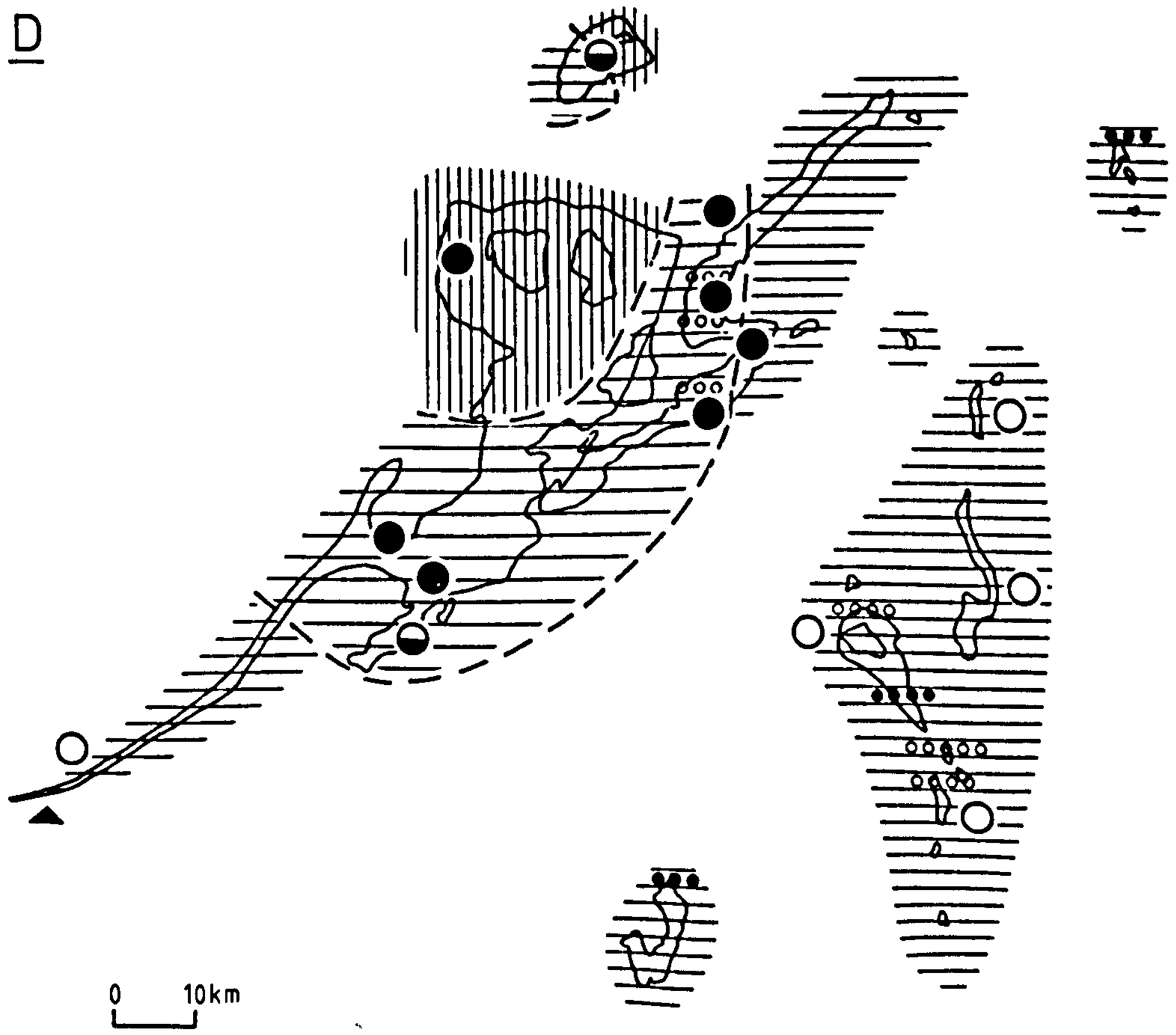
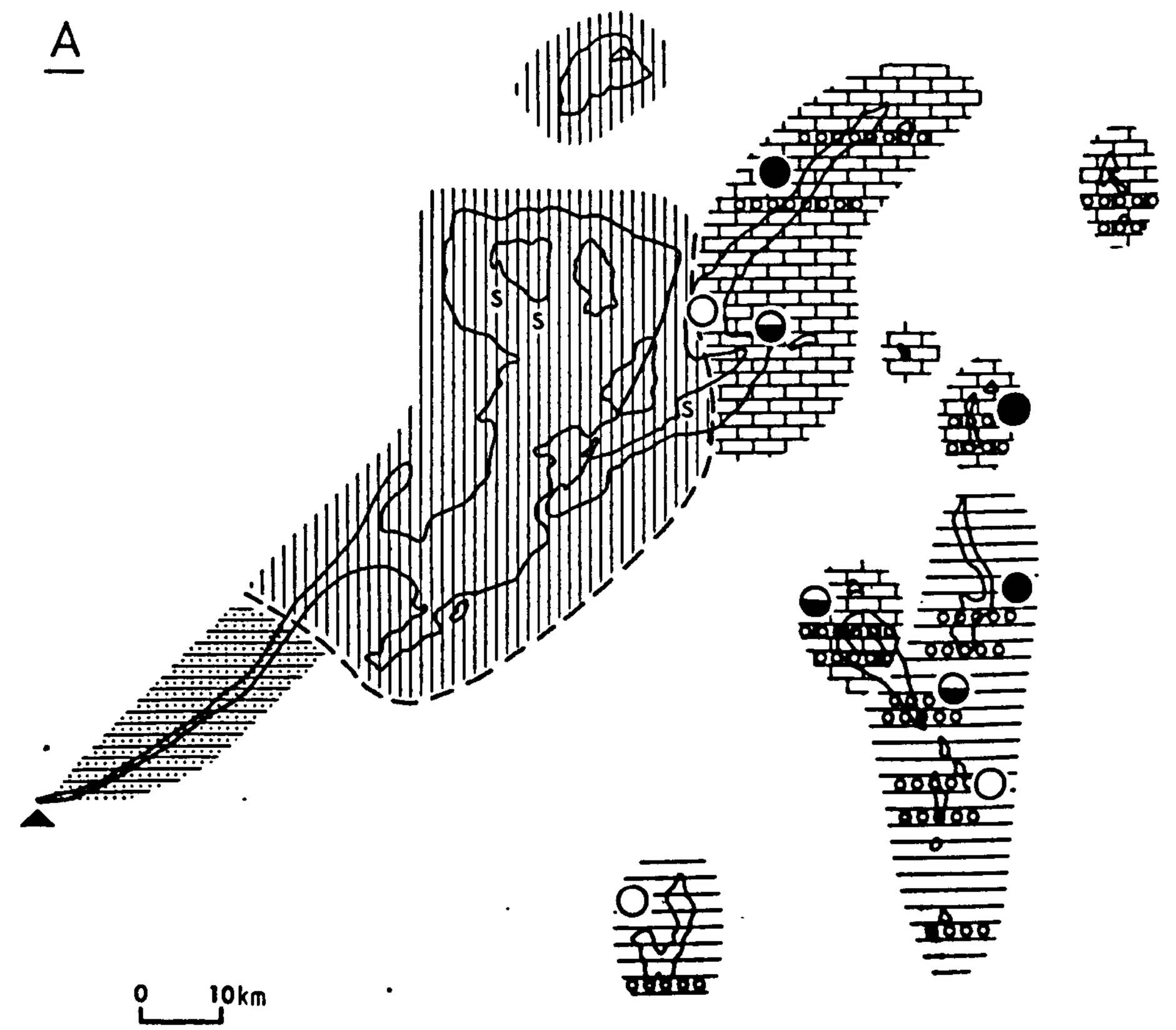


Fig. 5.37 : Neobeyrichiids

Non-palaeocope ostracodes



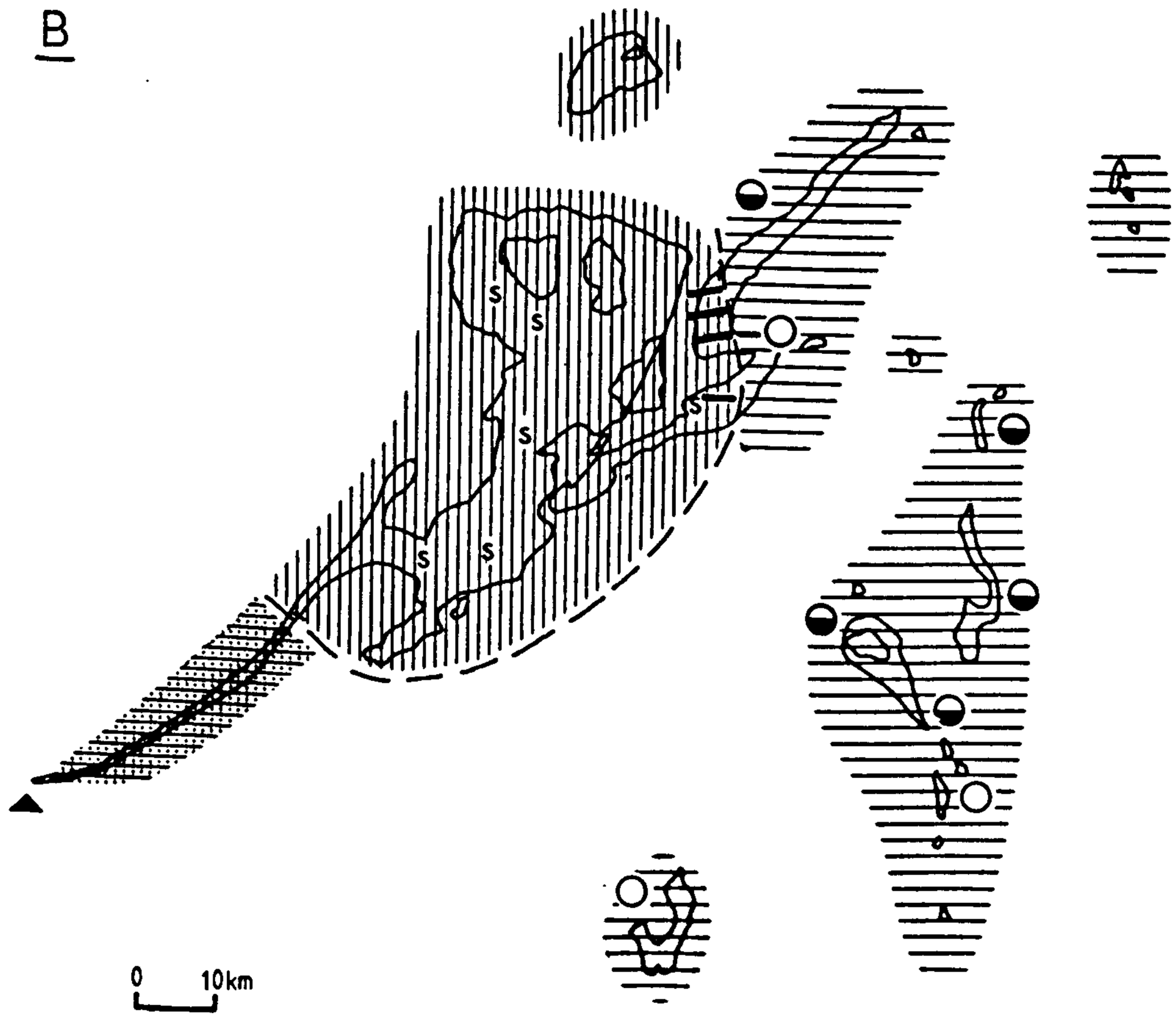
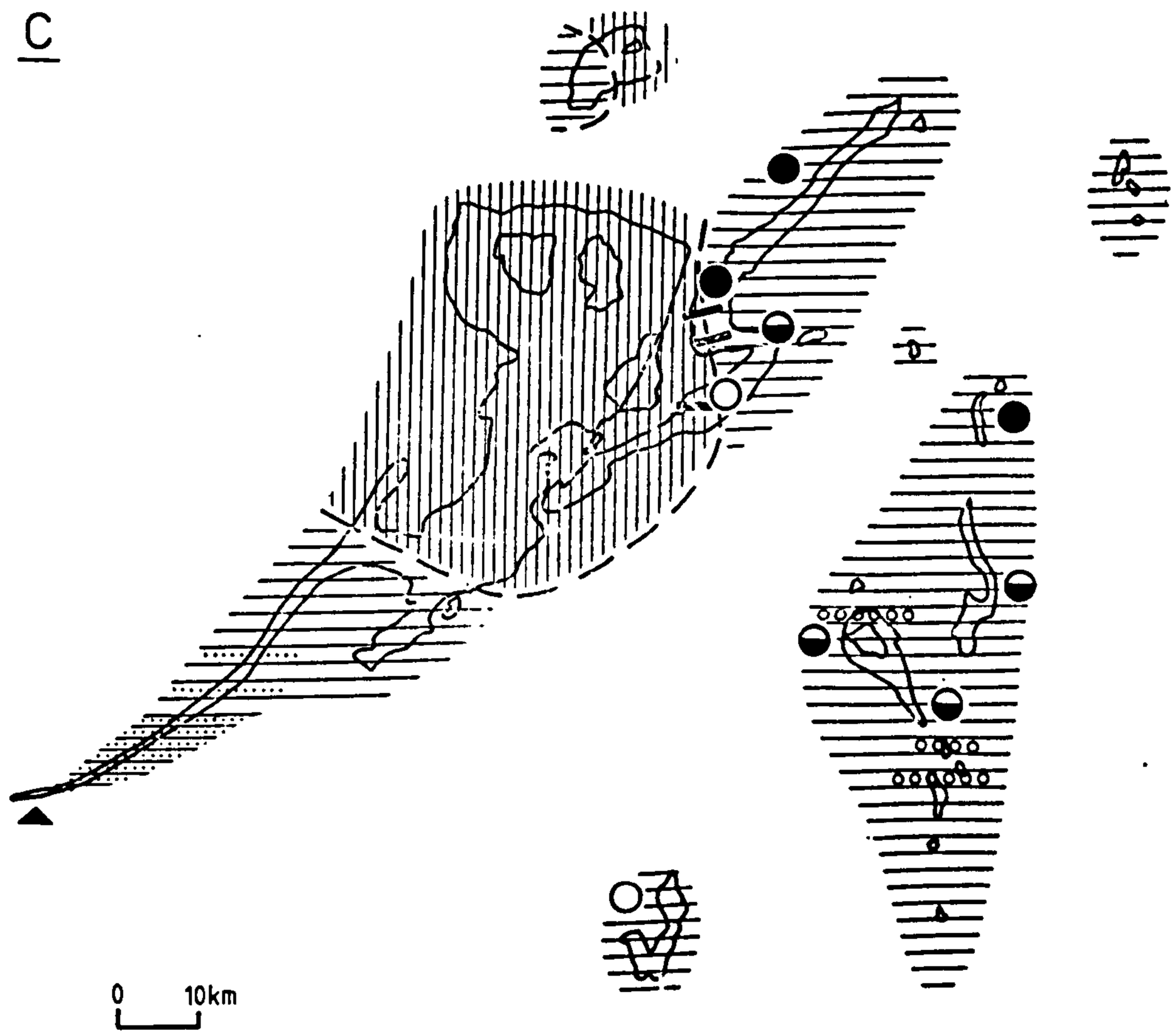


Fig. 5.38 : Non-palaeocope ostracodes

Non-palaeocope ostracodes



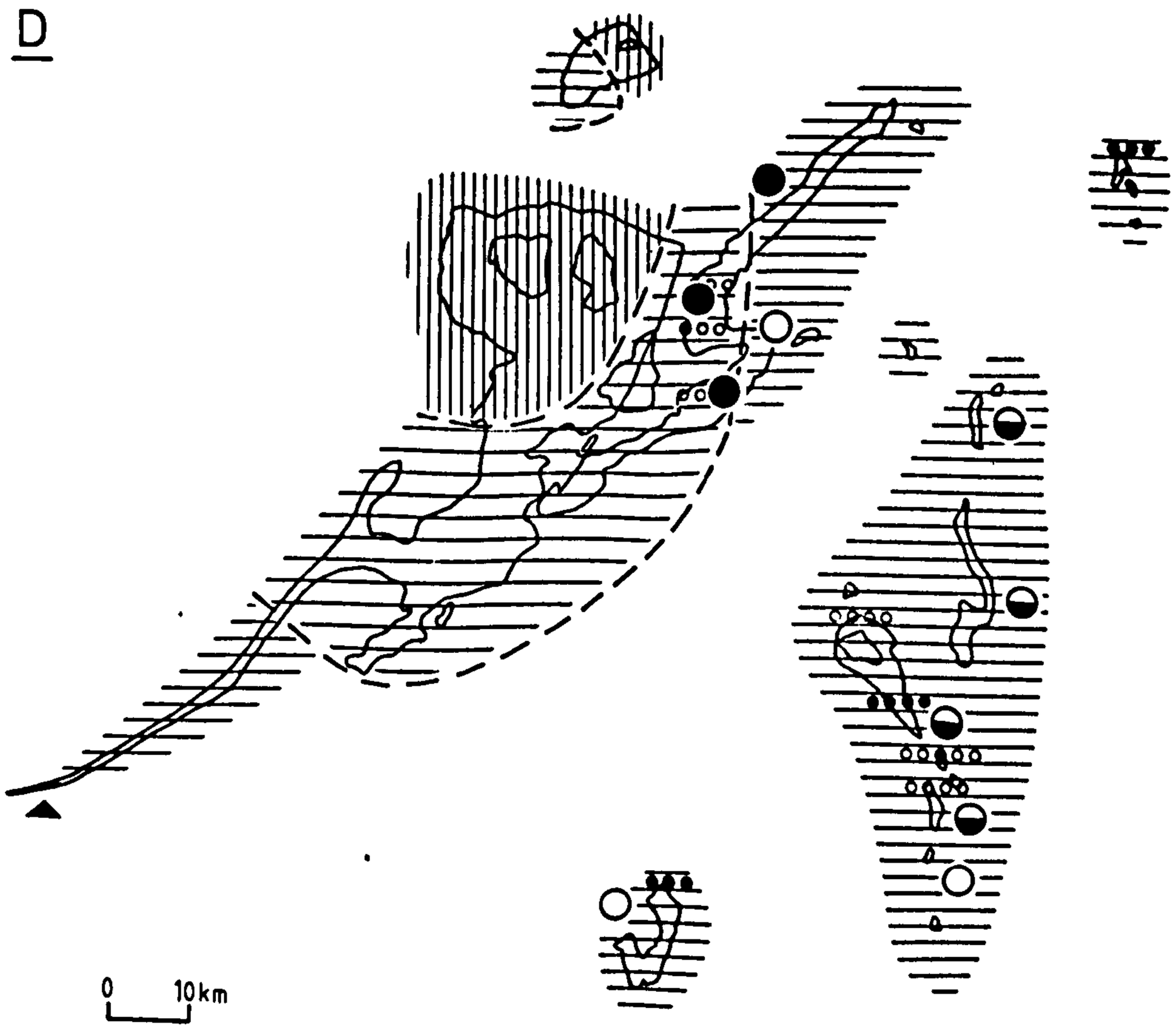


Fig. 5.38 : Non-palaeocope ostracodes

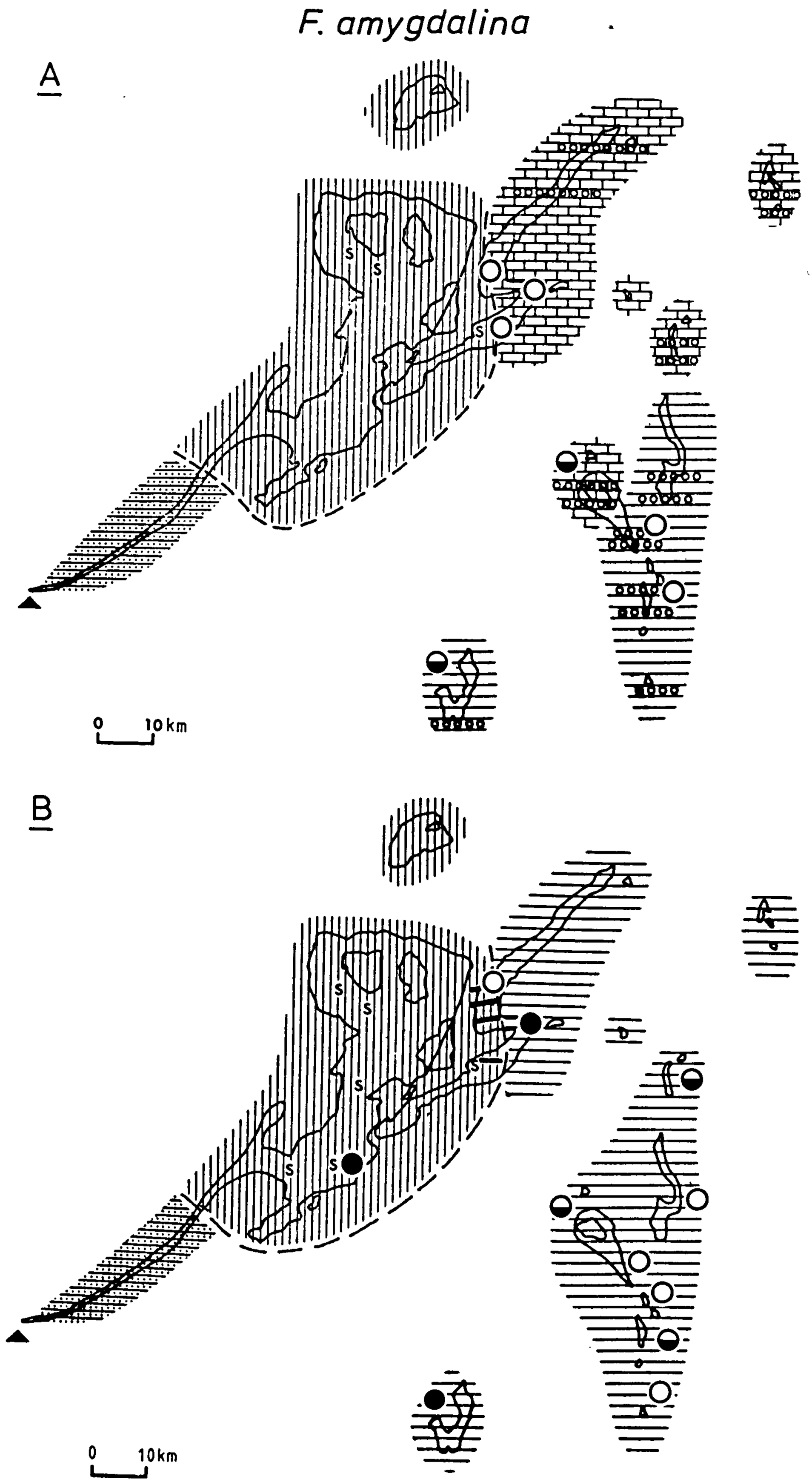
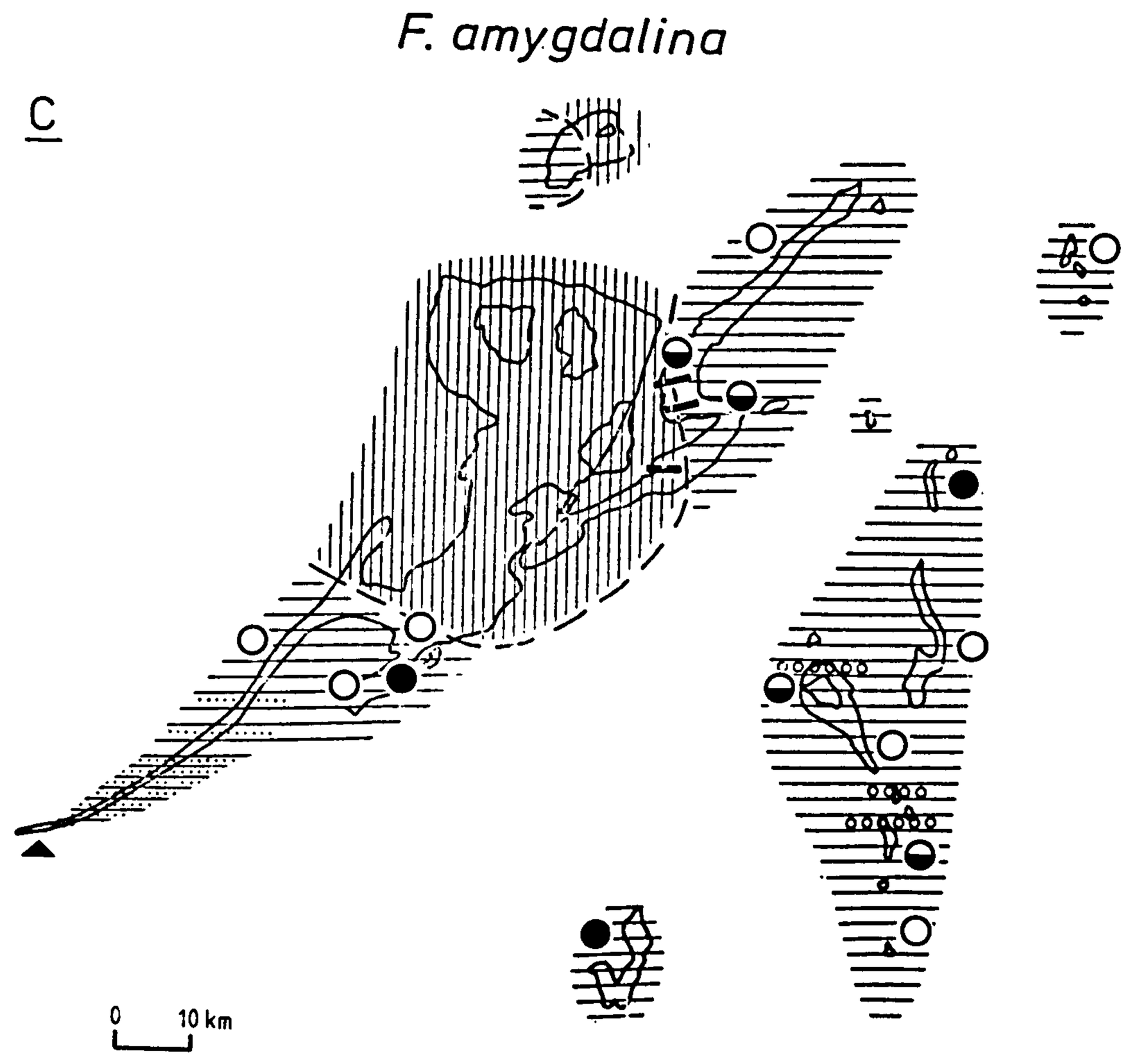


Fig. 5.40 : F. amygdalina



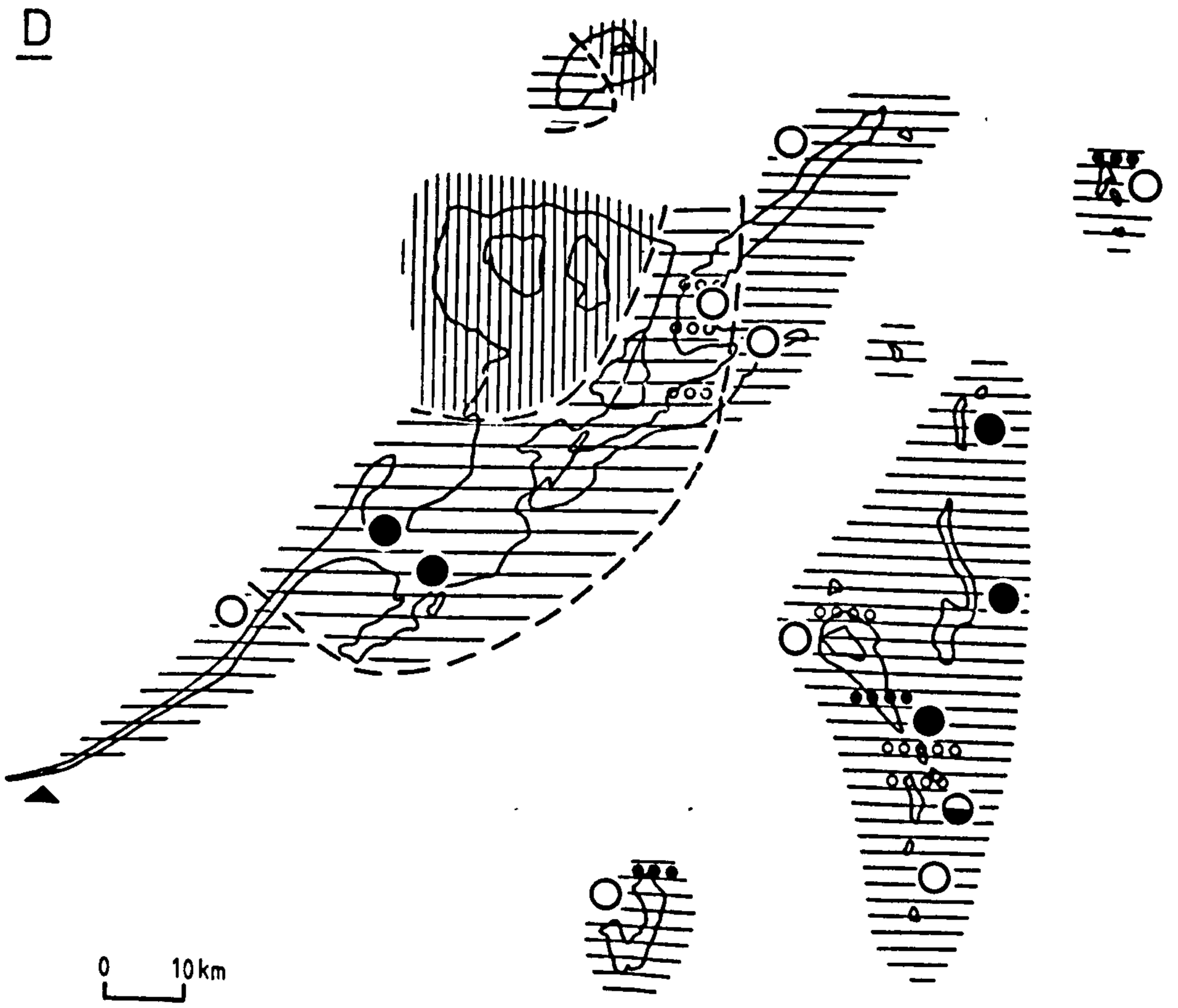


Fig. 5.40 : F. amygdalina

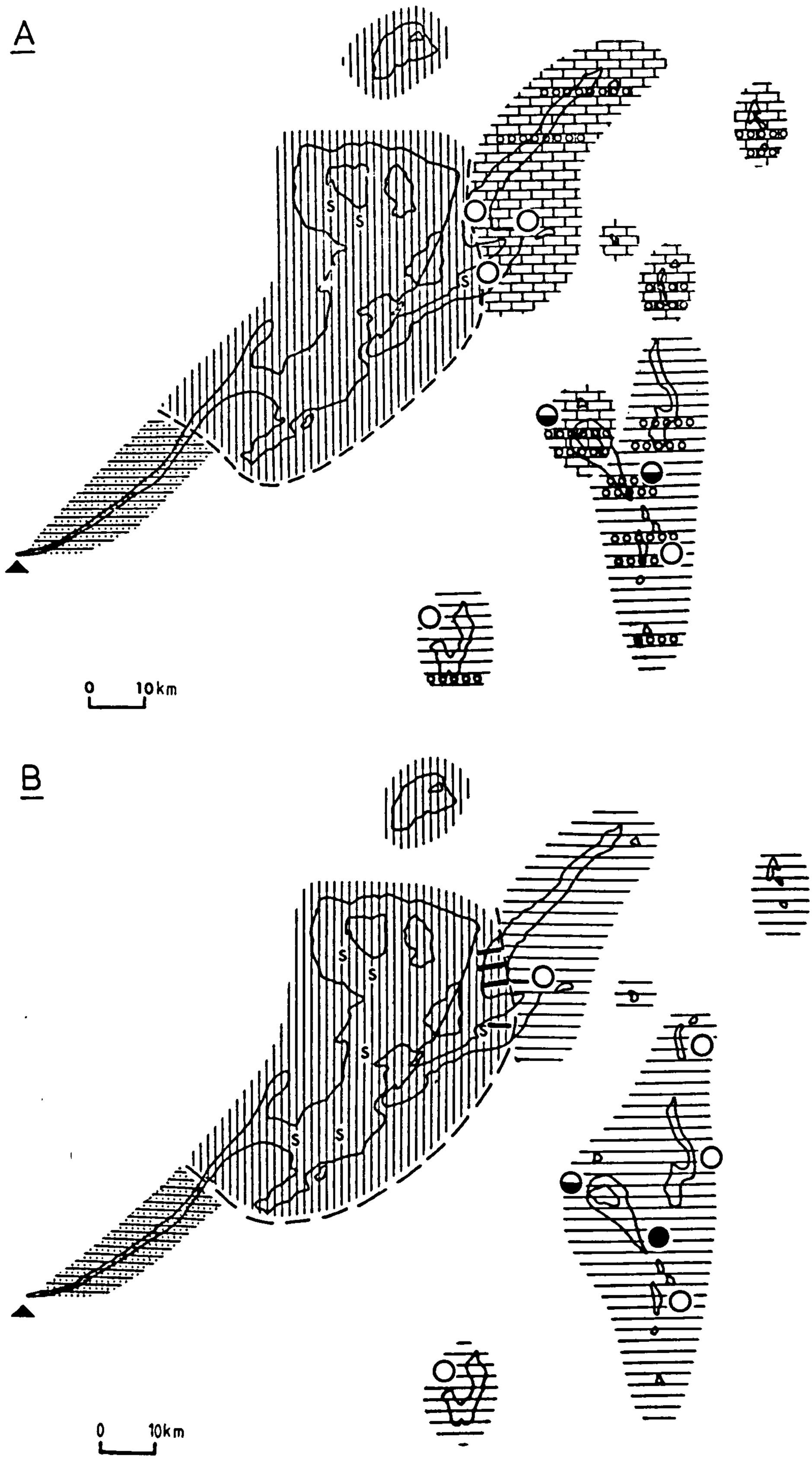


Fig. 5.41 : G. cymbaeformis

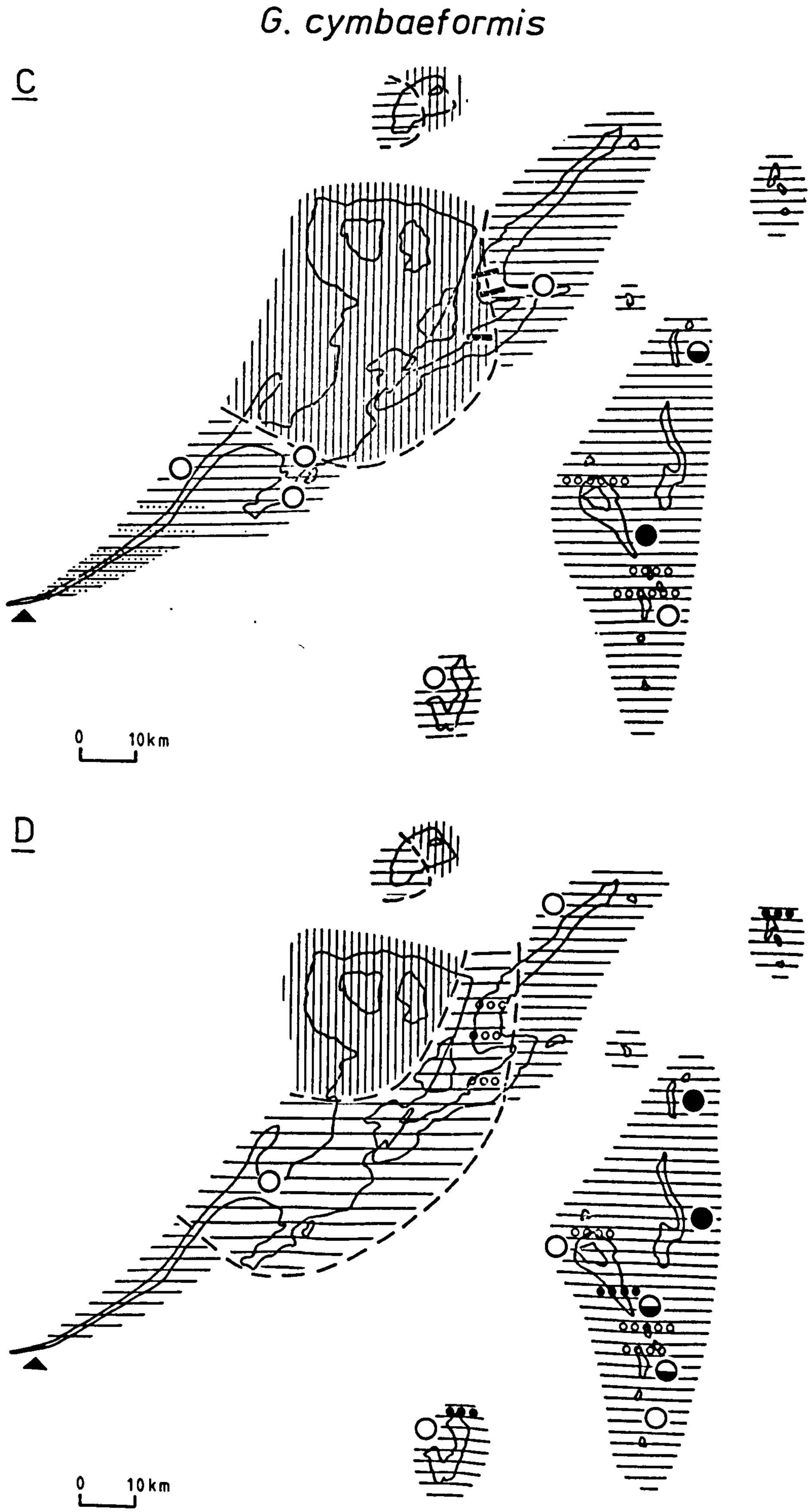
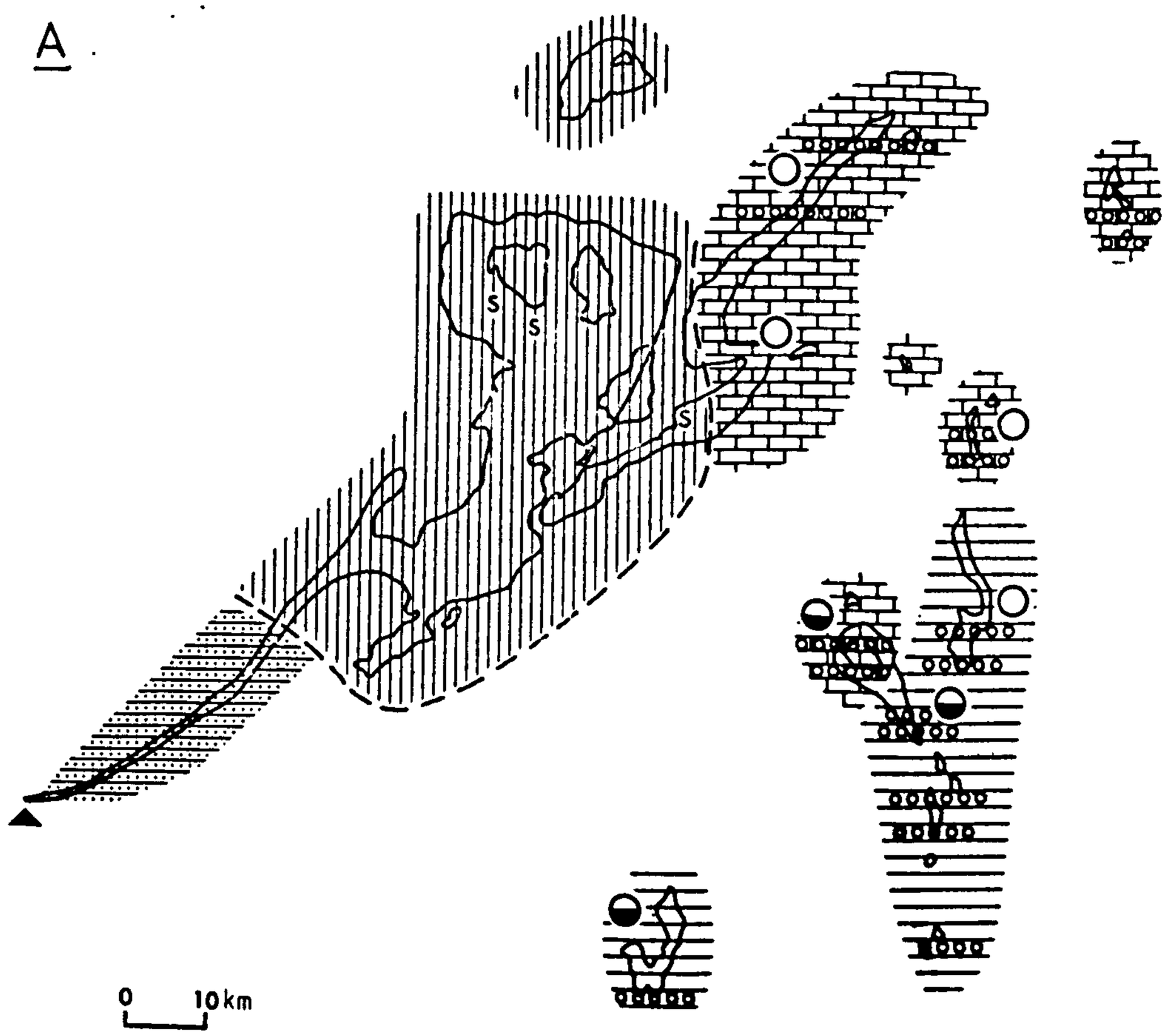


Fig. 5.41 : G. cymbaeformis

Pteronitella spp.

A



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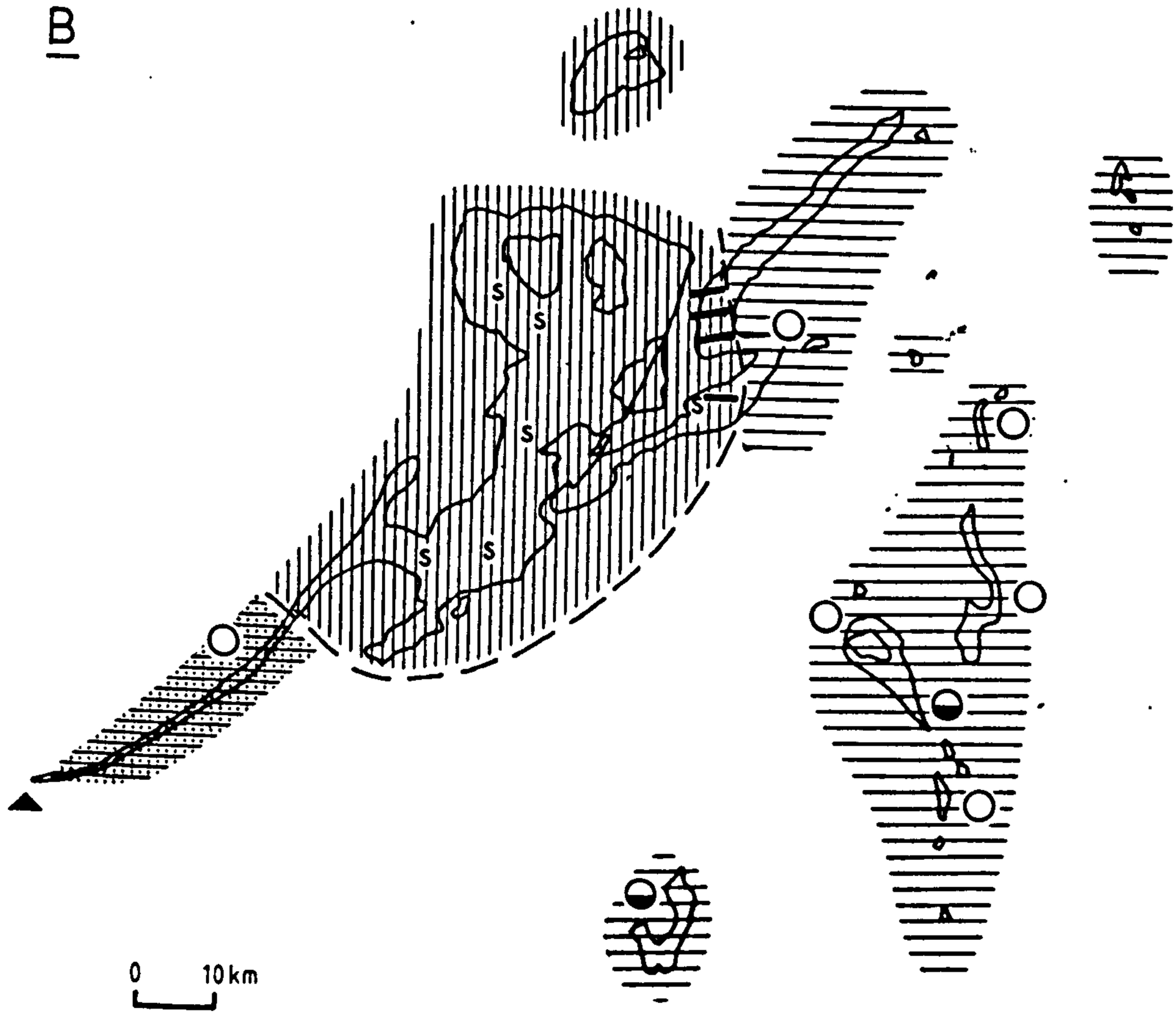


Fig. 5.42 : Pteronitella spp.

Pteronitella spp.

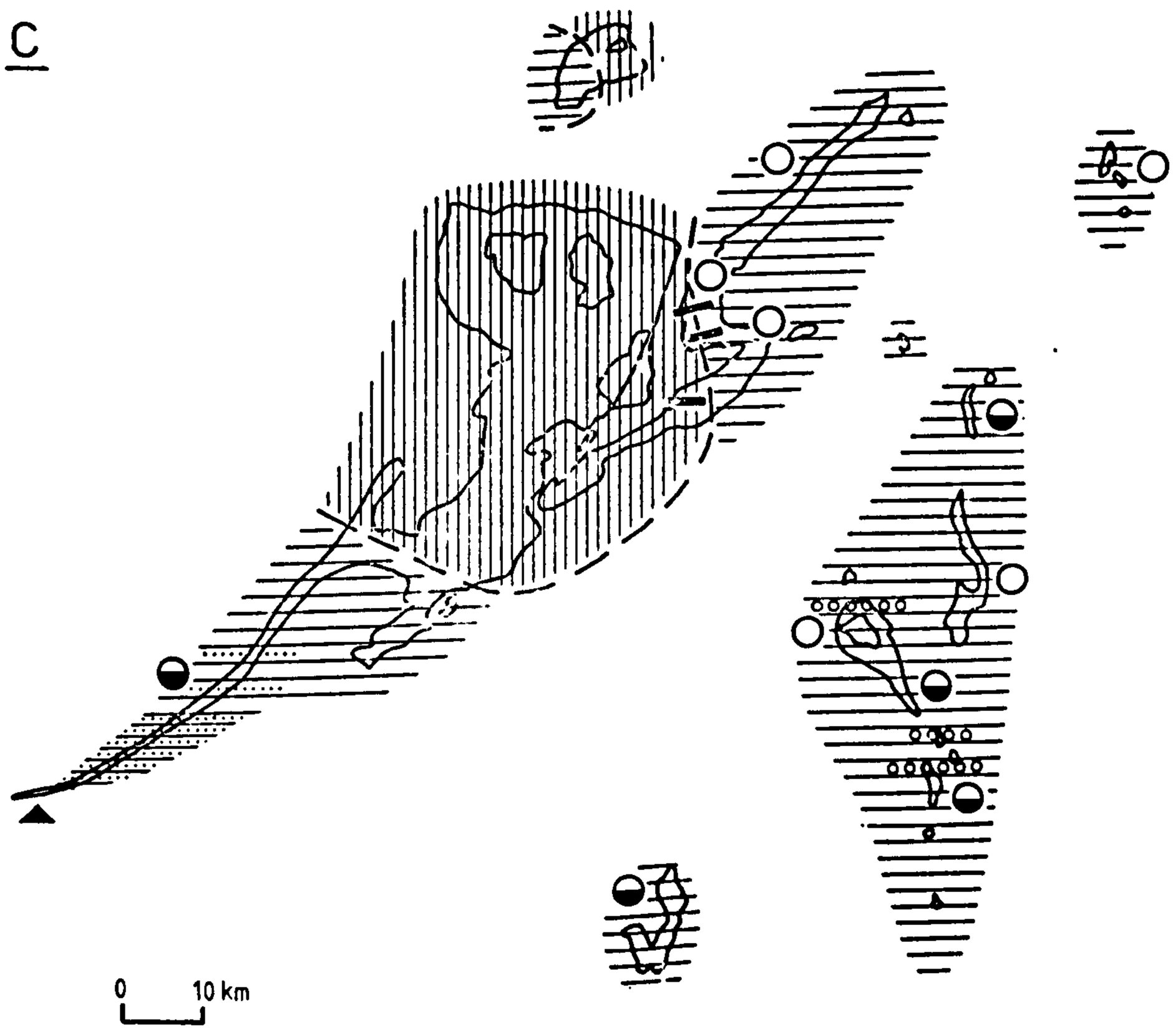
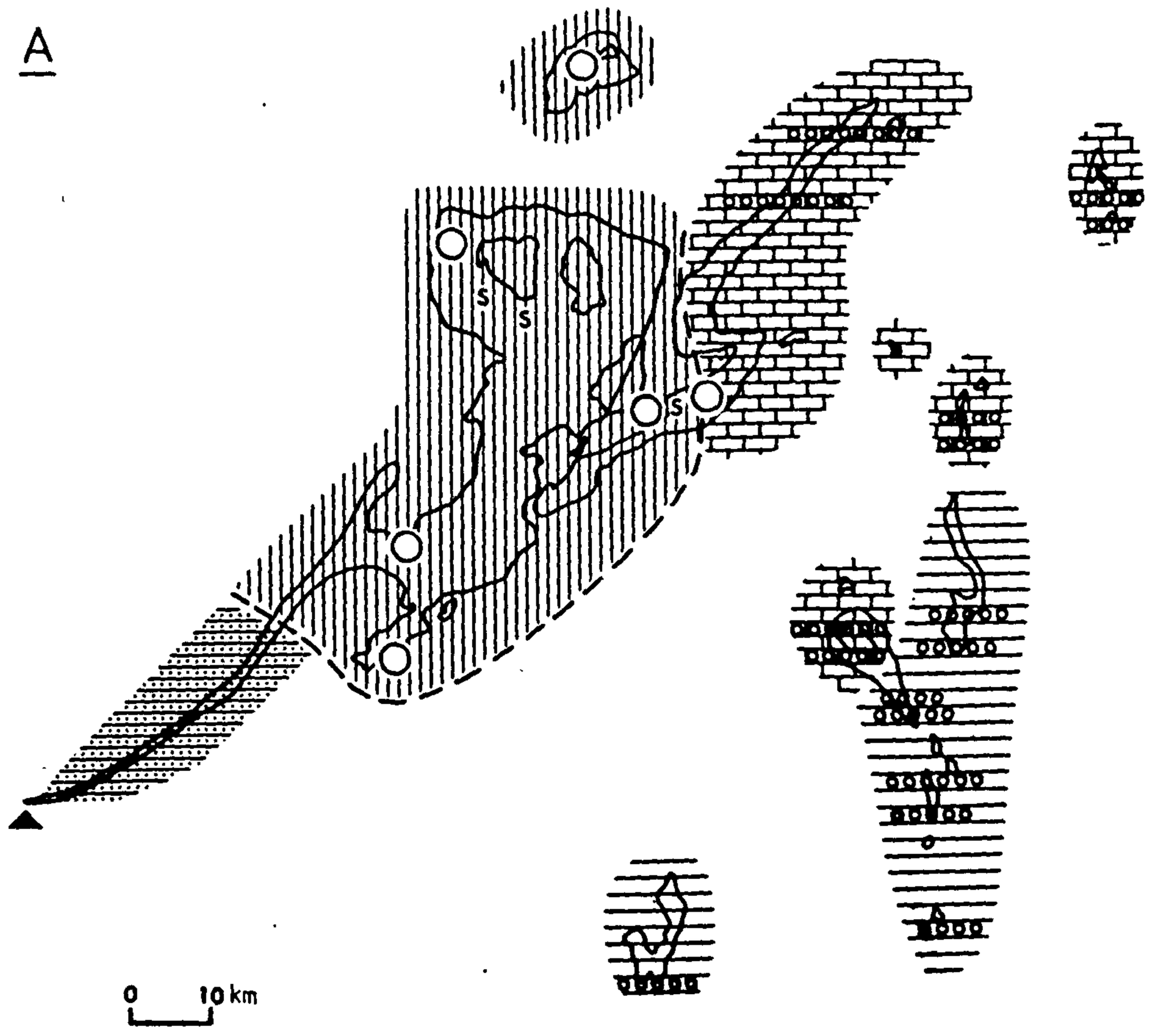


Fig. 5.42 : Pteronitella spp.

Pterinea spp.



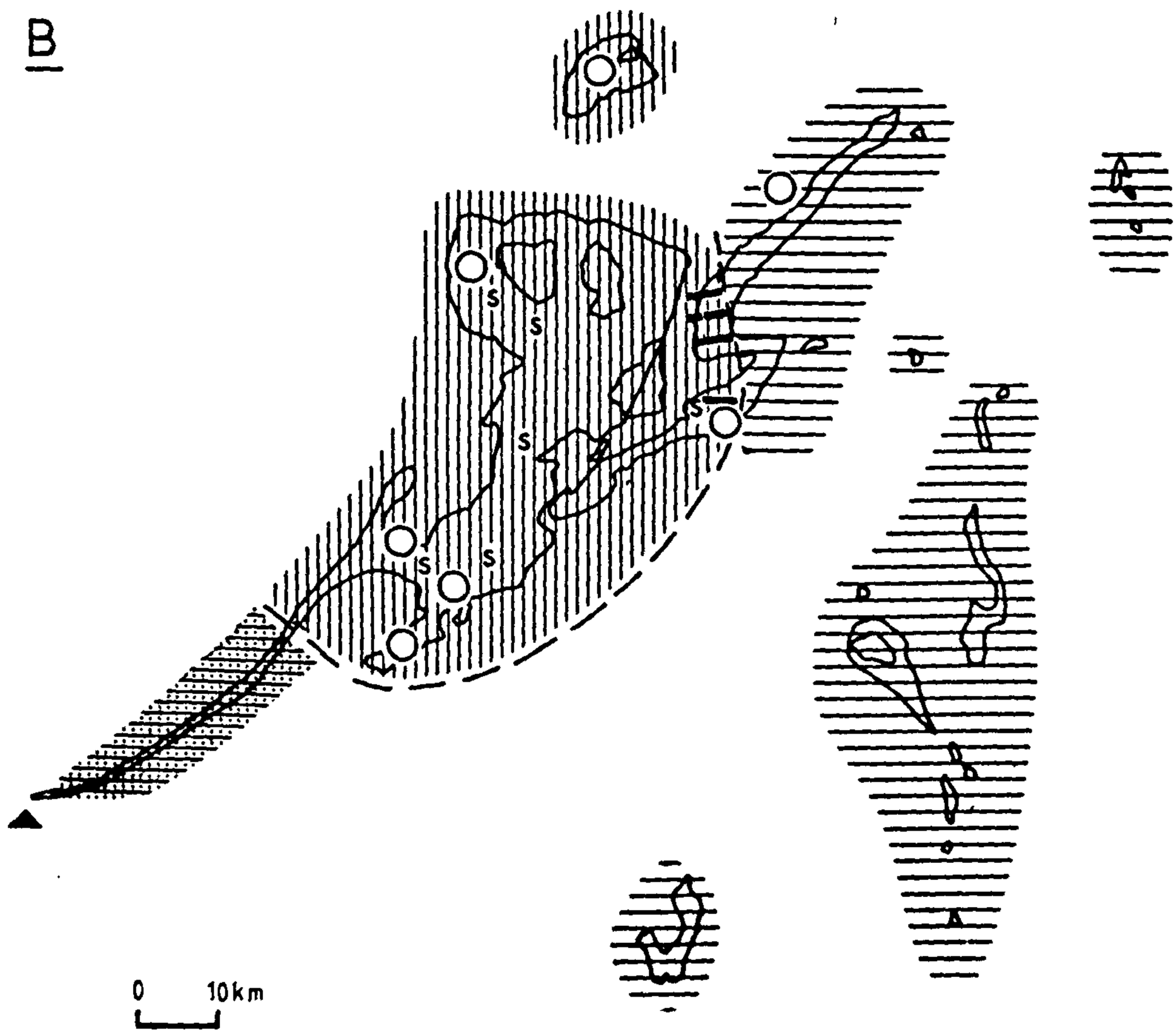


Fig. 5.43 : Pterinea spp.

Pterinea spp.

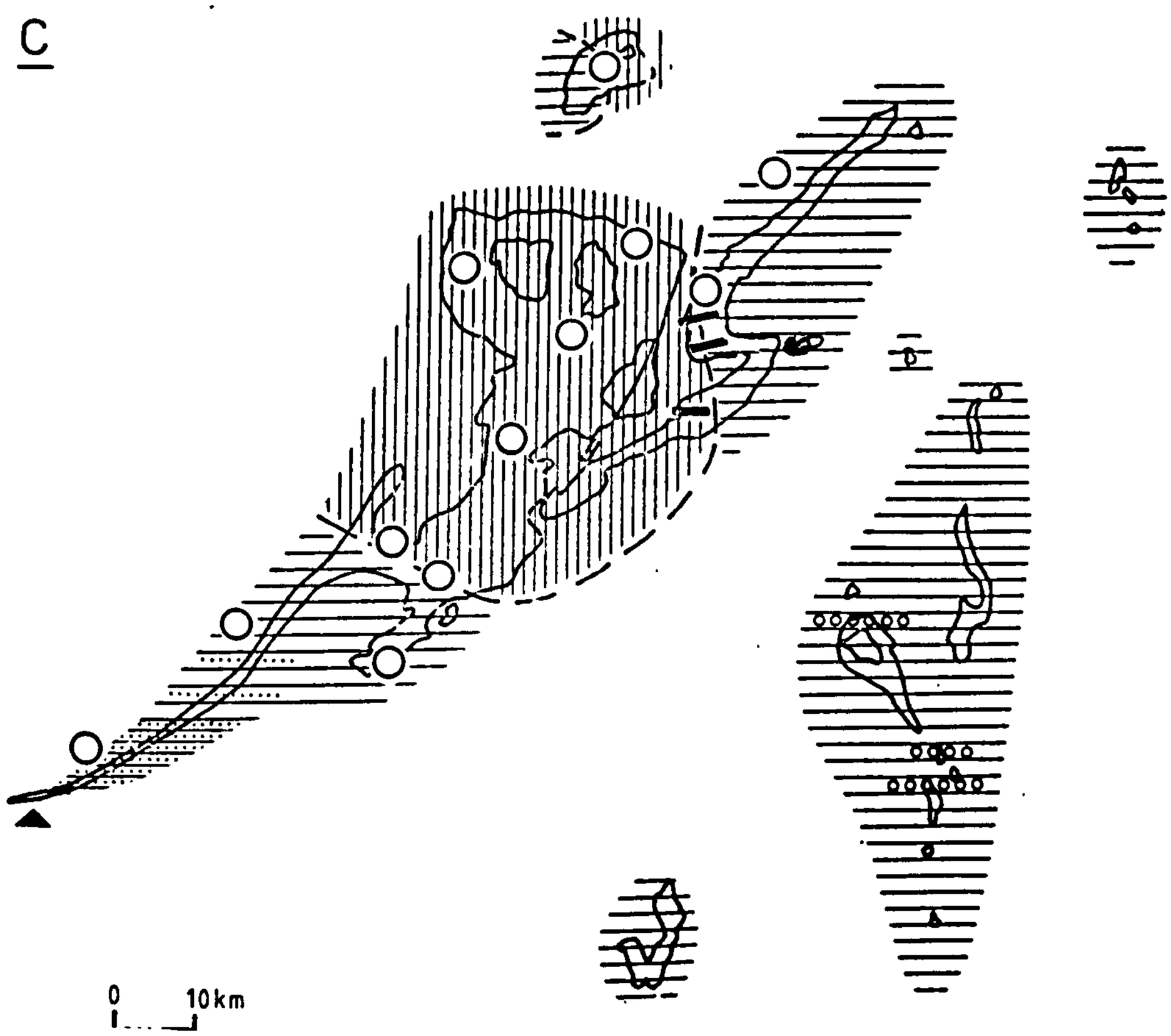


Fig. 5.43 : Pterinea spp.

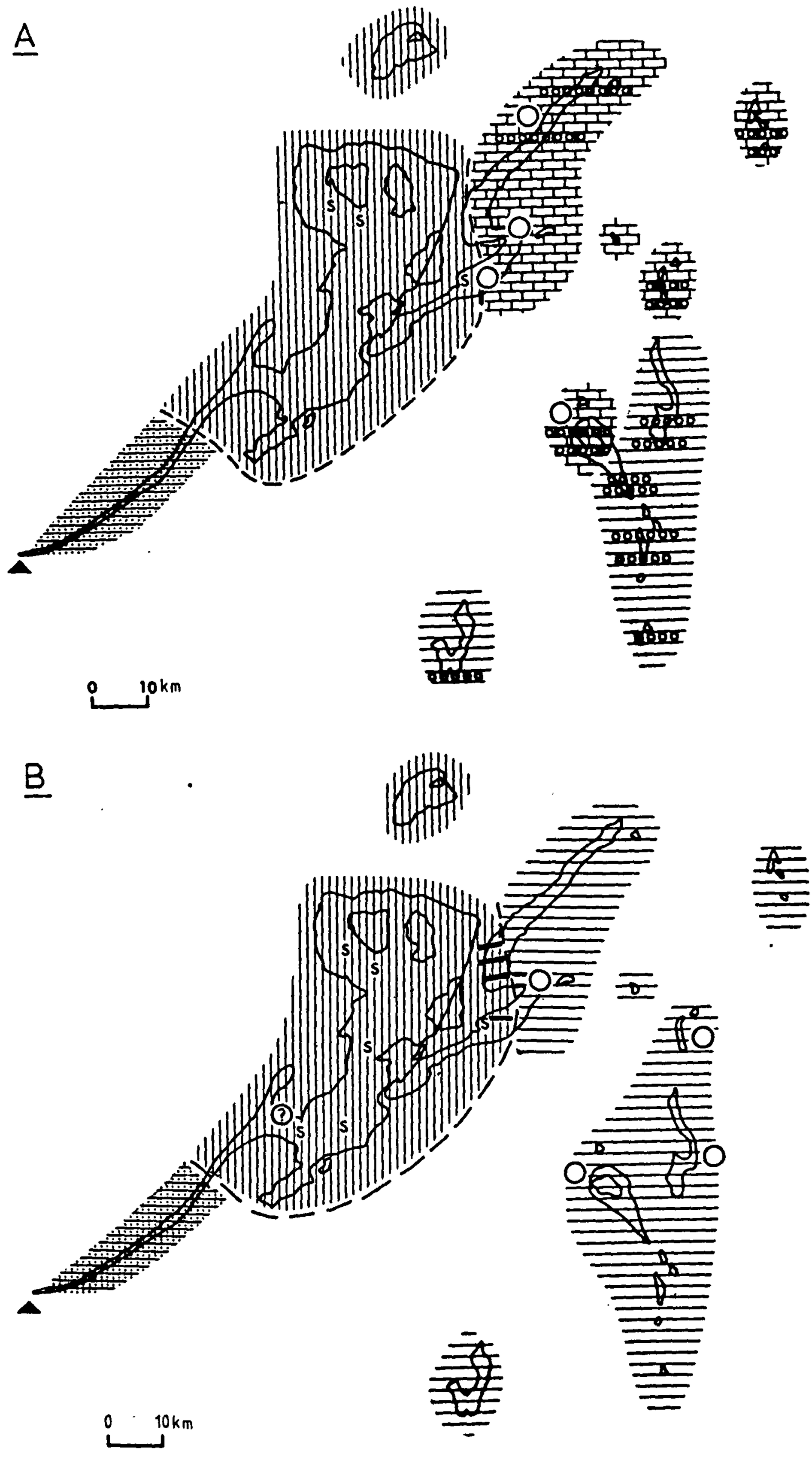
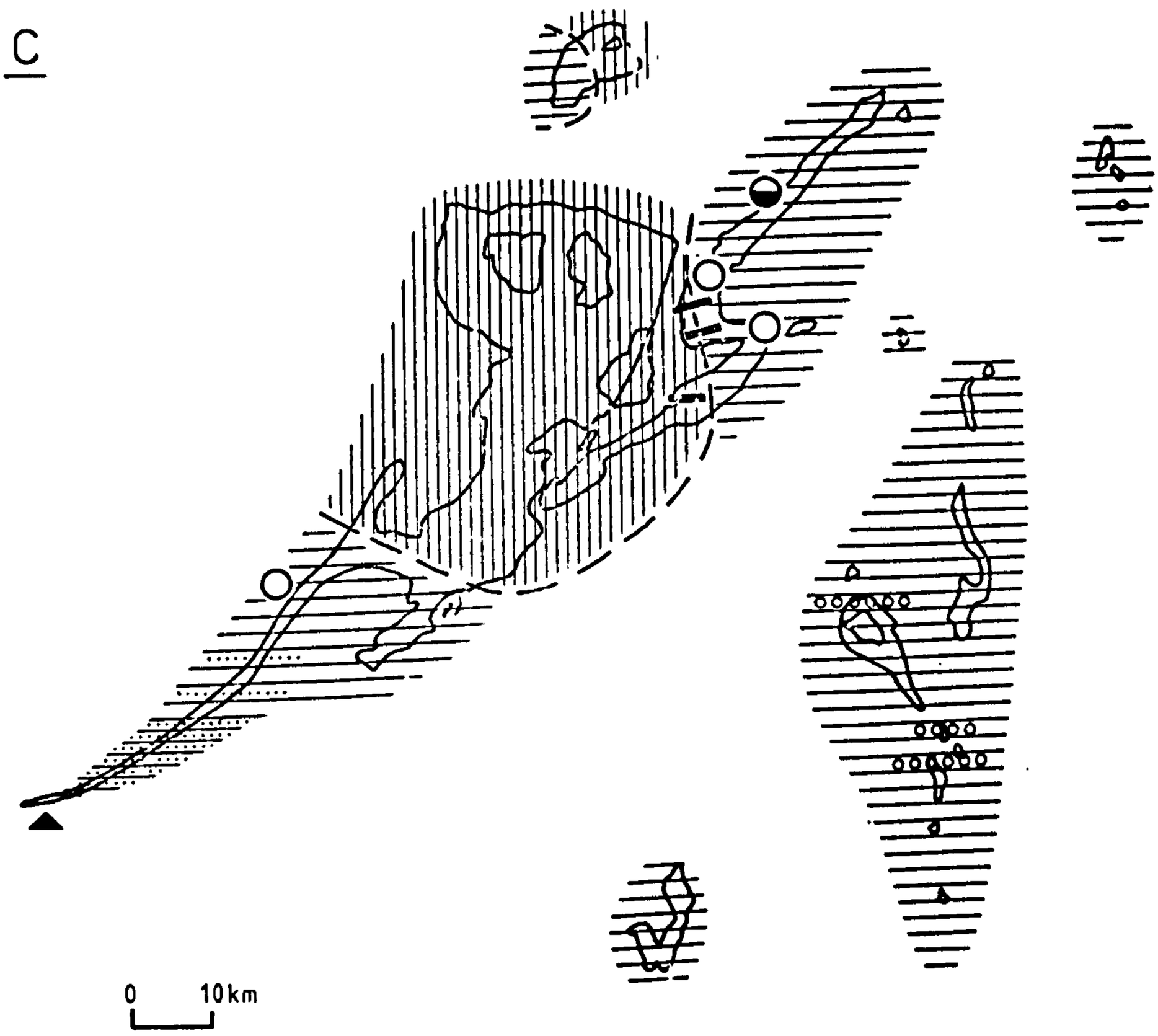


Fig. 5.44 : C. planulata



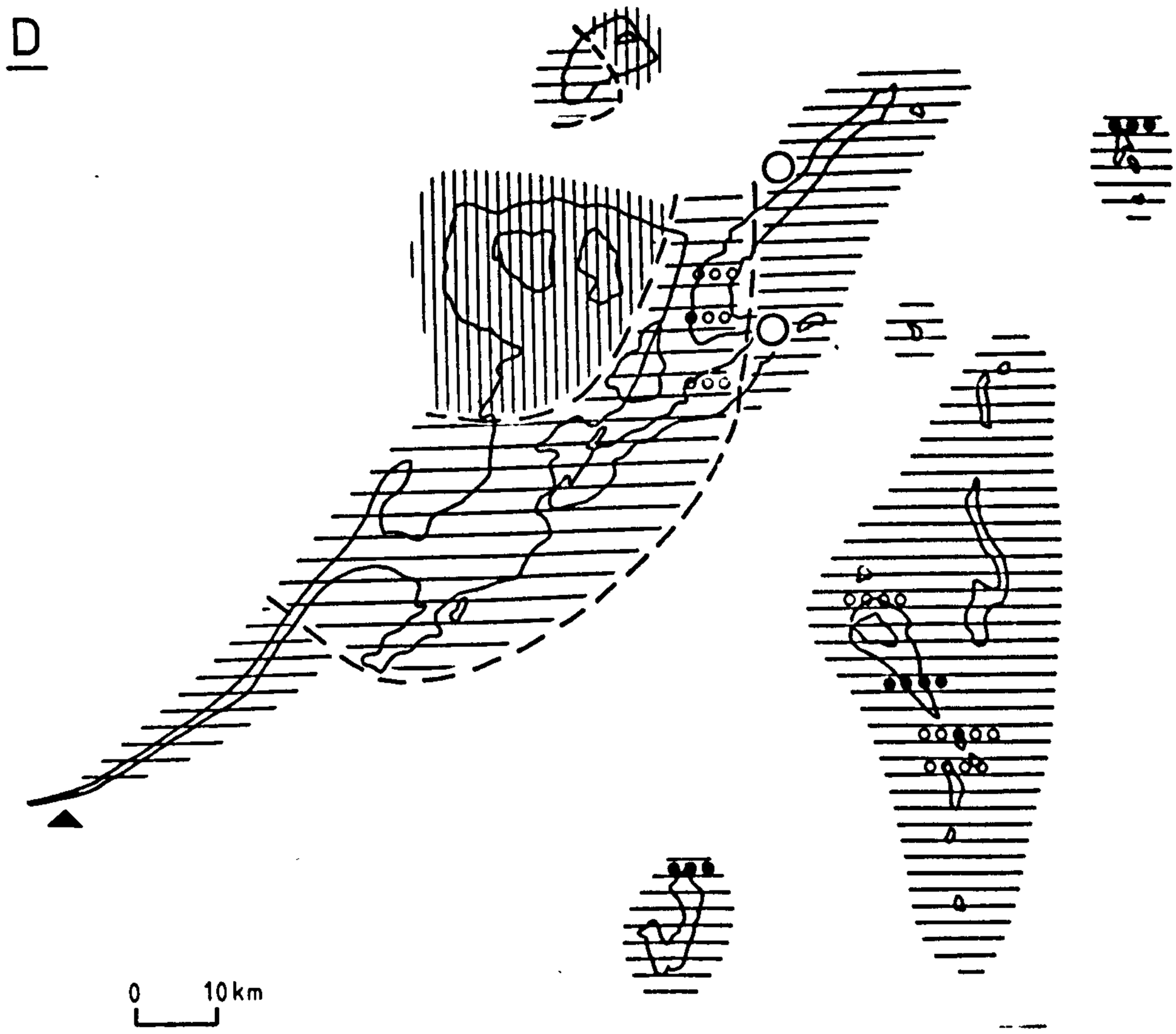
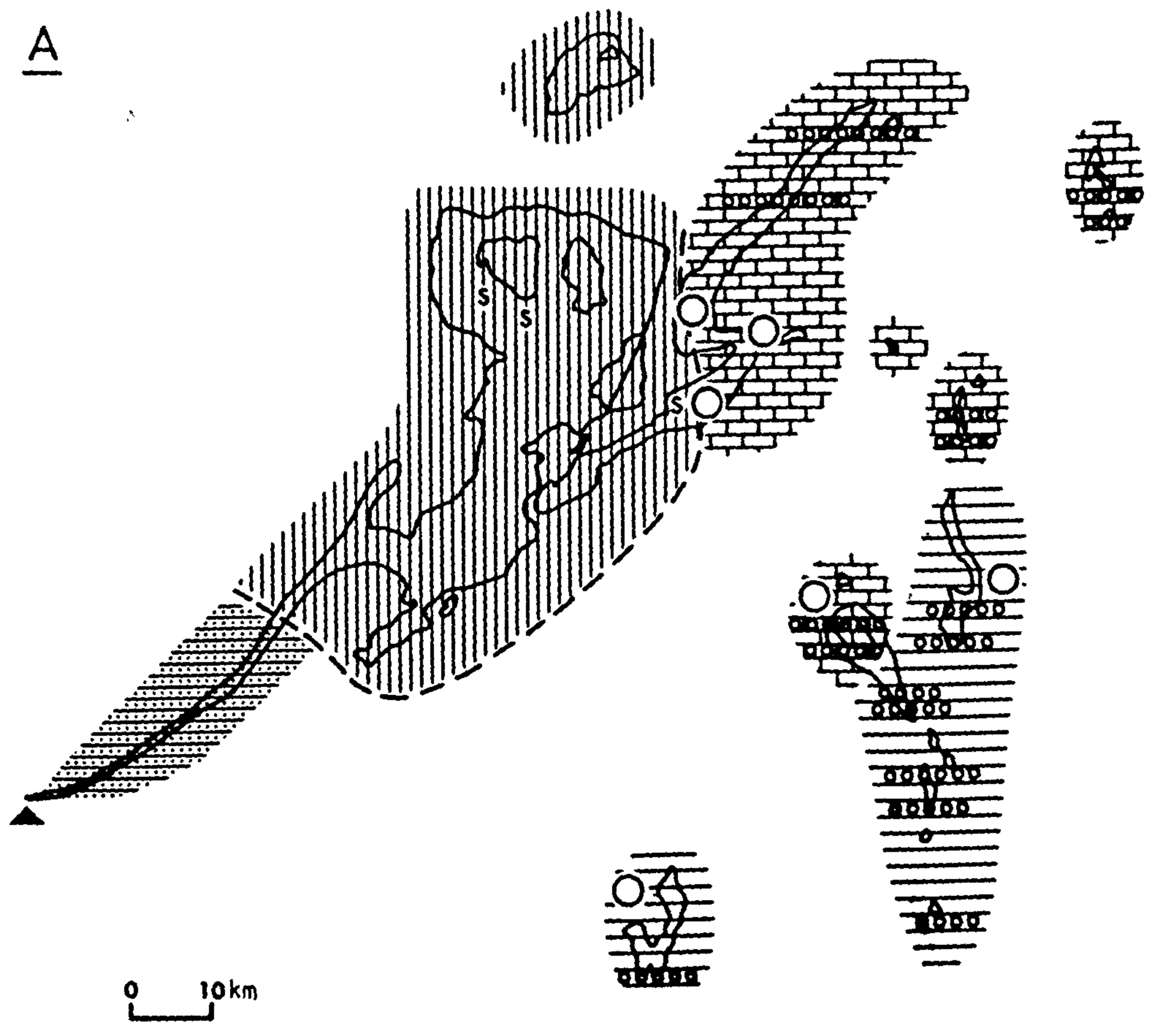


Fig. 5.44 : C. planulata

C. cornucopiae



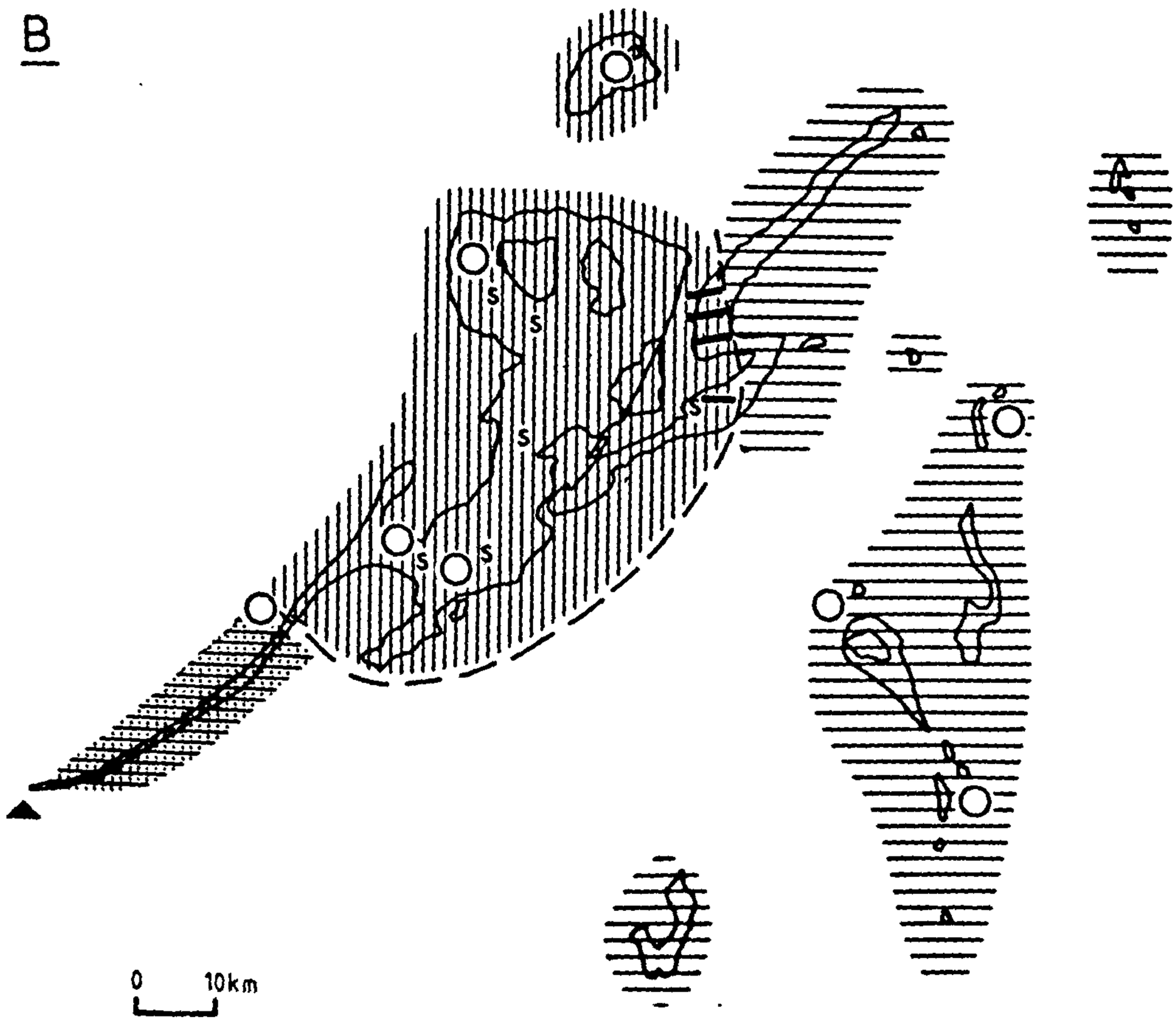


Fig. 5.45 : C. cornucopiae

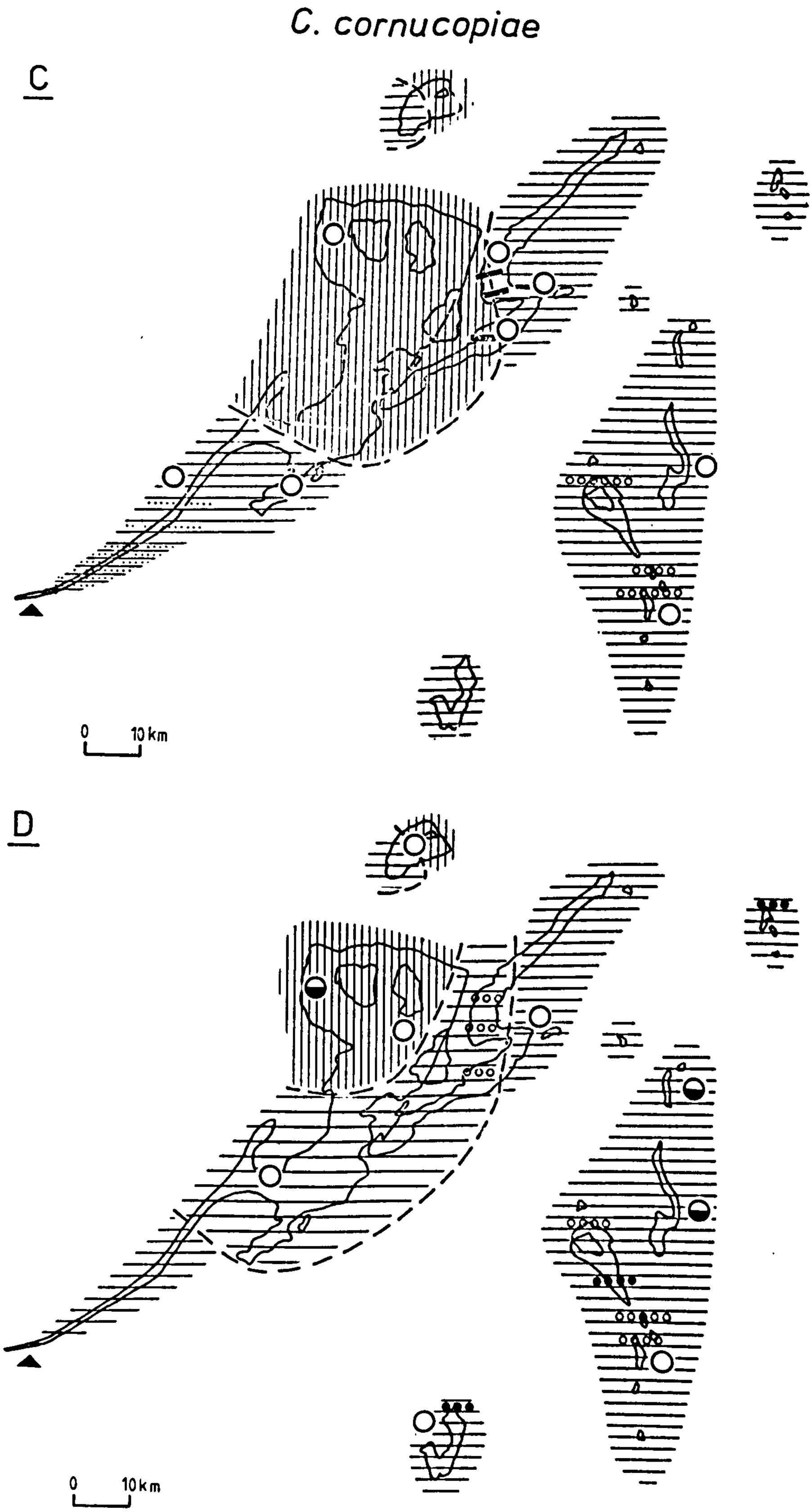


Fig. 5.45 : C. cornucopiae

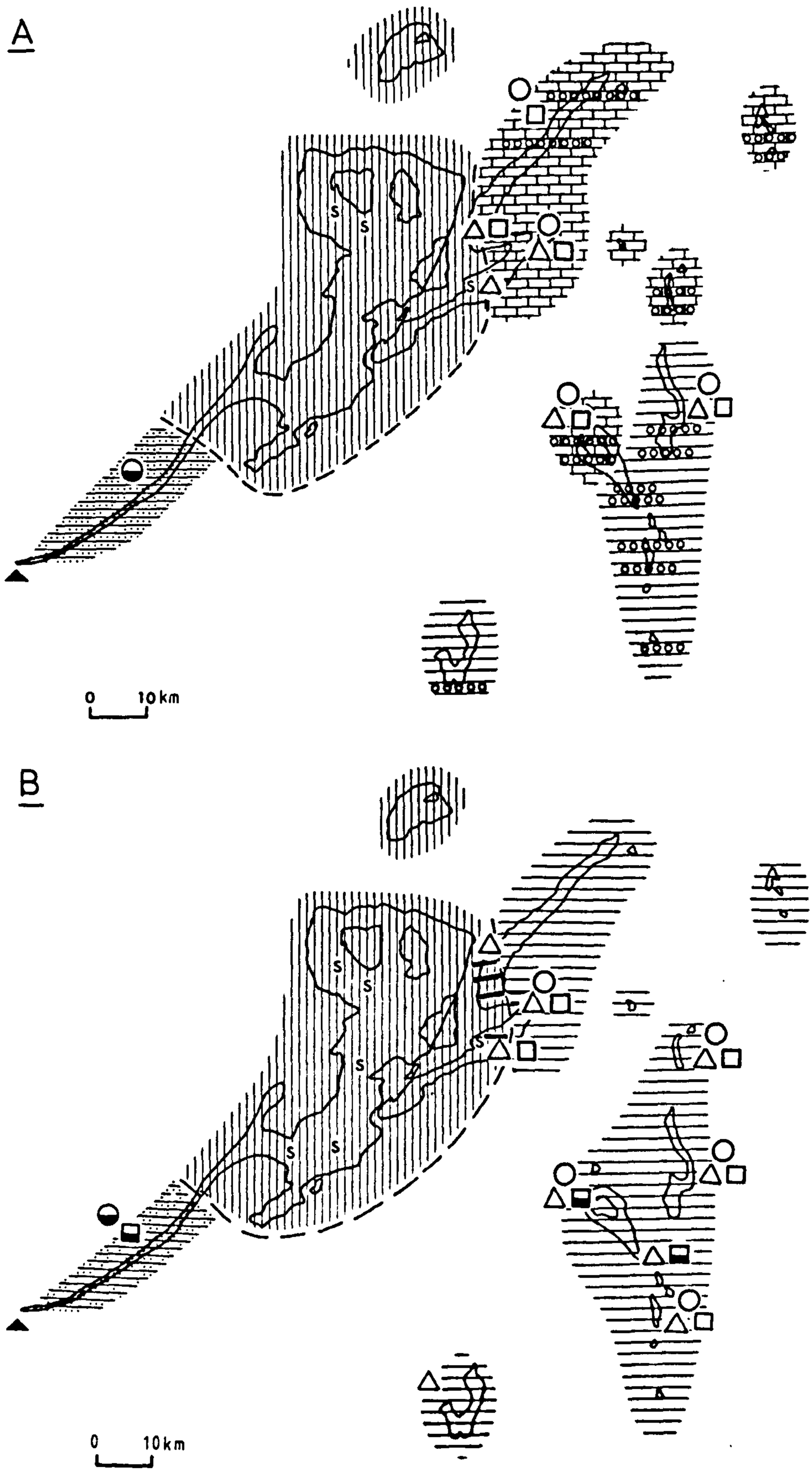


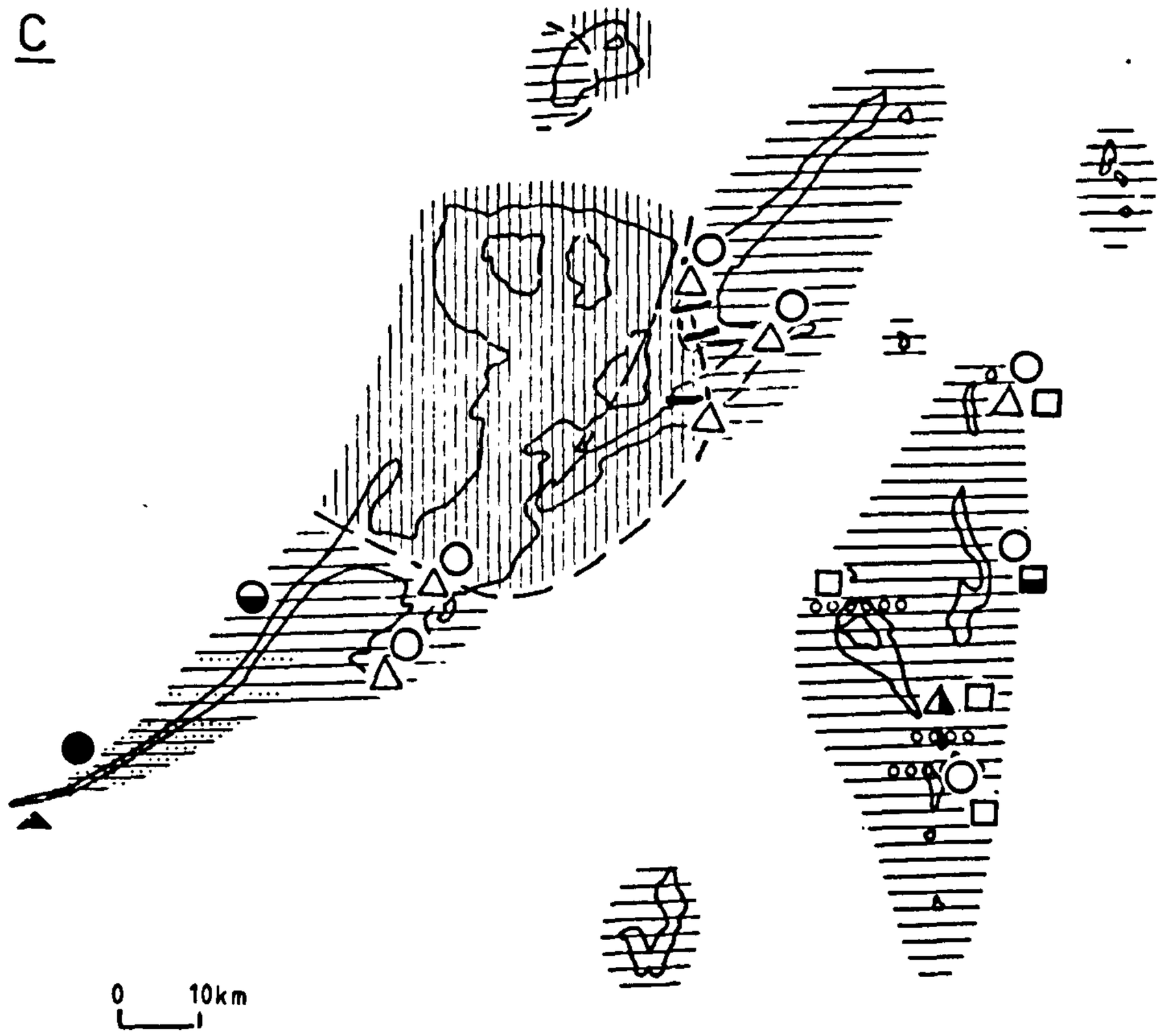
Fig. 5.46 : Gastropods

Gastropods - *B. lloydii* △

C. corallii □

Loxonema sp. ○

C



D

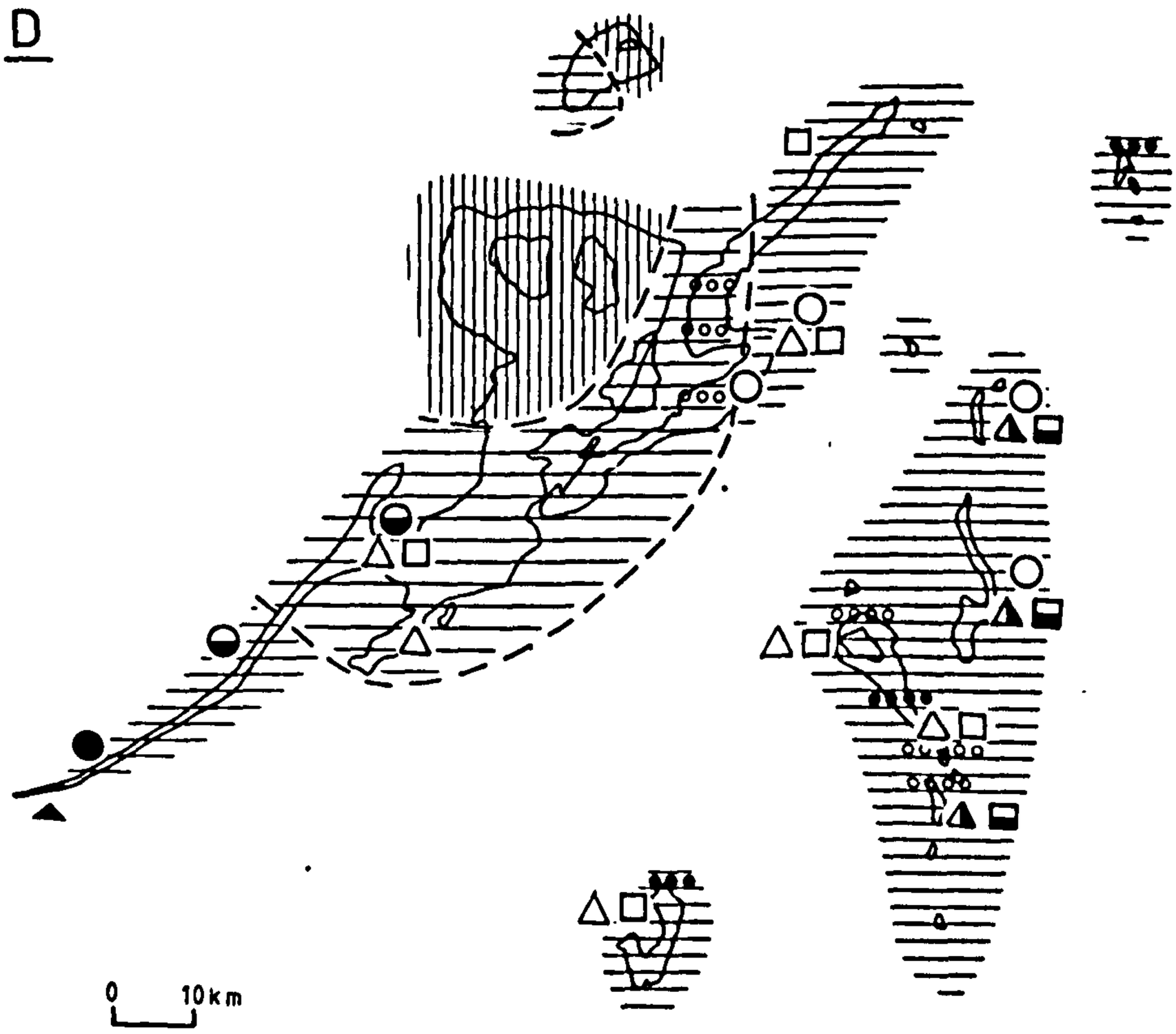
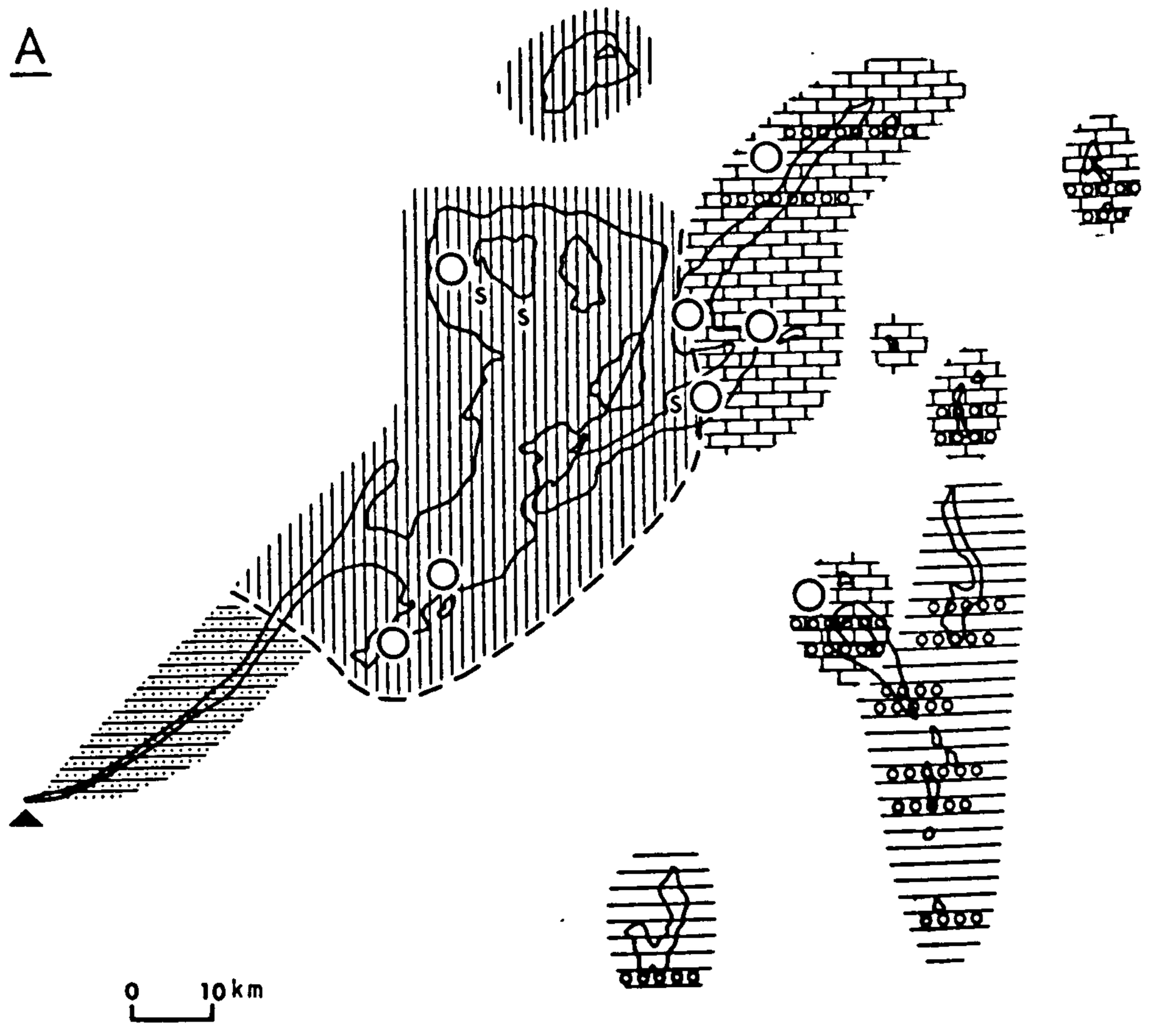


Fig. 5.46 : Gastropods

Orthocones



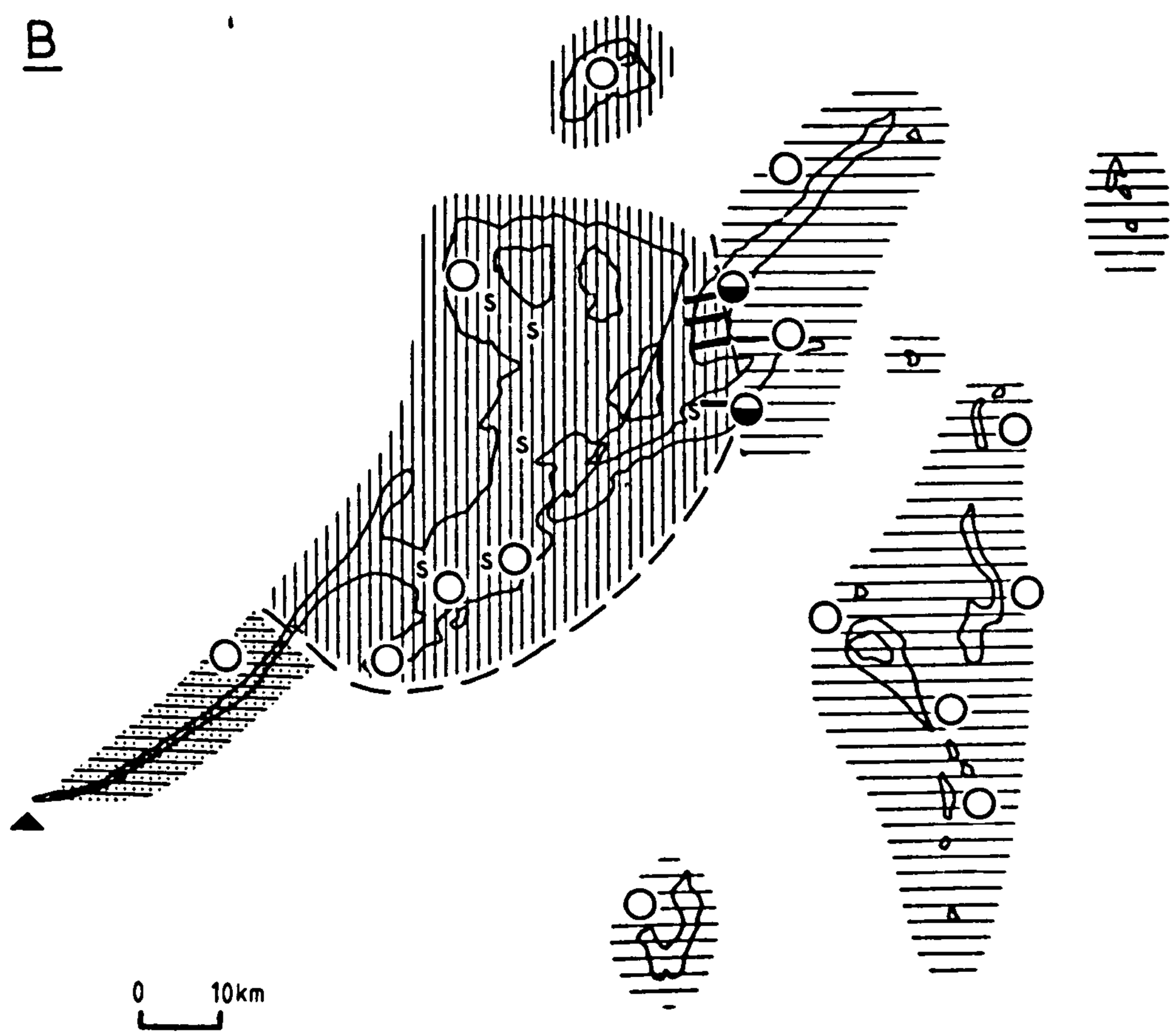
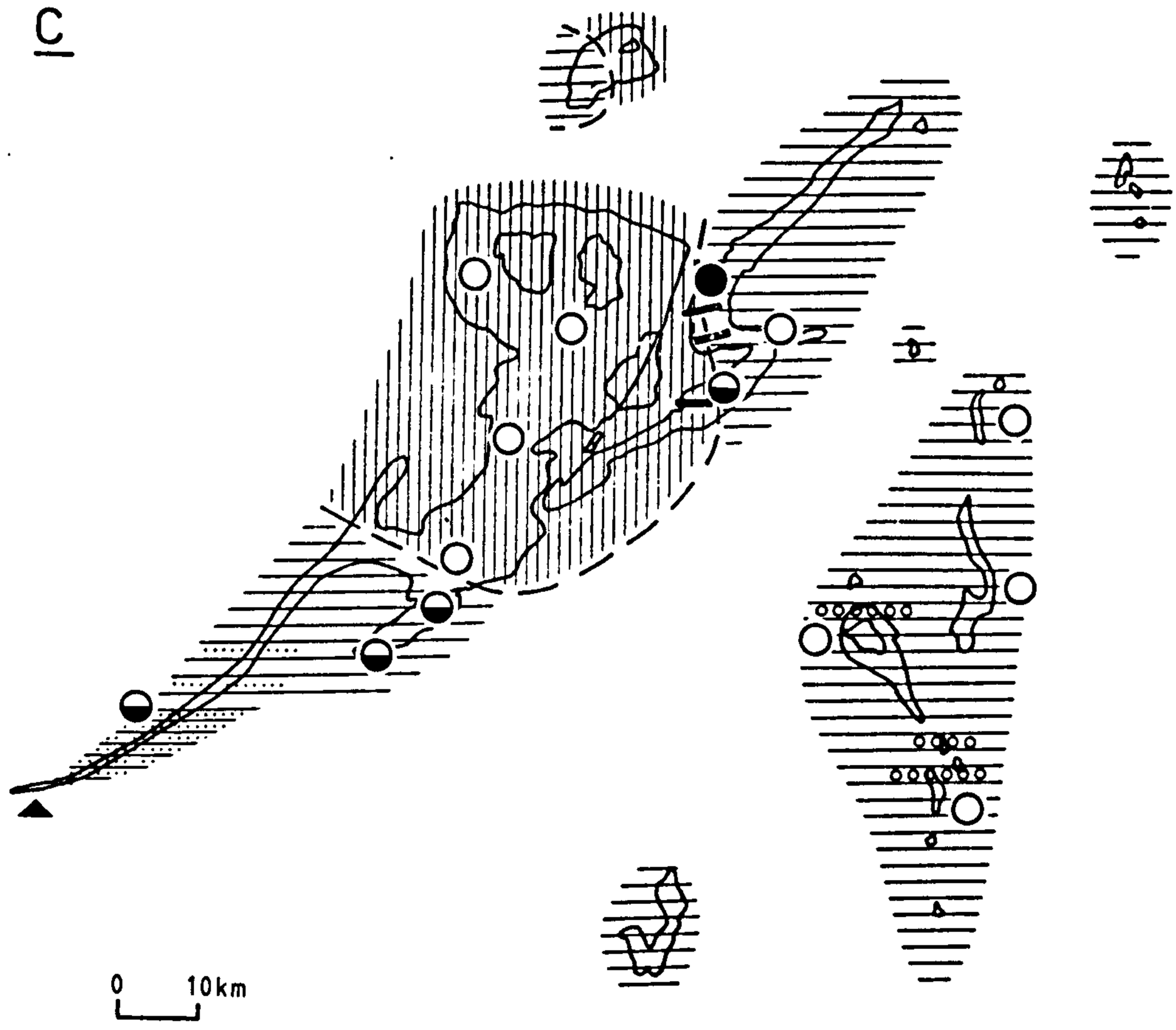


Fig. 5.47 : Orthocones

Orthocones

C



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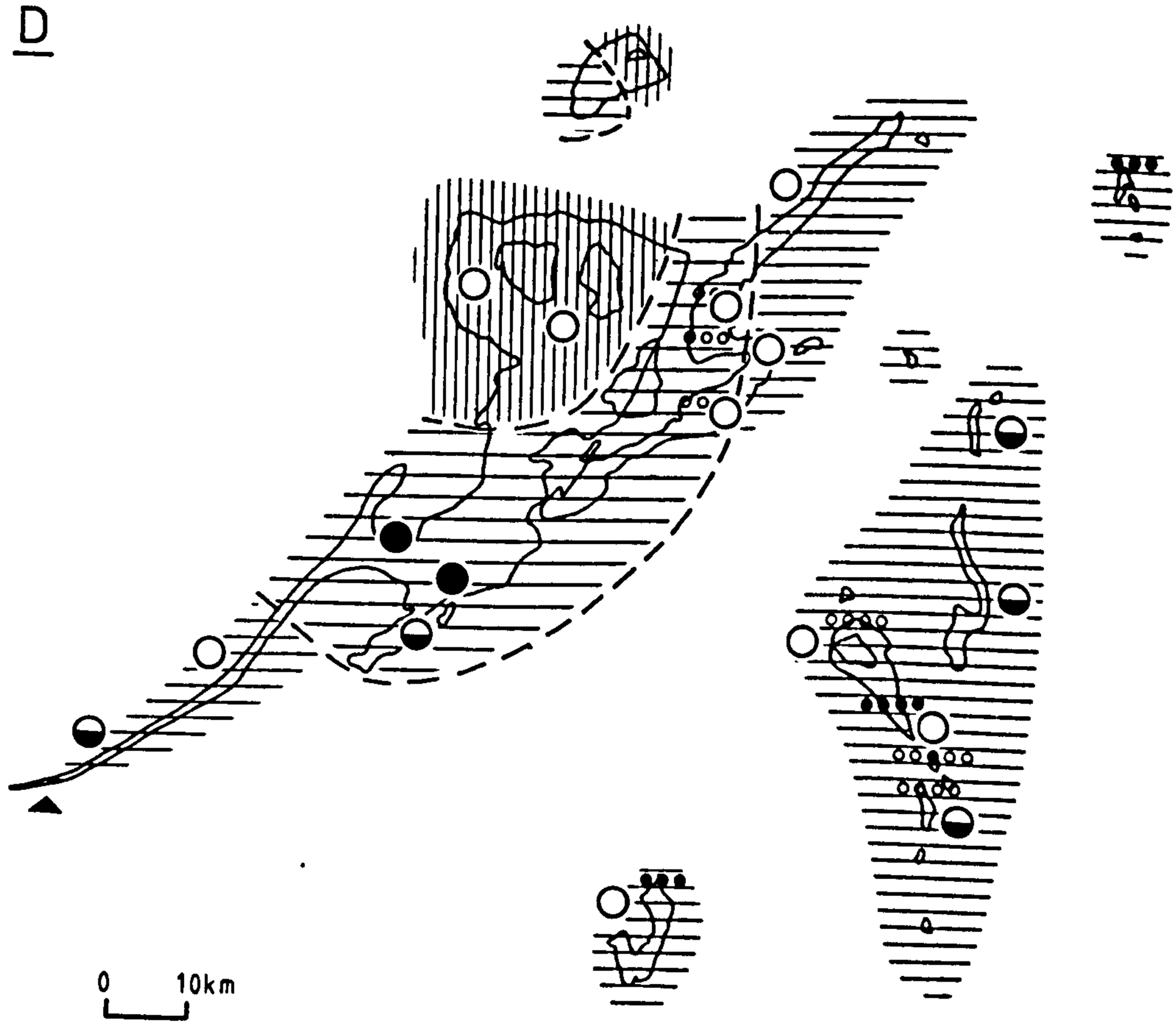
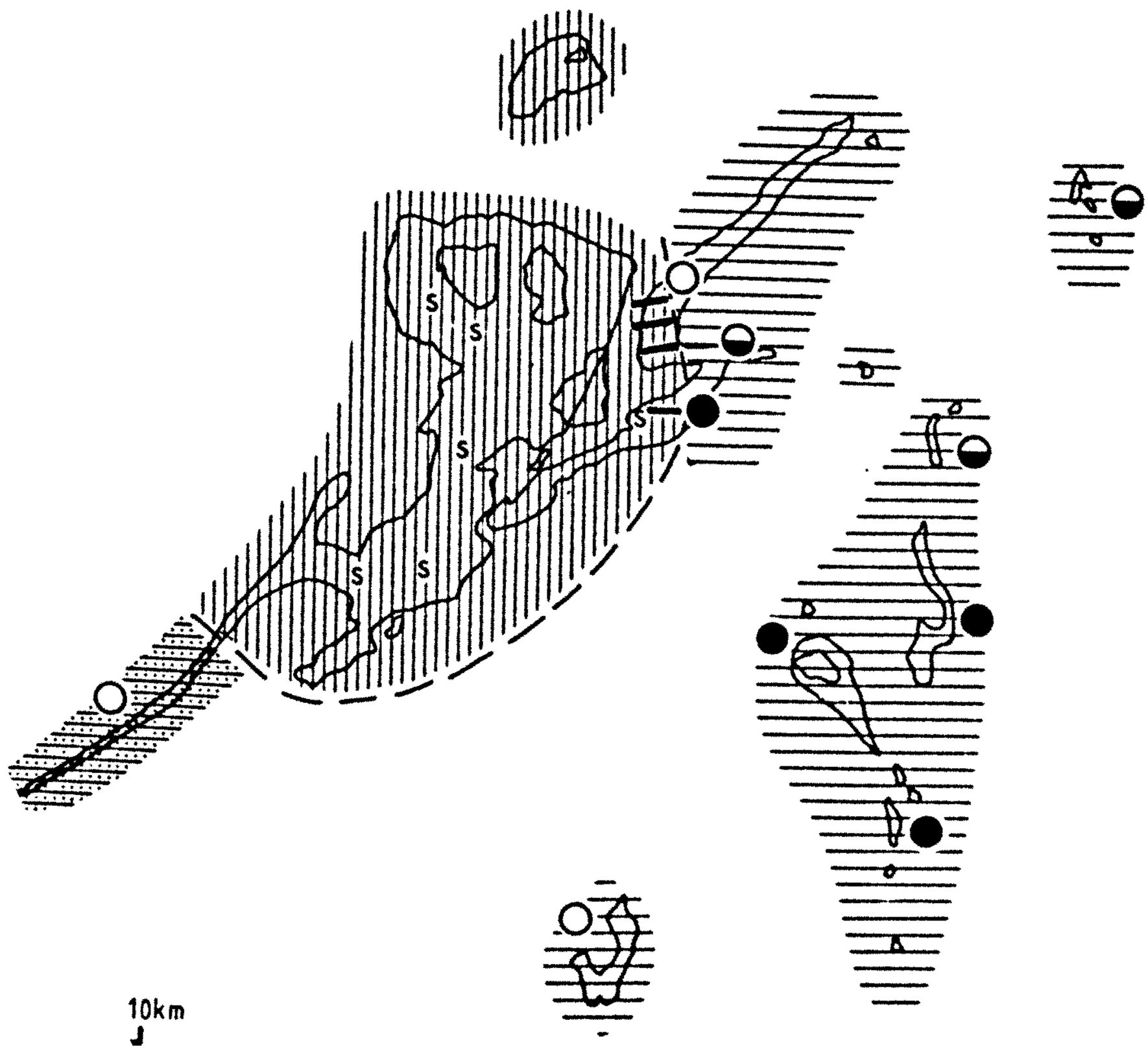


Fig. 5.47 : Orthocones

Bryozoa

A

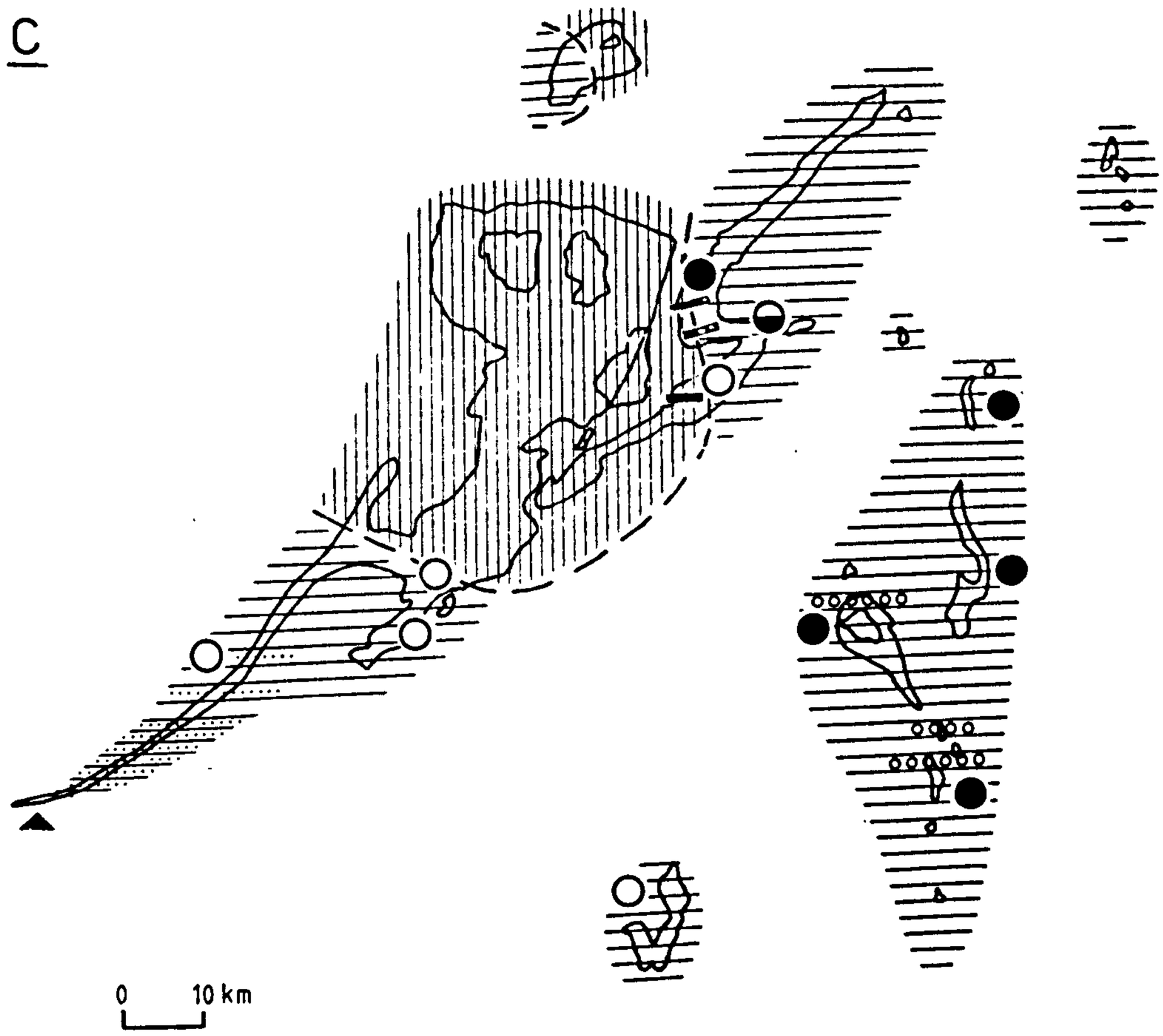
B



g. 548 : Bryozoa

Bryozoa

C



D

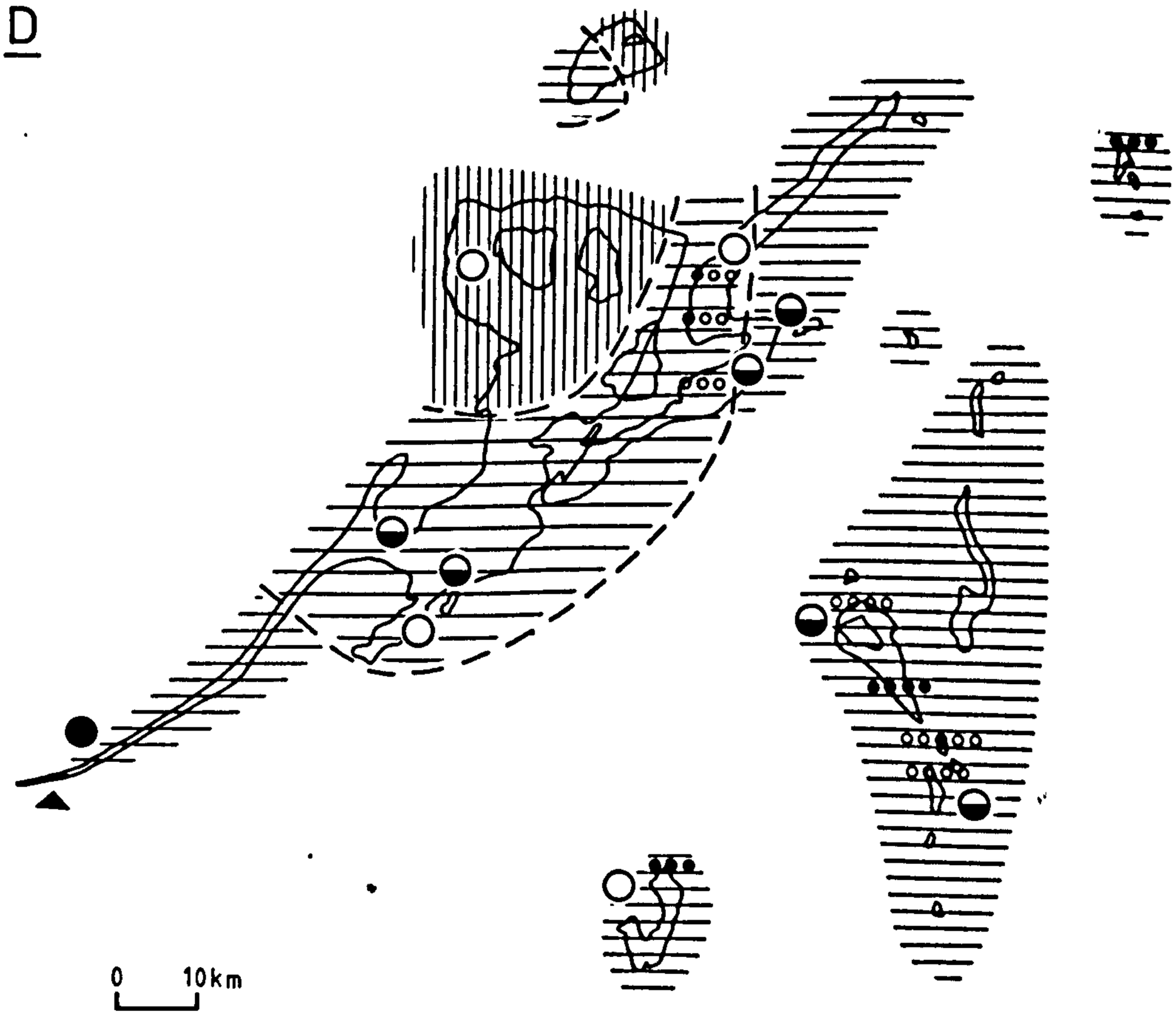


Fig. 5.48 : Bryozoa

CHAPTER SIX

LLB FACIES AND FAUNAS

The nature and significance of the facies distinguished in Chapter 5 are discussed. Palaeoecological analyses have been carried out on populations of several articulate brachiopod species, and surveys on sequences of calcareous siltstone facies.

The faunal and facies variation in the LLB are considered in relation to the brachiopod 'communities' of Calef and Hancock ('74); five sub-faunas are recognised for the LLB. The controls on the distribution of various fossils are evaluated in the context of the possible diachronism of the biostratigraphical divisions of the Ludlow Series. The palaeogeographical implications of the changing faunal and facies distributions through the LLB are discussed.

LLB BASAL CONGLOMERATES:

The interpretation of breaks in the sedimentary sequence has frequently, because of the assumption that sedimentation in the marine environment was continuous, involved a period of emergence and sub-aerial erosion. However, the recognition of many areas of non-deposition on the present sea-floor has meant that a submarine origin is now proposed for many such stratigraphical gaps. The environmental significance of the LLB basal conglomerates must be considered in relation to these alternatives.

1. Tites Point and May Hill:

Brookend borehole:

The basal LLB conglomeratic limestone units have been both bored and burrowed, and there is evidence that these horizons are hardgrounds. There is a cyclicity of sedimentation. Individual conglomeratic beds (up to 25 cm thick) are roughly graded, with the largest clasts in the lower parts. In some units up to 15 cm thick, an overall fining-upwards through several conglomerate-siltstone alternations finishes in siltstones with fine parallel lamination.

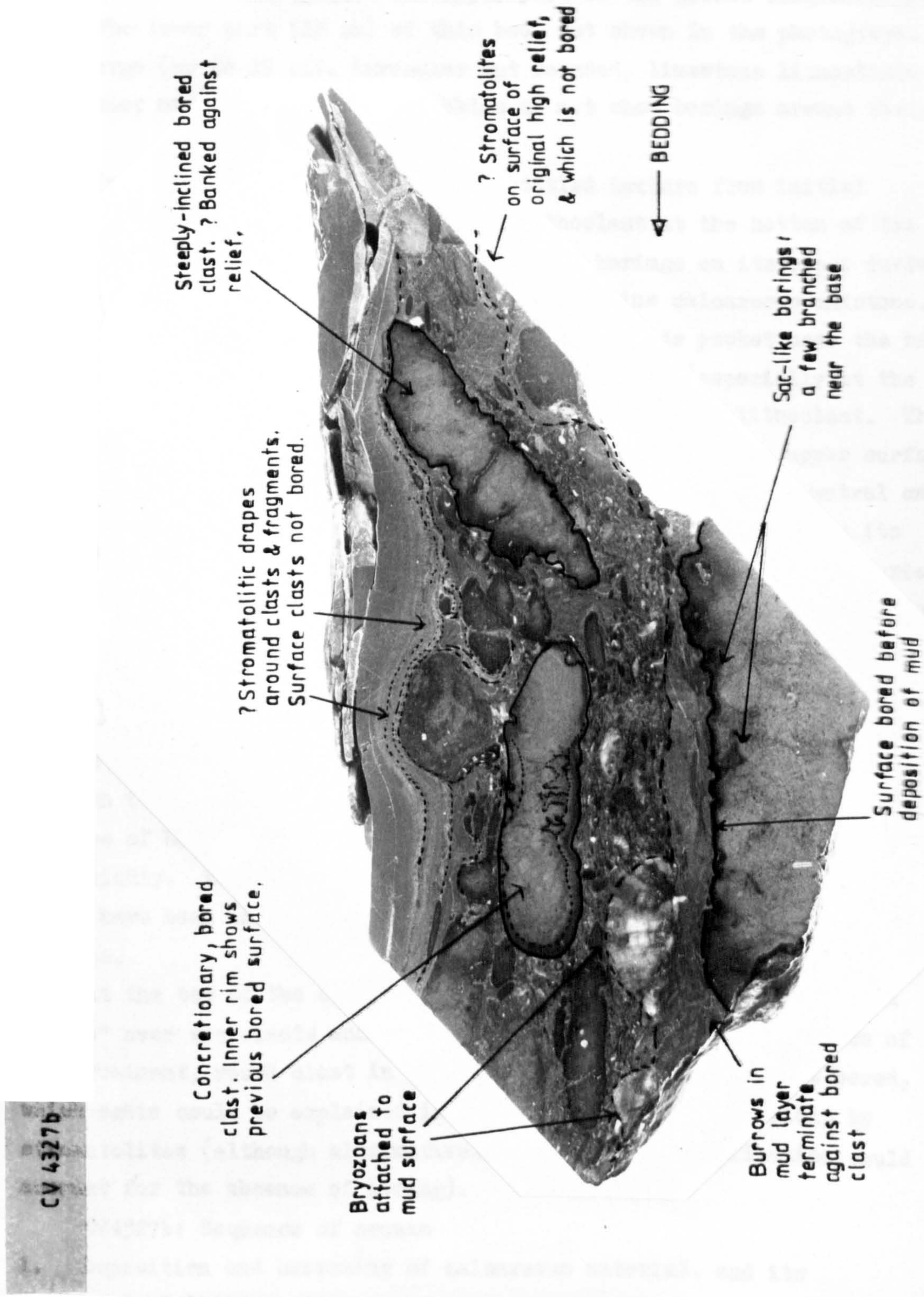


Fig. 6.1 : Brookend borehole core CV4327b (IGS) showing the upper part of the basal LLB conglomerate. (x 1)

a. Fig. 6.1p310 : CV4327b - The upper part of the lowest conglomeratic bed.

The lower part (13 cm) of this bed, not shown in the photograph, has large (up to 15 cm), irregular but rounded, limestone lithoclasts in a siltier matrix; these basal pebbles do not show borings around their rims.

In the photo, the clasts show a mottled texture from initial burrowing of the lime mud. The large lithoclast at the bottom of the picture has numerous, and fairly extensive, borings on its upper surface. Many are simple sac-like pits, infilled with fine calcareous mudstone. However, one longer boring (see overlay) has a side pocket near the base. The overlying muddy band has been well-bioturbated (especially at the LHS of the photo), the burrows terminating against the lithoclast. The muddy layer seems to have a large bryozoan attached to the upper surface which is not bored. Among the higher limestone clasts, the central one shows an inner, previous surface which has been bored as well as its outer rim. This clast, after boring, must have been temporarily buried, accreted more carbonate, been re-exhumed and bored again. Intraclasts in the bed are at various stages of lithification; only hard substrates will be bored.

At the RHS of the photo there is a steeply-inclined clast. This suggests that there was considerable relief on the horizon. The surface beneath (see overlay) may have been stabilised by stromatolites; the absence of boring could also be explained by stromatolites covering it too quickly. There are some small clasts and fossil fragments, that could have been incorporated in the stromatolite, aligned along this surface.

At the top of the conglomerate, there are several laminae which "drape" over the clasts and may be stromatolitic. The top surface of the prominent, round clast in the centre of the picture is not bored, which again could be explained if the clast was covered rapidly by stromatolites (although alternatively, inadequate lithification could account for the absence of boring).

CV4327b: Sequence of events

1. Deposition and burrowing of calcareous material, and its partial lithification.
2. Scouring→lag intraclasts. (Deposition of sediment has ceased).
3. Lithification followed by boring.

4. Covering of large lower lithoclast by sediment. Pre-lithification burrowing of sediment. Burrows terminate against intraclast.
5. Consolidation of sediment. ? Stromatolitic cover of surface (which is not bored). Attachment of large bryozoan.
6. No evidence of erosion above this sediment layer. Intraclasts and bioclastic debris are embedded in a calcareous matrix. Intraclasts are at all stages of lithification, with boring indicating a hard substrate. One intraclast shows evidence of boring followed by burial, accretion of a new outer rim, re-exhumation and re-boring.

   The bed could result from scour of a hardground deposit.
7. Laminae "draping" over irregular surface have incorporated shell fragments and small clasts: they may be stromatolitic. The upper surfaces of some of the top clasts is not bored.
8. Deposition of fine sediment.

b. Fig 6.2p313 : CV4327 - 12 cm higher in the sequence.

The photo illustrates the fining-up units of sedimentation.

The basal layers have a mottled appearance from burrowing. The shelly bed above has closely-packed, fine bioclastic debris, with some complete shells and small bored lithoclasts scattered in the matrix. One complete shell in the bottom part shows a geopetal infilling (see overlay). At the top of the bioclastic unit, there is a transitional boundary at the LHS with the overlying bioturbated siltstone. It contrasts with the sharp junction seen on the RHS, where the uneven, slightly corroded surface to the limestone suggests that this part was already lithified. Two fining-up sedimentary units overlie the siltstone.

c. Fig 6.3p314 : CV4281 - Approx. 4 m higher in the sequence.

The bed contains flattened, elongated limestone lithoclasts (the matrices of which have been burrowed) that have been extensively bored on both sides. Borings are narrow; a number show lateral pouches branching off near the bases of the main tubes. One clast in the lower part of the photo has a bryozoan growing off its upper surface. The surrounding calcareous matrix, which has an upper layer of rhynchonellids and other shells, has some areas of burrow mottling (especially LHS - see overlay). The discrete upper boundary of the calcareous band containing the shells may result from concretionary hardening in this region.

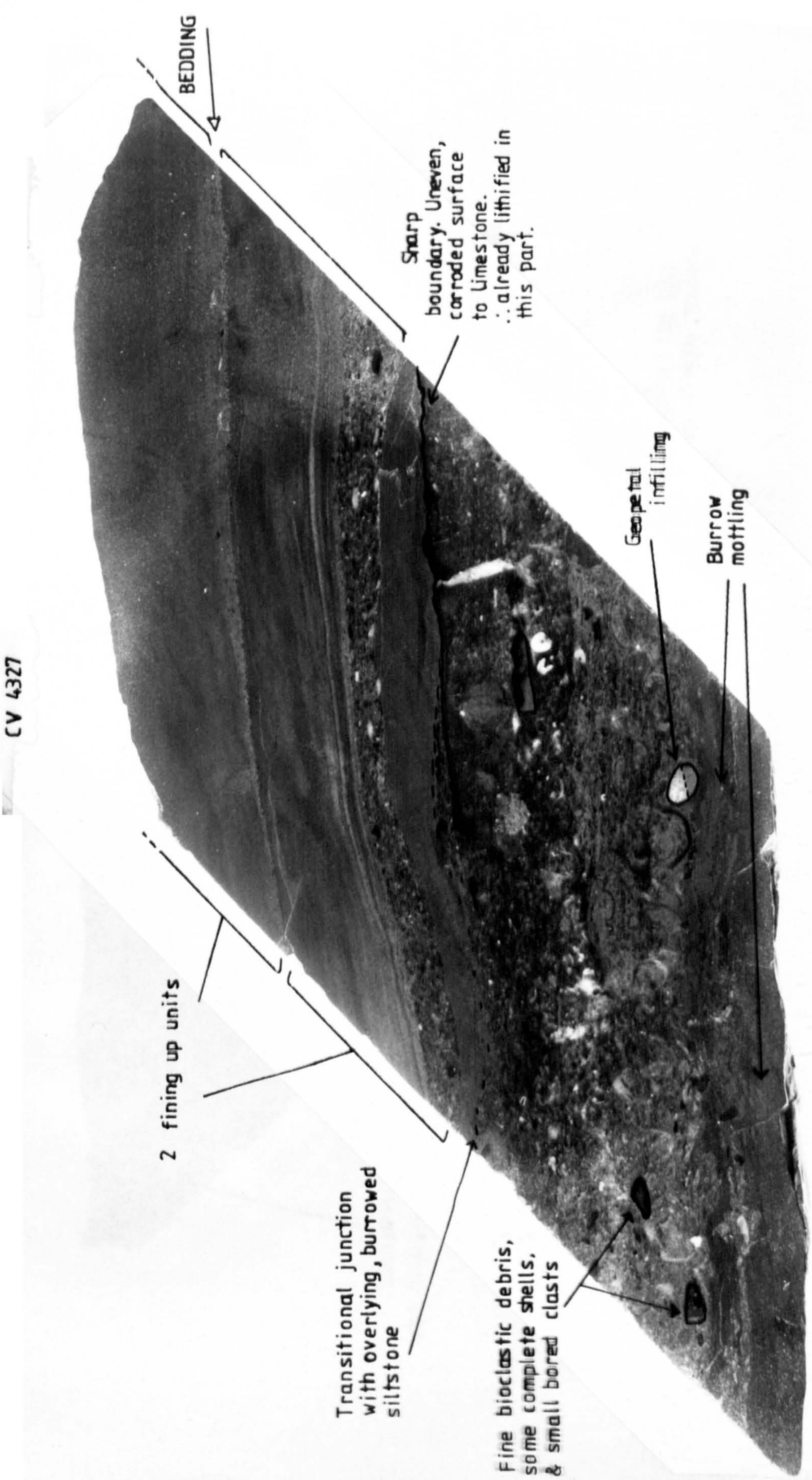


Fig. 6.2 : Fining-up units of sedimentation above a band of bioclastic material; Brookend borehole core CV4327 (IGS). (x 1)

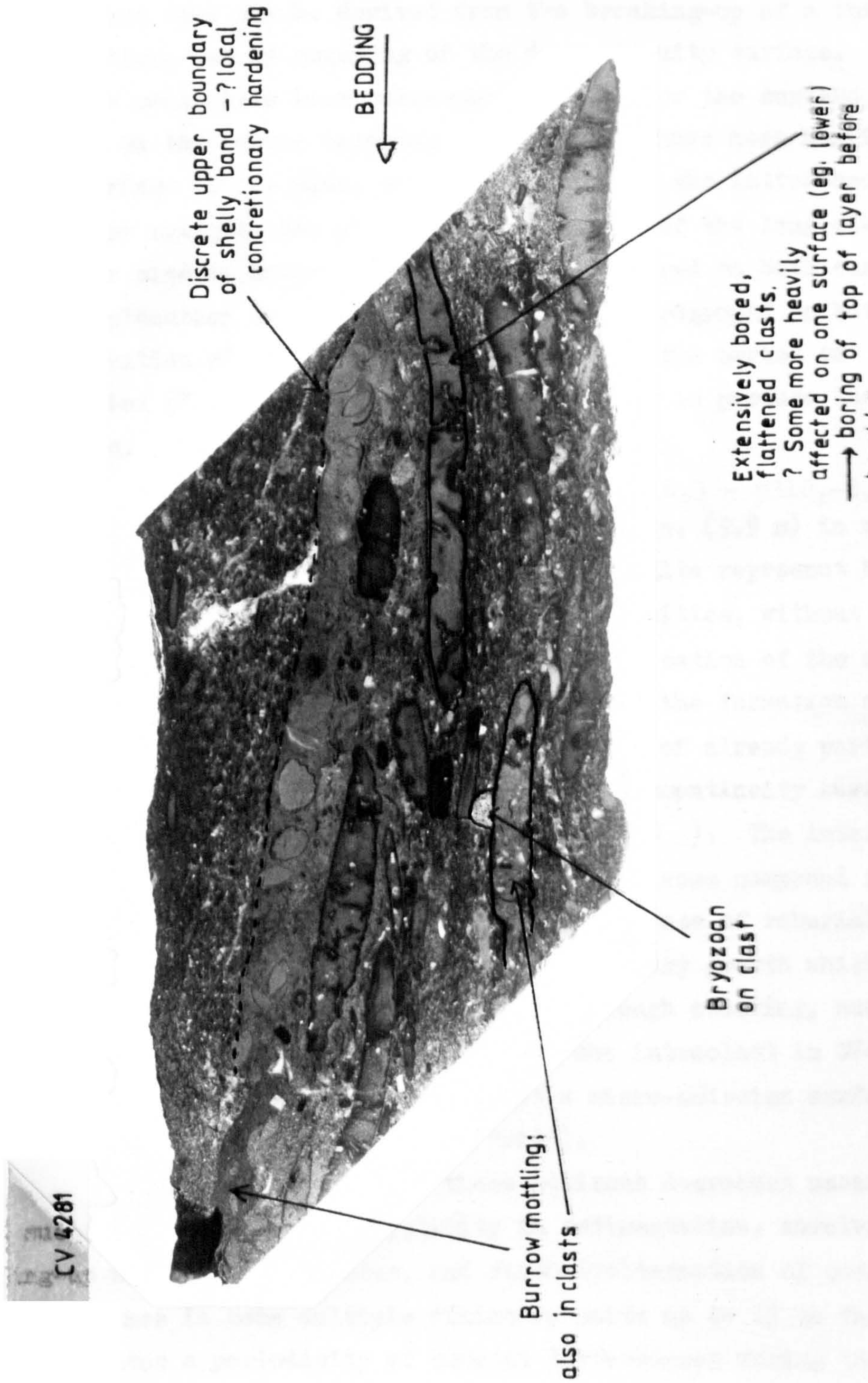


Fig. 6.3 : Conglomeratic limestone with bored clasts; LLB Brookend borehole core CV4281 (IGS). (x 1)

The flat shape, and relatively angular outline of the lithoclasts suggests that they may be derived from the breaking-up of a thin, well-lithified, bed by scouring of the discontinuity surface. These intraclasts could have been subsequently bored, or the surface may have been bored on top before breaking. Some clasts have more heavily stained borings on one side, which would support the latter sequence of events - for example, the present lower surface of the long clast on the RHS. Other clasts, however, are more equally bored on both surfaces. Another explanation could be of boring of the hardground on both surfaces after excavation of a horizontal gallery during the period of lithification (Bromley '75), and before breaking to produce the intraclasts.

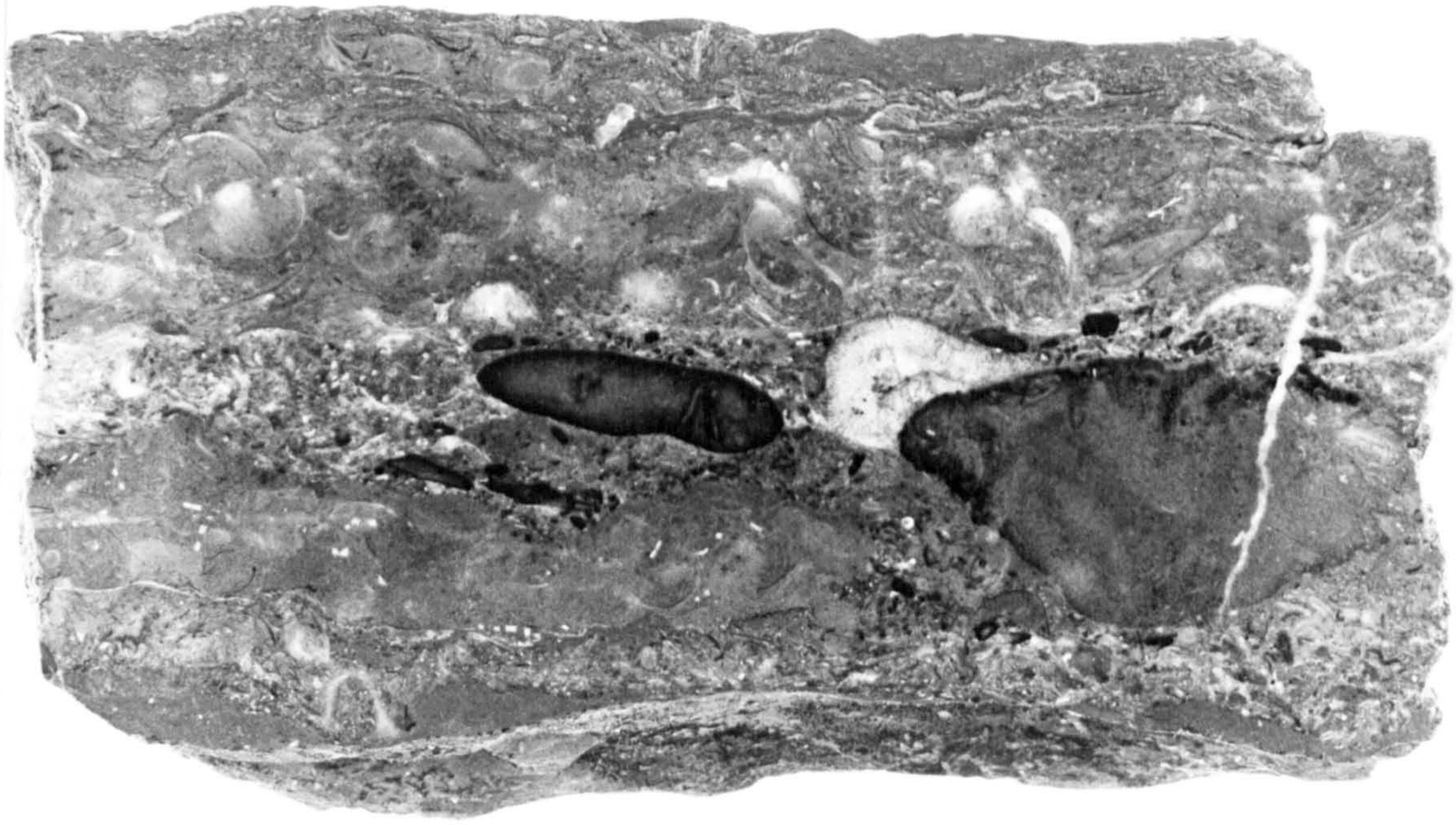
The Brookend bore-hole cores (Figs.6.1,6.2,6.3 - p310,-3,-4) show a series of fossiliferous limestone conglomerates, (9.5 m) in which numerous lithoclasts have bored rims. The deposits represent both interformational and intraformational discontinuities, without obvious large-scale erosion. The synsedimentary lithification of the sea-floor during the periods of non-deposition - that is, the formation of hardgrounds - was followed by boring. Scouring of already partly lithified sediment formed intraclasts at the discontinuity surface which are commonly bored (for example, CV4281, Fig.6.3). The interplay of deposition, scouring and lithification produced some compound intraclasts (- "hiatus concretions" of Voigt '68). A sequence of reburial of a bored intraclast, followed by further accretionary growth which was subsequently interrupted by re-exhumation through scouring, and then boring of the new surface is inferred for one intraclast in CV4327b, Fig. 6.1 . The cycle of events has left a micro-omission surface within the intraclast (ie. an inner "rim").

The frequency and extent of these horizons decreases upwards in the succession. There is a cyclicity in sedimentation, involving fining-up within conglomerates, and rhythmic alternation of conglomerates and siltstones in some multiple fining-up units up to 15 cm thick. This indicates a periodicity of current disturbances during their formation. The lower conglomerates in the succession are less shelly, but contain more numerous, and larger, bored lithoclasts. The interbedded clastic sediments are fine siltstones and mudstones, sometimes closely-laminated, in which fossils are infrequent.

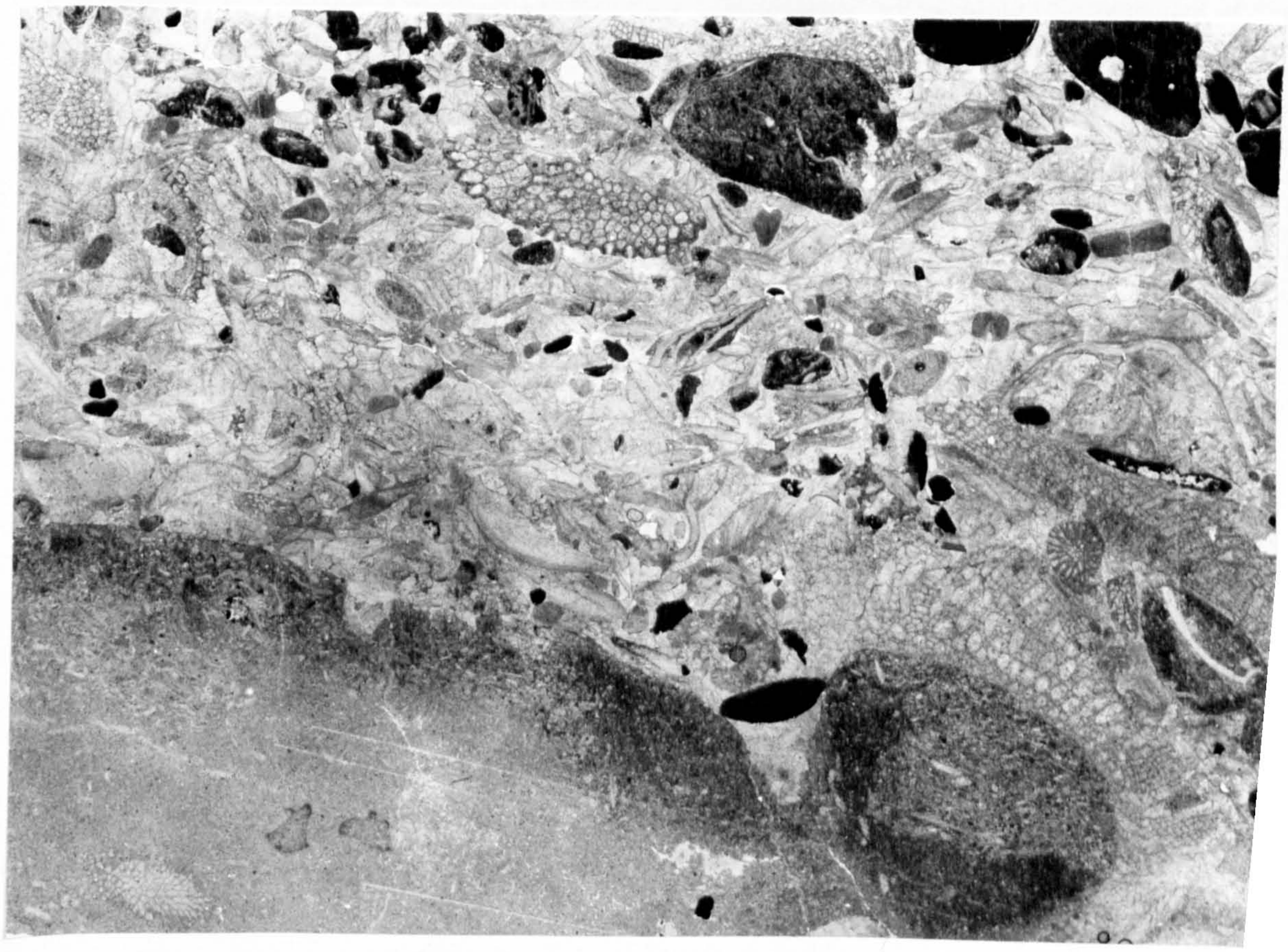
At May Hill, a similar, though thinner, sequence (3.1 m) of limestone conglomerates and siltstones is found. Bored lithoclasts of limestone and calcareous siltstone are found with shells, large bryozoa and bioclastic debris in the conglomeratic limestones. The lower beds are coarser with larger, more irregular, lithoclasts that are unevenly dispersed in the matrix. The interbedded fine muddy siltstones, which are well-burrowed in parts, have a sparse fauna. Phosphatic pebbles are occasionally found in both siltstones and conglomeratic beds. As further south, the conglomeratic beds decrease in prominence as the succession is ascended.

The basal LLB at Tites Point and at May Hill have a series of deposits indicating repeated discontinuities in sedimentation. Bromley ('75) noted that many fossil hardgrounds which represent the omission of hundreds or thousands of years of sediment in shallow oxygenated water are surprisingly little bored, so that the quantity of borings is not an indication of the duration of the depositional pause. He considered the chief factors inhibiting boring to be insufficient hardness of the sediment and burial by new sediment. Penecontemporaneous cementation is well-known in Recent shallow-water and supratidal carbonates (Bathurst '71), but hardgrounds are also common in deeper-water chalk sequences (Kennedy '75). In the LLB the interbedded fine clastic sediments indicate generally quiet conditions, but the formation of the lag intraclasts and hiatus concretions of the conglomerates requires periodic current scouring during lithification. There is no sedimentary or faunal evidence in the LLB for supratidal conditions. Early lithification is most characteristic of carbonates; other sediments are less susceptible to synsedimentary cementation. The more usual occurrence of shallow-water hardgrounds, the LLB palaeogeographical evidence of shelf-conditions, and the associated benthonic fauna suggest a probable shallow-water origin for the bored conglomerates.

The May Hill conglomerates include much bioclastic debris and are more shelly than the lower beds in the Brookend borehole sequence. Correspondingly, bored pebbles are more common, and bigger in the latter. The restriction of boring to the upper lithoclasts of the roughly graded, basal LLB conglomerate at Tites Point suggests that completion of lithification, and then boring, took place after deposition of the conglomeratic material. The general absence of erosion of the bored

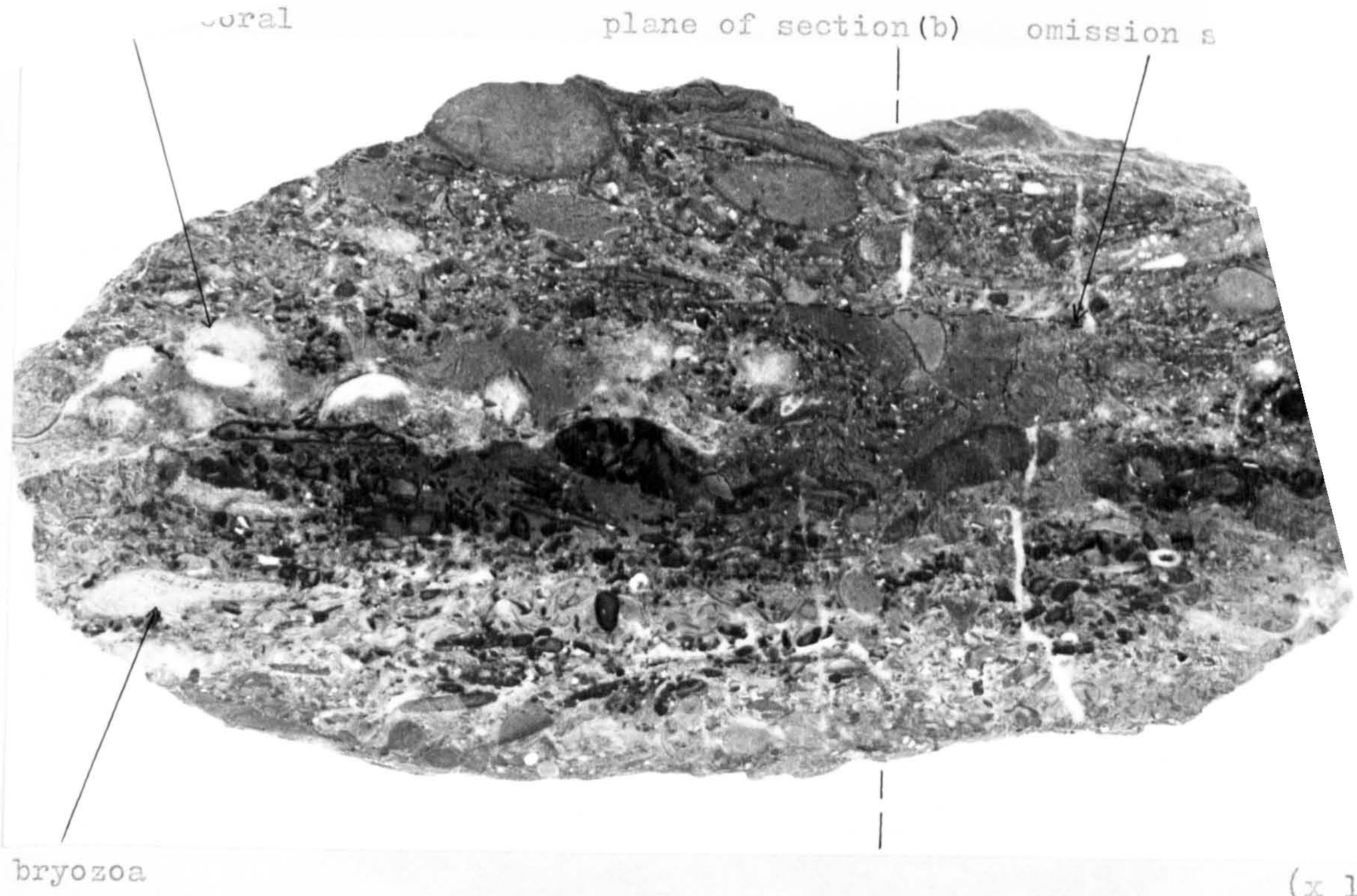


a : Conglomeratic limestone of basal LLB, Longhope by-pass. Clasts (originally of bioturbated lime mud) are bored, and one (RHS) has a large bryozoan attached to it. The matrix is composed of shells and bioclastic debris. (x 1)



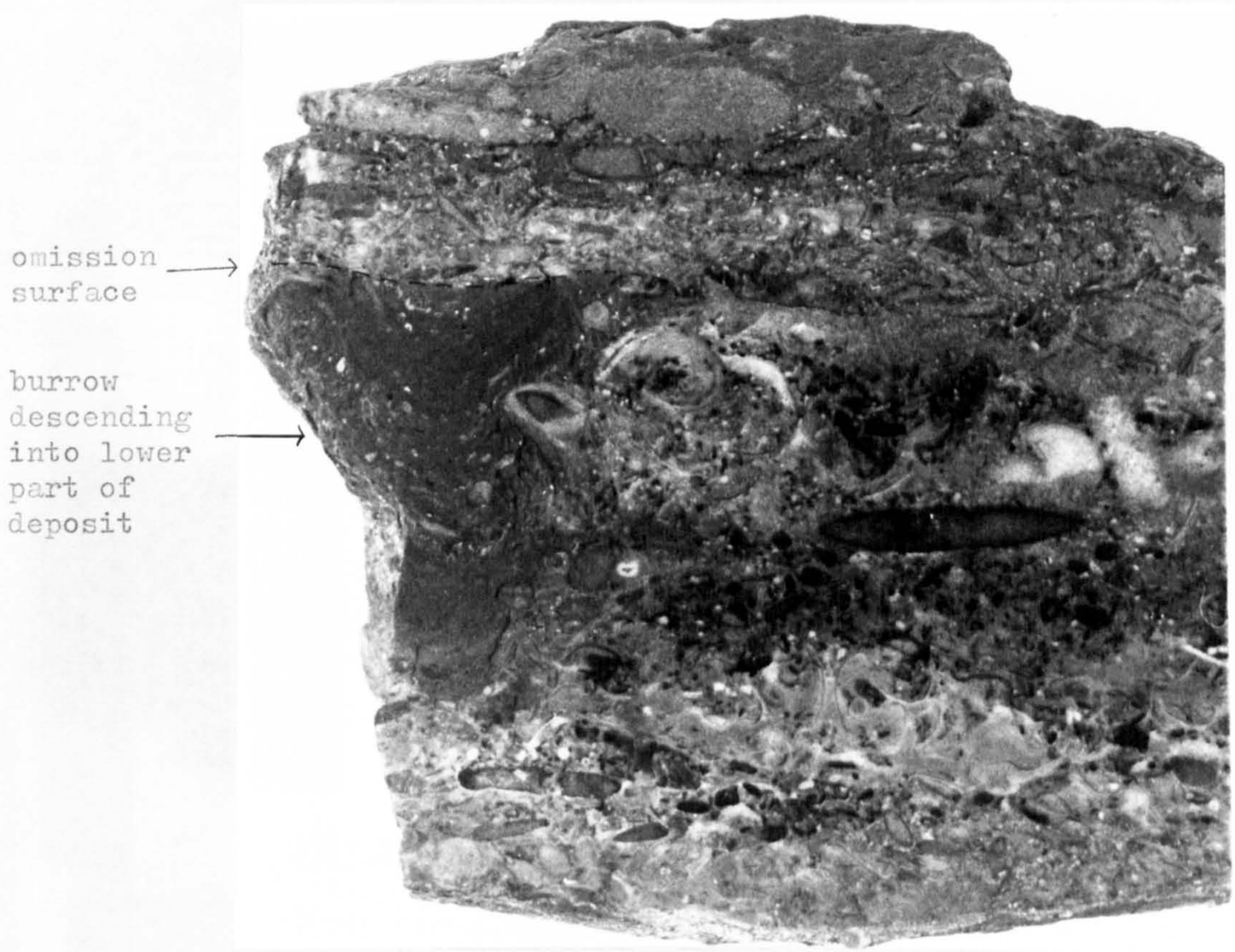
b : Thin section of basal LLB conglomerate, Wood Green. (x 6) The large clast (at the bottom) which has a bored rim has a bryozoan growing on its surface (RHS). Other clasts and shells in the matrix also have attached bryozoa.

Fig. 6.4 : Basal LLB conglomerates, May Hill.



(x 1)

a : Conglomeratic limestone containing many flattened bored clasts in central part. Large bryozoans are prominent in the matrix which also has fragments of compound coral. The omission surface of (b) is indicated on the photograph.



b : Section at right angles to (a) showing a large burrow with meniscus-fill structure descending from omission surface. A bored clast is clearly visible in the centre of the picture. (x 1.5)

Fig. 6.5: LLB conglomerate, Wood Green (WG-Ja).

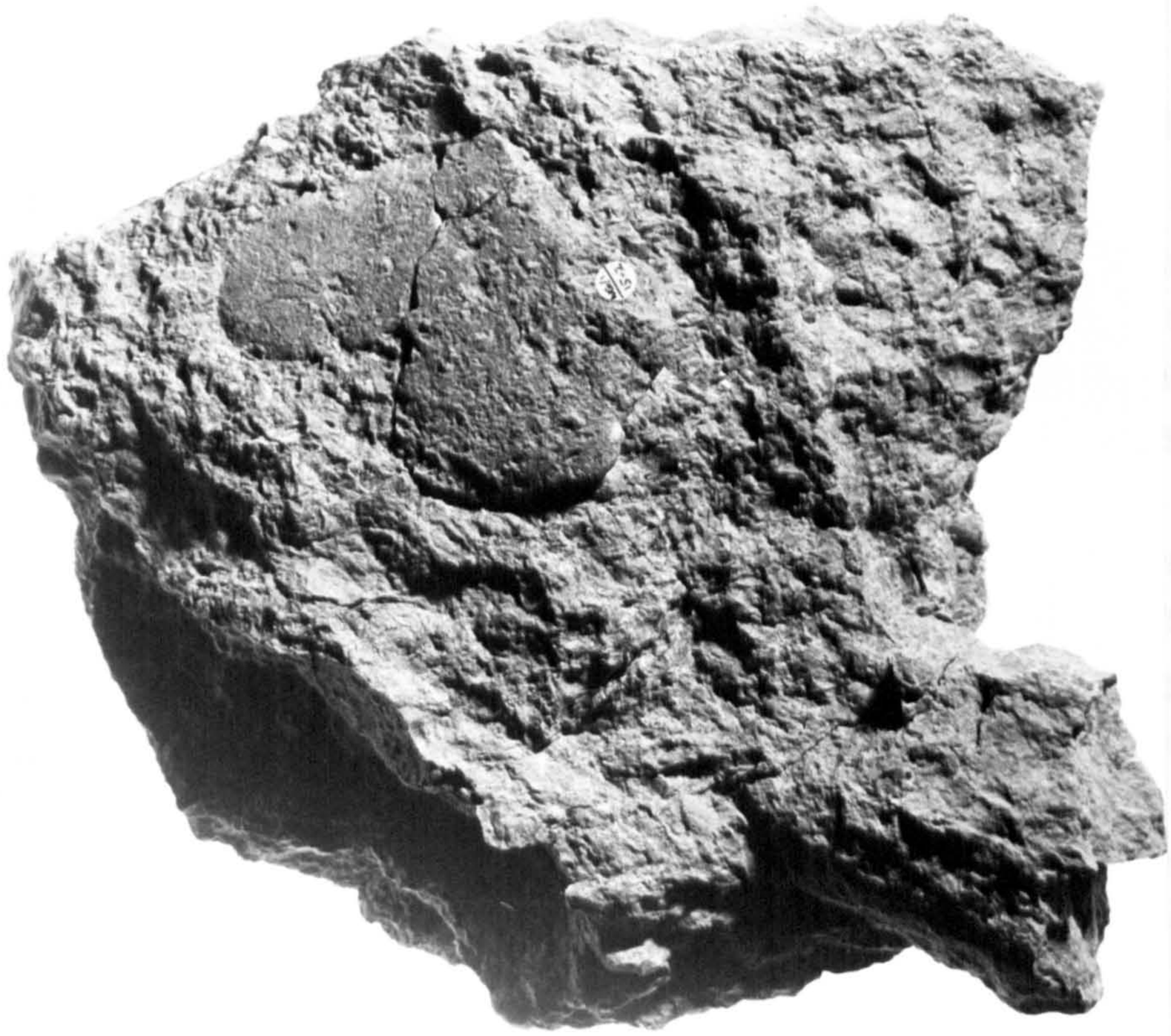


Fig. 6.6 : Basal LLB conglomerate, Wood Green. (x 1)
Surface view, showing pitted exterior to clast which, in section, is seen to be bored.

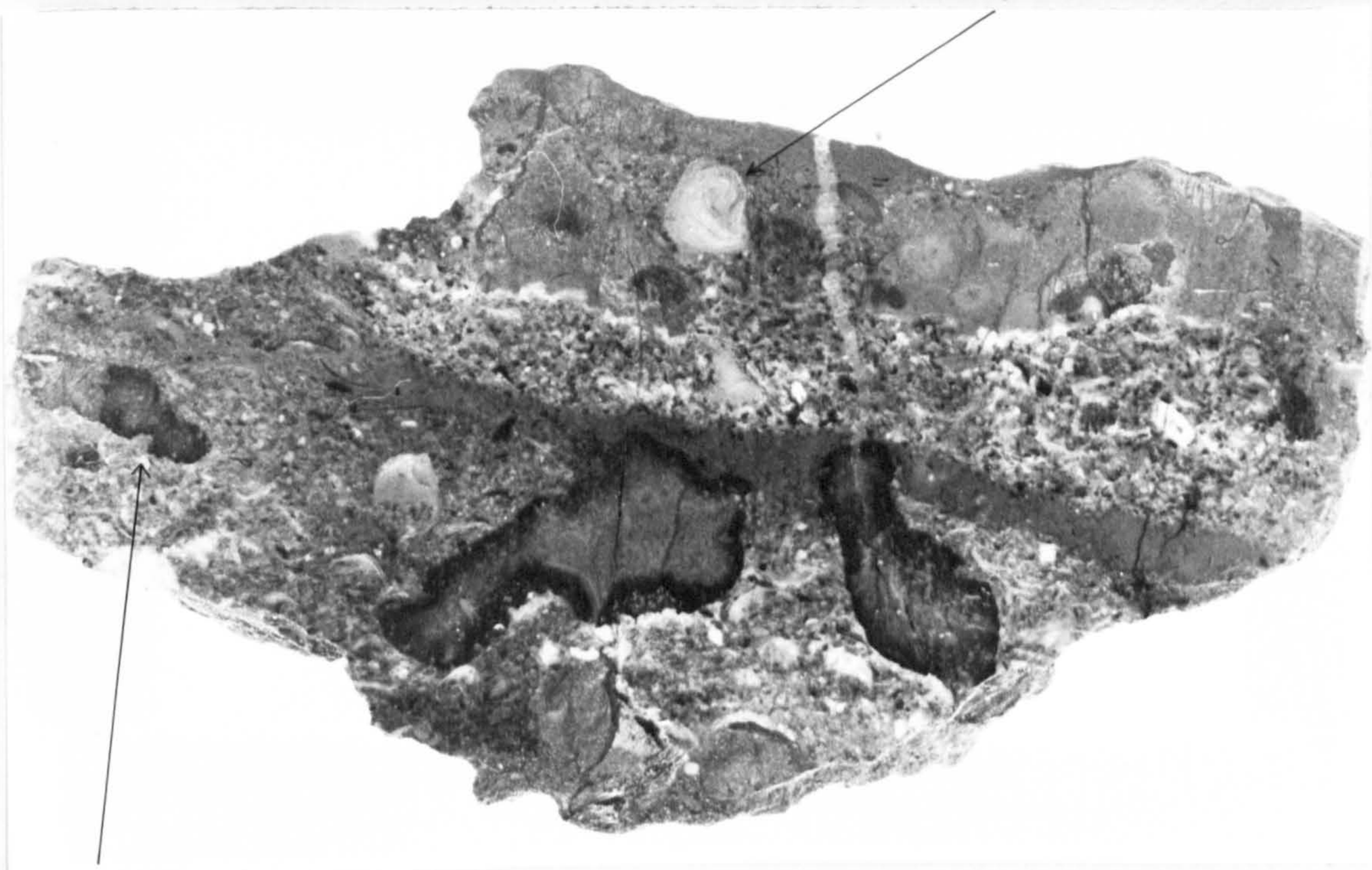


Fig. 6.7 : Conglomeratic limestone, LLB Perton. (x 1.2)
Irregular clasts of bioturbated lime mud have corroded rims with a few borings. There is a bryozoan with a layered structure encrusting a shell fragment at the top of the picture.

surfaces indicates that the lithoclasts have not travelled far after being bored. Similar conclusions are reached for pebbles on which large, intact bryozoans are attached - for example, at May Hill - Fig. 6.4 p317. More fossiliferous beds in which small bored, and broken, lithoclasts are scattered among shell debris appear to have suffered more extensive transport or reworking (for example, WG-Jal, Fig. 6.5 p318). Hence, it may be inferred that environmental energy was greater at May Hill than at Tites Point.

The Aymestry Limestone is not developed in these areas; an unconformity or lateral faunal and facies changes are alternative explanations for this. Lawson ('55) preferred the former for May Hill, because of the thinness of the succession, the sharp contact and faunal contrast between the basal L. Blaisdon Beds and the underlying U. Flaxley Beds, and regional evidence of instability and erosion provided by the widely developed limestone conglomerates and the Gorsley succession (Lawson '54). He proposed that the limestone conglomerates might be derived from the erosion of previously consolidated Aymestry Limestone. In this study, a few fragments of compound corals were found in the matrix of May Hill conglomerates, but no diagnostic UBB fossils; nor did the Brookend borehole core yield any UBB fossils from the conglomeratic sequence. Therefore, non-deposition of the Aymenstry Limestone is probable. It is not possible to assess whether lateral faunal and facies changes can explain its absence, however.

In these areas, conglomeratic and phosphatised horizons, and bone-beds occur at several levels. For instance, Cave and White ('71) reported a limestone conglomerate with bored pebbles at Tites Point from a level taken as the base of the Whitcliffe Beds, and several bone beds with phosphatic pebbles occur higher in this division. At May Hill, phosphatised fragments become more frequent in the top LLB, and a phosphatised limestone conglomerate (LH-I) is used to indicate the LLB-ULB boundary here. A similar horizon marks the base of the LWB at May Hill (Lawson '55).

Clearly, numerous diastems and discontinuities in the succession are indicated locally, accompanied by varying amounts of erosion. The boring of the basal LLB conglomerates is consistent with hardground formation - that is, with a submarine origin during periods of non-

deposition. Periodic current scouring is responsible for accumulation of shells and debris, formation of intraclasts, and grading of the beds. However, boring and bryozoan encrustation are inferred to have occurred *in situ* in many beds during stable periods. The interbedded fine, clastic sediments show that intervals of quiet sedimentation alternated with those of omission and erosion.

2. Woolhope to the Abberleys:

The basal LLB at Perton, Chances Pitch and Woodbury include a series of conglomeratic limestone beds, developed at the top of the Aymestry Limestone facies. There is no evidence of a marked stratigraphical break in these sequences. However, at S. Woolhope (Squirrell '56), the Aymestry Limestone is absent in the thinner, southern sequences, in which the conglomerates are also much coarser. In the Ledbury district, there are 12.5 m of bryozoan-rich conglomeratic beds (Clencher's Mill member) representing the Leintwardine and Whitcliffe Beds; the lower 8-9 m are thought to be the former. The "normal" thicker LLB sequences further north have conglomeratic beds mainly in the lower part. The thickness and frequency of these conglomerates becomes greater towards the south (Phipps and Reeve '67).

In the three sequences studied, the faunal and facies changes at the UBB-LLB boundary are transitional. For convenience, at Perton and Chances Pitch, the lowest limestone conglomerate was taken to mark the base of the younger division. At Woodbury, the equivalent bed had a clearly UBB fauna, and so a higher conglomeratic band without diagnostic UBB fossils was selected here. These shelly limestone conglomerates appear intraformational. Many of the lithoclasts are very similar in composition to the matrices, and only become clearly visible when weathered. A few small lithoclasts show signs of boring - for example, CP45 Fig. 6.10p323. The pebbles, of fossiliferous limestone, limestone and calcareous siltstone, are commonly, irregularly arranged in a shelly and debris-rich, calcareous matrix. "F." *fibrosa* is abundant in the basal beds at Perton, and at Woodbury, where some planes have numerous, convex-up specimens. This fossil has been variously described as a bryozoan, stromatoporoid and coral - if a bryozoan, its lunulitiform structure is considered to be adapted for an epifaunal strategy, resting on the broad base of the cone. Recent colonies of this form are relatively tolerant to sedimentation but not to turbulence (Ryland '70).

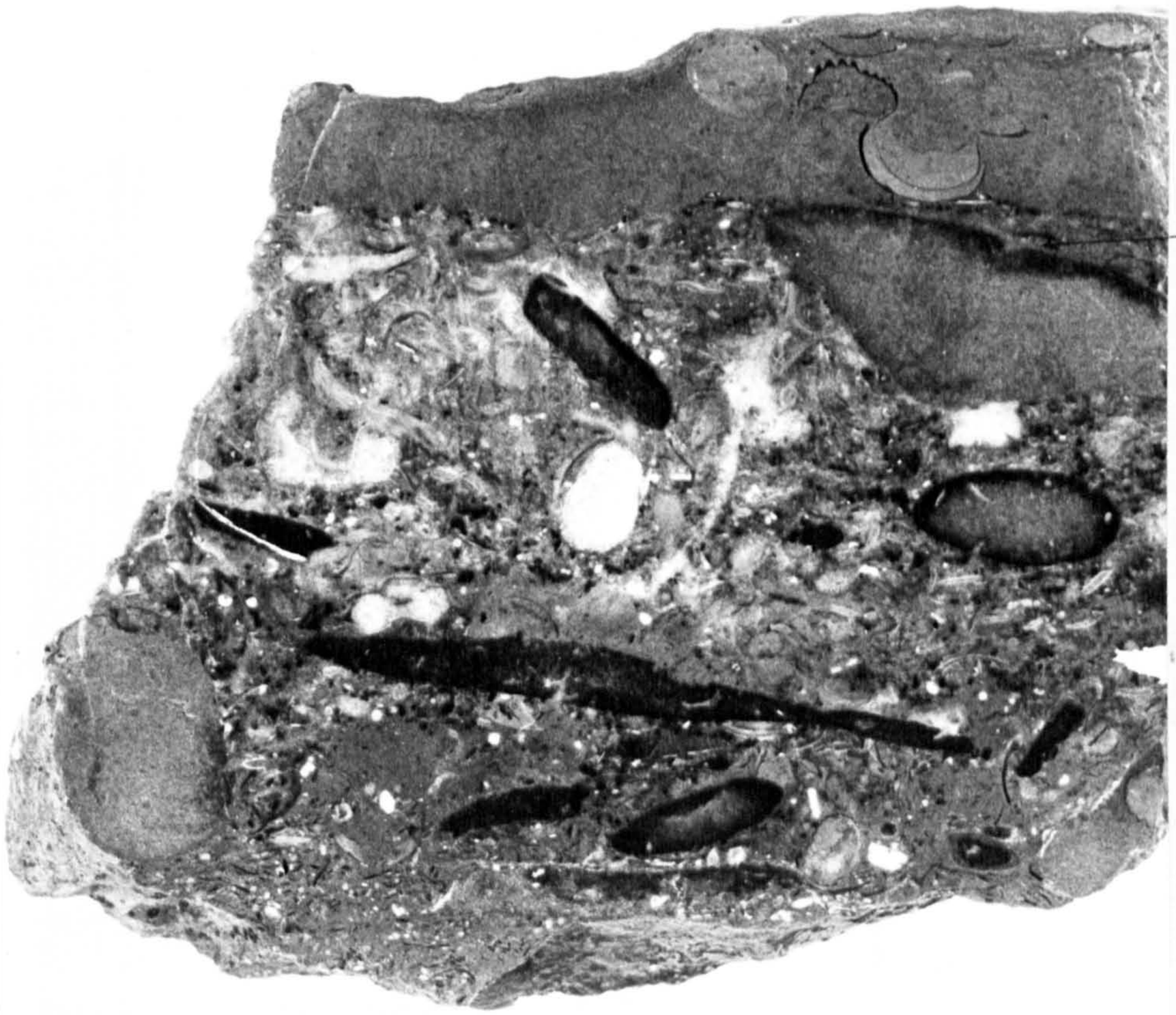


Fig. 6.8 : Conglomeratic limestone, LLB Woodbury. (x 1.75)
Clasts of bioturbated lime mud have corroded rims with some small sac-like borings. The clasts vary greatly in size and shape.

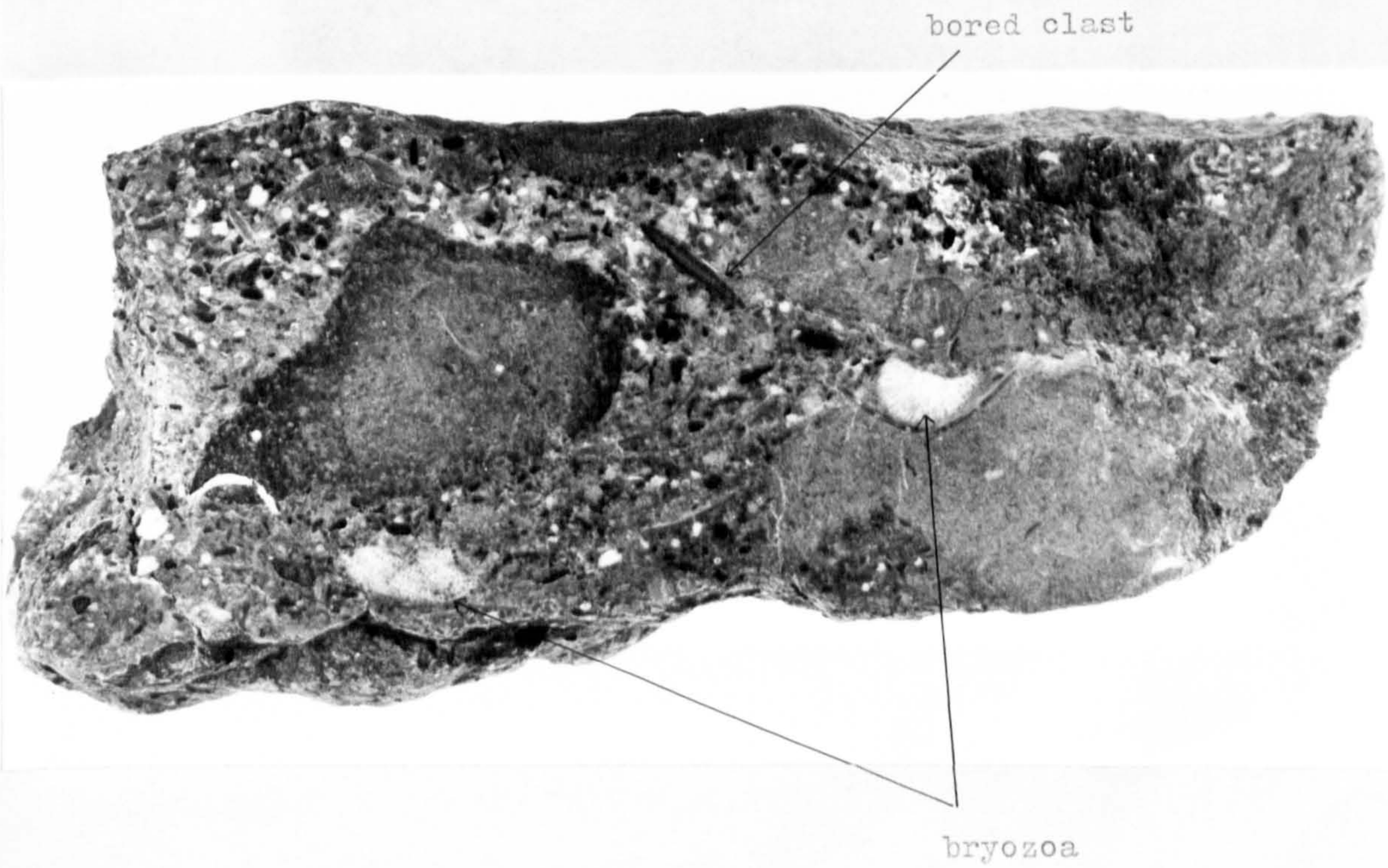


Fig. 6.9 : Basal LLB conglomerate, Lye. (x 2)
Calcarenite clasts, one of which has borings in its rim, lie in a matrix of fine bioclastic debris. Large bryozoa are common.

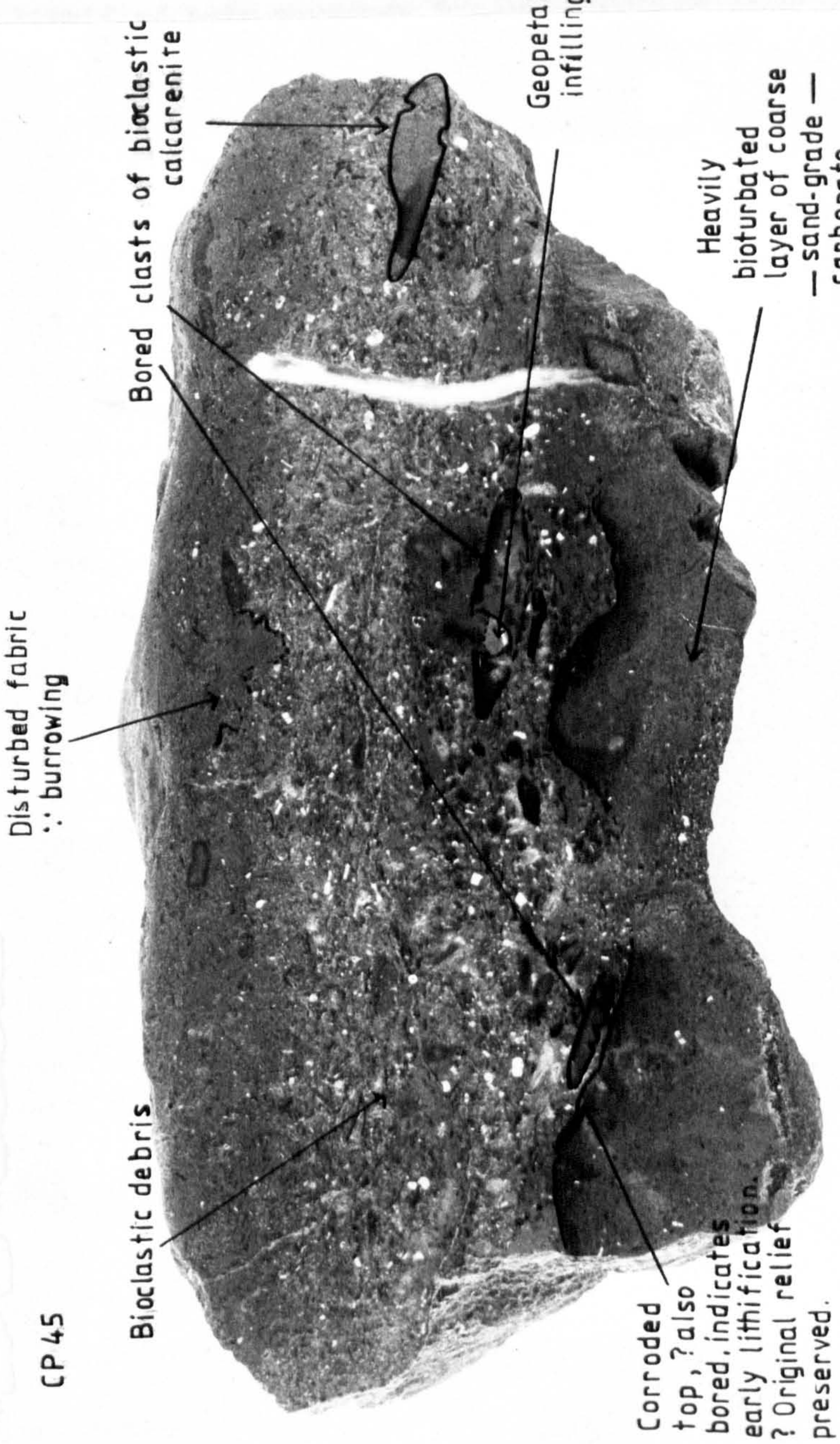


Fig. 6.10 : Conglomeratic limestone with some bored clasts; LLB Chances Pitch. (x 0.85)

The conglomeratic limestone beds, which often have sharp bases, are considered to show pauses in sedimentation. Periodic scouring of partly lithified beds accounts for both the formation of lithoclasts and accumulation of shells. The general absence of boring could be explained by insufficient hardness of the substrate, faster renewal of sedimentation, or by the unsuitable environment for the boring organisms. There is not sufficient evidence to discriminate among these alternatives, but all could relate to a more offshore, or deeper, environment of deposition. There is no sign that sub-aerial erosion was involved in the formation of the conglomerates.

3. Lye, Wenlock Edge - Aymestrey:

Dean borehole: Fig 6.11p325 BDH 541, The

A single conglomeratic horizon occurs at the level of the UBB-LLB boundary. The underlying beds are nodular UBB limestones (Aymestry Limestone facies). Many nodules are concreted, well-bioturbated, calcareous sediment, which has been broken up after partial consolidation. The lower part of the core shows this very well: the small triangular intraclast has become detached and rotated after being burrowed and lithified. The sharp boundaries of the upper part of the large, basal nodule (compared with the diffuse transition into the muddy matrix seen lower down) indicate that lithification was further advanced in this upper part. The intraclasts which have been extensively bored around their rims are composed of similar, well-burrowed, muddy limestone. However, the horizontally-disposed intraclast on which only the upper surface is corroded, although some burrow traces are visible in the matrix, has an inner rim indicating a previous outline (BDH 541). Subsequent growth has therefore been accretionary, during temporary burial. This clast possibly has a different parentage from the more angular and extensively bored clasts.

Lithified UBB sediments here have been scoured and rapidly redeposited without current reworking, to leave a haphazard arrangement of intraclasts in the matrix. The level of the bored horizon represents a period of non-deposition of sediment.

The restriction of corrosion to the upper surface of the accreted intraclast probably indicates that the lower part was embedded in sediment. Lithification of intraclasts at the sediment surface

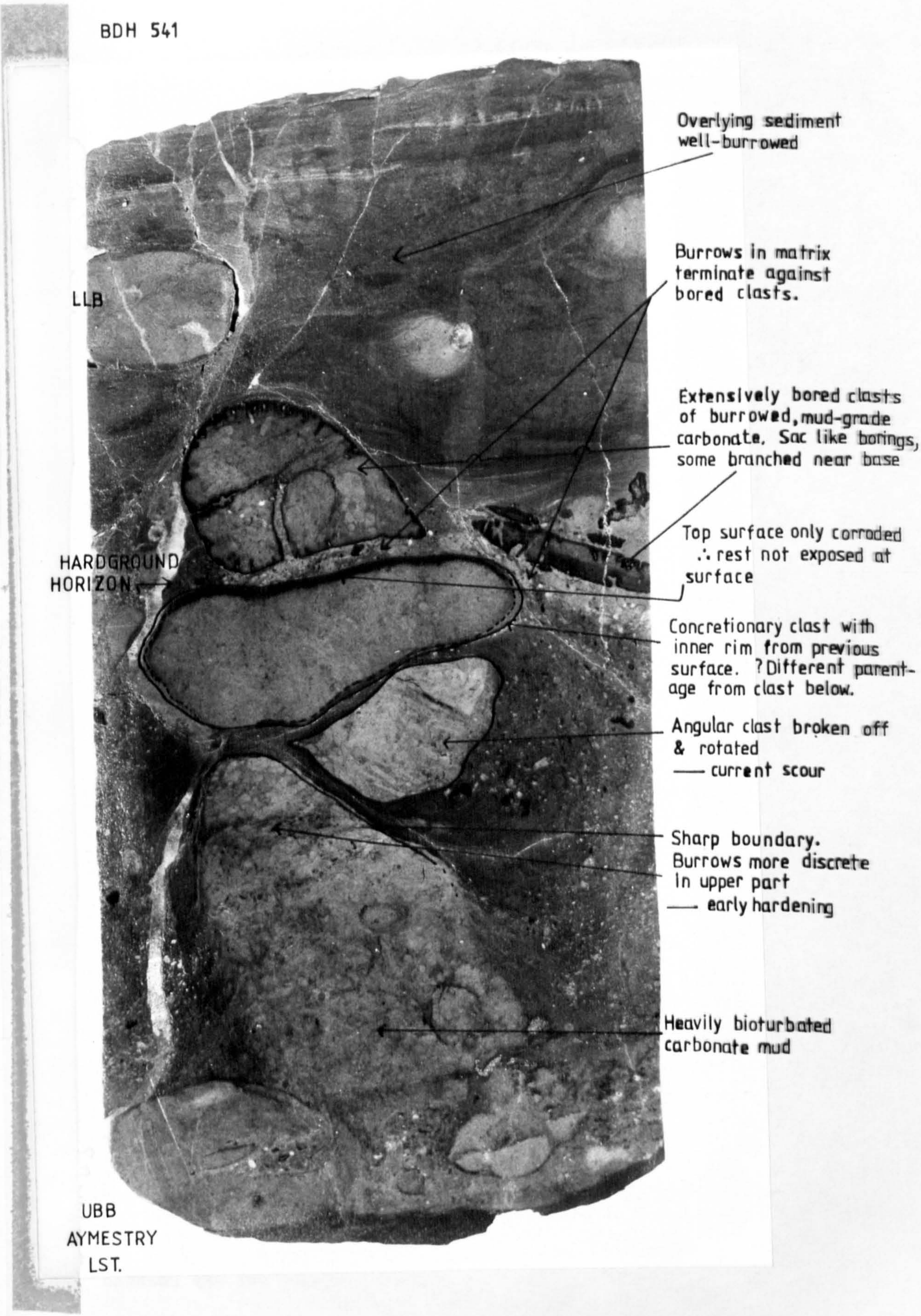


Fig. 6.11 : Bored conglomerate at the UBB-LLB boundary; Dean borehole, NE Wenlock Edge (IGS). (x 1)

preceded boring, for which hard substrates are required. Many of the borings are simple, narrow, sac-like tubes, but a few have lateral branches developed near their bases (for example, in the long, thin lithoclast of BDH 541). The calcareous matrix surrounding the bored lithoclasts is bioturbated.

The sediment overlying the conglomeratic level is fine and muddy, with numerous diffuse, sub-horizontal, burrow traces. There is no evidence of further erosion prior to redeposition of sediment above the bored horizon.

Sequence of events:

1. Deposition of calcareous substrate and its bioturbation. Concretionary growth of nodules.
2. Scouring during early lithification→lag intraclasts.
3. Accretion of some intraclasts (eg. horizontal one) during temporary burial.
4. Cessation of deposition. Lithification of intraclasts at surface followed by boring. Accreted intraclast is partially re-exhumed and corroded on top surface.
5. Pre-lithification burrowing of calcareous matrix around bored lithoclasts.
6. Inhibition of boring by burial with sediment.
7. Bioturbation of overlying sediment.

The Dean borehole (SJ.678.000), at the NE end of Wenlock Edge, has evidence of erosion of the partly hardened UBB, then a period of omission during which further lithification of pebbles at the discontinuity surface was followed by boring. Renewal of sedimentation (LLB) took place without further movement of the bored lithoclasts because the outer, bored surfaces have not been re-eroded (Figs 6.1E p325). Development of a conglomeratic horizon at the top of the UBB was reported from NE Wenlock Edge (Shergold and Shirley '68), and the Bengry Track at Aymestrey (Lawson '73(a)). In the present study, evidence of erosion of the top of the Aymestry Limestone in the main quarry at Aymestrey (p125) indicates a disconformity at the UBB-LLB boundary. A clean-swept erosion surface was proposed by Shergold and Shirley ('68) for SE Wenlock Edge, where there is a sharp contact between the two stages.

At Lye, a series of coarse pebbly limestones are found in the basal LLB. These beds have bioclastic, shelly matrices, with irregular, limestone and calcareous siltstone, pebbles (Fig 6.9p322). They most resemble the basal May Hill conglomerates. (Only a few small lithoclasts are clearly bored; however, the Lye conglomerates were not studied extensively).

In the NE Wenlock Edge conglomerates, ooliths occur in one locality, and the large ostracode Leperditia, which Berdan ('68) suggested might be adapted to temporary sub-aerial exposure, was recorded commonly at this level (Shergold and Shirley '68). These suggest very shallow conditions, and possibly emergence at the end of UBB times. The Dean borehole horizon may be explained by submarine cementation. There is widespread evidence of at least one period of non-deposition and erosion at the UBB-LLB boundary. The Lye deposits indicate repeated pauses in sedimentation in this area, consistent with the thin succession; bone-beds and phosphatised fragment beds higher in the succession show repeated periods of non-deposition.

Boring organisms:

(Boring = penetration of hard substrates)

Records of boring organisms from Palaeozoic rocks are very limited. The ichnogenus Trypanites was proposed by Bromley ('72) for a spectrum of more generalised, pouch-like, single entrance excavations (which can be attributed to polychaetes, bivalves, thoracican barnacles, sipunculids, and other groups). Most Palaeozoic borings in hardgrounds are of this type (eg. Hecker '70, Kennedy '75). However, the ichnogenus covers a wide range of sizes and shapes of excavations and is probably a heterogeneous grouping (Warme '75).

The borings in the LLB conglomerates appear comparable with those attributed by Seilacher ('69) to acrothoracican barnacles. He described borings which extended only a few millimetres into the substrate, and had narrow (about 1 mm), drop - to slit - shaped apertures. The pouches were separate, although commonly gregarious. He recognised an evolutionary trend from parallel-sided excavations in the Palaeozoic to the development of side pockets near the base in Mesozoic and Caenozoic examples. The LLB borings include some with basal branching.

Bryozoan borings are similar in dimensions but are connected by a network of stolons (Warme '75). Such patterns are not seen on the

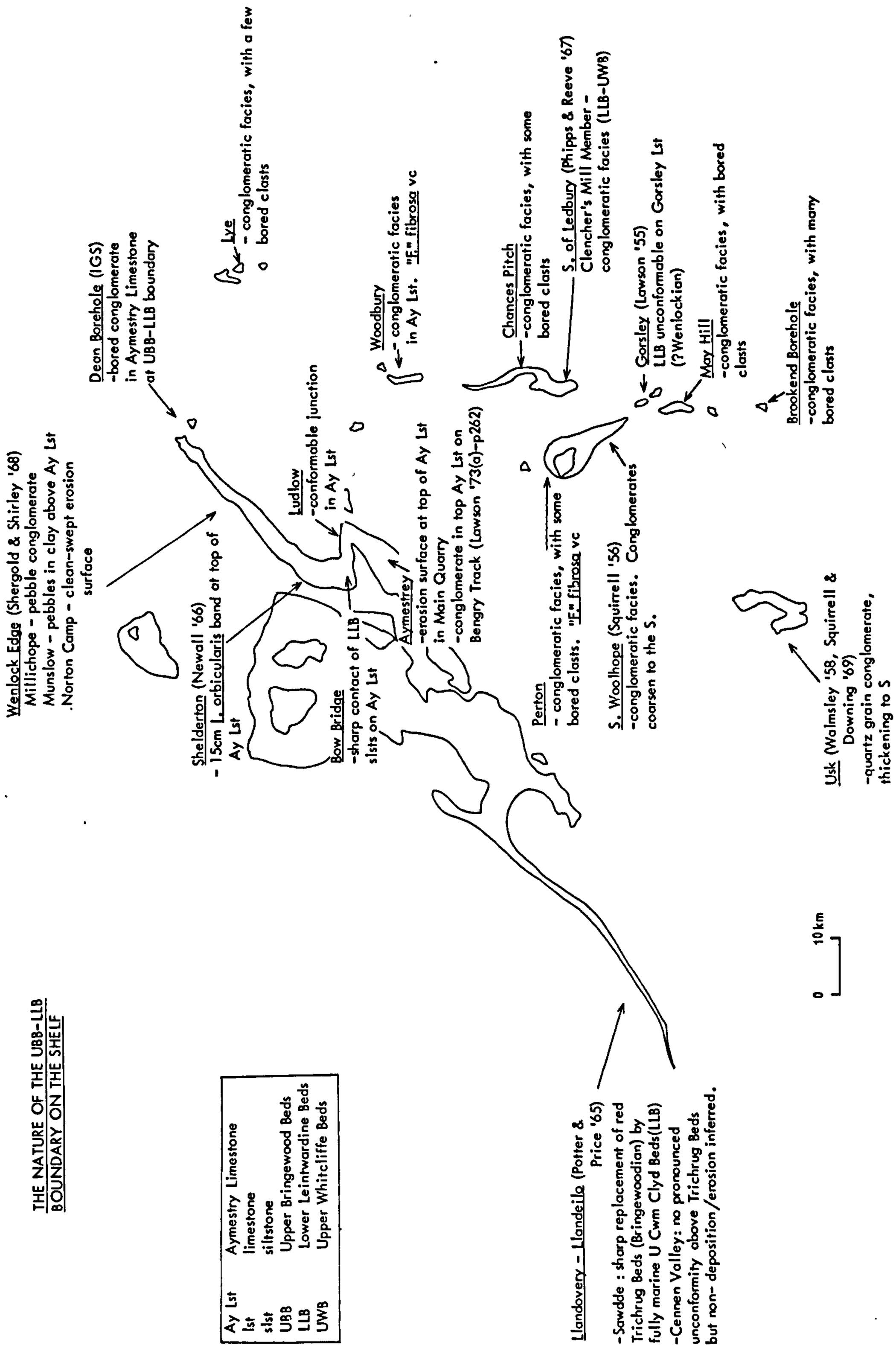


Fig. 6.12 : The nature of the UBB-LLB boundary on the shelf.

surface of LLB lithoclasts. Sponges are important borers in Mesozoic and later hardgrounds. Clionid sponges make microscopic to small macroscopic cavities which gradually become interconnected into internal galleries. The LLB borings are single excavations, however. Their small size eliminates most other groups of boring organisms (such as bivalves, sipunculids and polychaetes).

Conclusions:

The nature of the sediments at the UBB-LLB boundary on the shelf is shown in Fig 6.12p328. There is abundant evidence of environmental instability. Intermittent sedimentation and erosion is inferred for the series of basal conglomerates. The distribution of conglomerates with boring, for which a hard substrate is required, is concluded to reflect shallow-water, and hence probably, nearshore conditions. Borings may have been made by acrothoracican barnacles. The frequency and extent of conglomerates increases to the SE, but is also affected by the Gorsley axis. Active uplift in this region, perhaps with emergence (Lawson '54) is reflected in the coarsening, and increase, of conglomerates, and thinner successions of adjacent areas. Boring of conglomerates is more prominent further SE, in the Tites Point area, and here, hardground formation at discontinuity surfaces appears probable. A submarine origin can explain the conglomeratic beds without recourse to widespread sub-aerial exposure and erosion. The bored lithoclasts demonstrate the early lithification of both mud-grade (eg. Wood Green: WG-Jal) and sand-grade (eg. Lye, Chances Pitch: CP45) carbonates. In the Recent, the latter lithifies more quickly than the former. (Shinn '69, Taylor and Illing '69).

The lateral variation in the character of the basal LLB sediments closely parallels the regional palaeogeography shown in the isopachyte map - Fig 1.4 p9 .

PHOSPHATISED HORIZONS

Phosphatised fragment-beds and conglomerates are found in several areas at the top of the LLB (Map C). Similar horizons and bone-beds are developed at the top of the ULB in some of the shelf inliers (eg. Gornal-Ball '51, May Hill - Lawson '55, Usk-Squirrell and Downing '69). The environmental significance of these horizons is important

for a palaeogeographical interpretation.

There is little evidence in modern sea-floors of the formation of bedded phosphorites, although concentrations of phosphorus are found in insterstitial waters of shelf seas (eg. D'Anglejan '67). Bromley ('67) noted that most phosphate/phosphorus is released from descending organic matter above 1000 m depth, so that for large amounts to accumulate, a much reduced depth, probably above 300 m, is required. If direct precipitation from sea-water, or colloidal deposition, is to occur, a shallow-water environment is again needed. Bromley ('67) reviewed the literature on authigenic phosphorites and their interpretation. Shallow, warm water, particularly between 30-300 m, is generally considered the most favourable conditions for the formation of phosphorites, although a few deeper occurrences have been reported (McKelvey et al. '53). Locally-enriched interstitial waters, especially in restricted basins, may enable phosphatic nodules to form in deeper waters.

Bushinski ('64) suggested that phosphorites form within sediments by phosphatisation of calcium carbonate under quiet conditions, with enrichment by periodic winnowing out of the fine non-phosphatic material. He proposed depth alternations to account for the changing environmental energy, in a range from 30-200 m. Areas of oceanic upwelling in warm climates relate closely to phosphorite deposits. Various chemical and biochemical controls have been advanced to explain this, and depth ranges from 50-1000 m (Bromley '67). In restricted basins (such as Norwegian fjords), Kaplan and Rittenberg ('63) proposed that deposition of phosphate takes place in areas where stagnant, high phosphate, basin waters mix with oxygenated shelf waters.

Phosphatisation is generally associated with shelly and fragmental conglomerates in the LLB. These horizons are developed in some sequences of the shelf and shelf edge regions. At May Hill, a phosphatised limestone conglomerate (LH-I) was taken to mark the LLB-ULB boundary. The bed contains lithoclasts of widely-different sizes associated, especially in the upper part, with small phosphatic nodules and a rich shelly fauna. At Shelderton, there are several phosphatised and limonitised conglomeratic beds at the top of the LLB. The LLB-ULB boundary here was taken at the appearance of N. lauensis, in a thick, fossiliferous, conglomerate which had numerous phosphatic fragments, worn and encrusted fossils, and some large, irregular pebbles of shelly

limestone (SR/2-g).

The conglomeratic nature of these examples shows that erosion of consolidated sediment has taken place. The pebbles of limestone in SR/2-g at Shelderton are of a very different lithology from the local sediments, and so are probably derived from other areas. Fossils and phosphatised pebbles are very closely-packed in these beds. Large orthocones are worn and encrusted with bryozoa, but ostracode valves are commonly unbroken. Therefore, it appears that the beds have been accumulated during breaks in deposition of sediment, and contain elements which have undergone extensive reworking or transport together with others which have not, concentrated by winnowing out of the fine sediment. Phosphatisation is consistent with such an origin. Although it is possible that the nodules did not form in situ, they do not appear greatly abraded and are inferred to be formed in this area. At May Hill, small phosphatic pebbles occur in several beds in the top metre of LLB, including a detrital limestone bed with worn valves of A. reticularis and L. depressa. Phosphatisation can again be explained by sedimentary discontinuities in the sequence. Several of the lithoclasts in the conglomerate are similar in lithology to the enclosing matrix, which suggests that they are derived locally by scouring of the partly lithified sediment. An intraformational limestone conglomerate at this level at Perton (PL/A-A) does not have phosphatic nodules, nor is as shelly. It is possible that it does not represent a similar break in deposition, but reflects a period of increased current activity.

Phosphatisation appears to be associated with discontinuous sedimentation in the thin shelf sequences, and is inferred to have occurred during quiet periods of non-deposition. Fragmental and conglomeratic beds result from occasional erosive current activity on the partly lithified sediment. At the shelf edge, similar periods of non-deposition of sediment alternated with normal sedimentation. The proposal of phosphate deposition concentrated at the edge of a restricted basin (Kaplan and Rittenberg '63) needs consideration because of the development of several phosphatised pebble beds at Aymestrey and Leintwardine, near the gravi-lauensis level. The appearance of the Gotland species N. lauensis and C. puellaris at this level does not seem consistent with increased restriction of the basin, though. Environmentally, the presence of the phosphatised beds may justify an

environmental interpretion of relatively shallow-water conditions, probably above 300 m and possibly much less.

PALAEOECOLOGICAL ANALYSES

The terminology used here to describe fossil assemblages follows the definitions by Boucot ('53), "life assemblage" denoting *in situ* fossils, and "death assemblage" referring to transported faunas.

Fossil assemblages consist of autochthonous and/or allochthonous components, and may have accumulated over long periods of time. Factors such as fossilisation bias, selective destruction of the less robust types and current winnowing further modify the composition of the faunas. Conclusions following from application of standard ecological techniques to fossil-bearing strata must take into account the complex of parameters involved in the formation of a fossil assemblage.

Size-frequency graphs:

A number of studies based on population dynamics have been carried out to distinguish between "life" and "death" assemblages of fossils. Interpretation of simple size-frequency plots of distribution, to differentiate altered and unaltered populations, differs fundamentally among workers.

Boucot ('53) argued that invertebrates with very high reproductive rates typically show high infant mortality, which for life assemblages would produce positively-skewed graphs of population distribution. Then, transport of shells would result in a bell-shaped curve, because of current sorting. The mean size of individuals would be related to the strength of the currents.

Craig and Hallam ('63) disputed the two basic assumptions in this work. Firstly, they proposed that, as most bottom-dwelling marine invertebrates have planktonic larval stages, the high mortality rate of juveniles might be expected to affect these forms, and not the young benthonic forms once they have successfully settled. Their work on living populations of *Mytilus edulis* indicated a relatively low mortality in the juvenile forms. The shape of the size-frequency graph depended primarily upon the interaction of growth and mortality rates, which can produce both skewed and normal distributions for living populations. Craig and Oertel ('66) carried out a more comprehensive computer analysis generating models for life and death assemblages

produced by varying growth, mortality and recruitment rates, and again emphasized the inherent variability of the resulting size-frequency graphs for life and death assemblages.

These conclusions oppose the view that the characteristically bell-shaped distributions of fossil assemblages represent death associations (Boucot '53, Olson '57), and are largely produced by selective removal of the small shells by currents, together with their preferential solution and destruction. Hallam ('67) reiterated that the Gaussian size-frequency graphs for some molluscan thanatocoenoses could be explained without invoking size sorting as a significant factor. He attributed the lack of small individuals partly to their selective destruction, but this acted only as a modifying factor on population distributions that reflected mainly the growth and mortality rates.

Nevertheless, the winnowing out by currents of small forms from fossil assemblages can be demonstrated using flume experiments (Newall '66). It is important to realise, though, that their absence does not necessarily indicate that the association is a death assemblage, and that other mechanisms can be responsible for such a population structure.

The general rarity of small forms in many life assemblages (Rudwick '70) has been discussed by several authors (eg. Broadhurst '64, Worsley and Broadhurst '75), and can be attributed to a number of factors. Worsley and Broadhurst ('75), in their study of Silurian atrypid communities, found that the smallest individuals were always larger than the first growth lines on specimens, and the smallest sizes had therefore been lost. They considered the shell pockets and clusters to be <u>in situ</u>, with many specimens preserved in their life attitudes. Collection failure could be discounted because smaller specimens of <u>Dicoelosia</u> were found in the assemblages, and preservation failure should be accompanied by only partial preservation of some larger shells, which was not noted. Selective removal by currents would again affect other species as well, as would the action of predators and sediment feeders (Segerstrale '62). A low infant mortality rate could be responsible to some degree (Craig and Hallam ('63) - although Thayer ('75) has more recently questioned the validity of this with regard to animals which have a high reproductive potential). Worsley and Broadhurst favoured premature death of young specimens, followed by their removal by currents after decay of the anchoring pedicles. They quoted observations by

Bockelie of small dead Mytilus shells floating free in water buoyed up by gases, formed during decomposition of the living tissue, trapped inside the shells. For brachiopods, where the musculature serves to open the shell from its naturally closed position (in contrast with bivalves) this mechanism may be more effective than for bivalves. Yonge ('62) commented that young individuals of many bivalve species are byssally-attached, although the adult forms are free-living; Stanley ('70) correlated this with the need of smaller, lighter forms for security against current removal. A similar strategy is developed in many brachiopod species, in which the pedicle becomes non-functional during ontogeny, the larger, heavier, individuals lying free on, or partially buried in, the sediment (for example, Davia - Tucker ('64). Loss of the anchoring device of small forms could lead to their selective removal by currents.

Several workers have cited recruitment failure in living populations to explain the lack of small forms (Brookfield ('73), Neall ('70), Paine ('69)), suggesting the exclusion, by adults in an area, of juveniles. Thayer ('75) investigated this hypothesis on living brachiopods, and concluded that the necessary conditions for the model were not fulfilled - he commonly found young terebratulids attached to older forms, and prolonged brooding (which would lead to lack of dispersion from the area) is known in many living brachiopods (McCammon and Buchsbaum ('68), Rickwood ('68)). He proposed that "patchy" settlement of larvae could account for the low proportion of young individuals which characterizes many living populations.

Thus, a positively-skewed graph of size-frequency distribution appears fairly atypical even of living populations. Studies on life assemblages (eg. Rudwick '65, Hallam '67) have commonly shown bi- or polymodal population histograms, which may be explained by diverse factors, such as seasonal growth variations, episodic recruitment, mixing of populations and periodic catastrophic events. Clearly the parameters interacting on a population are so numerous, and the resulting distributions correspondingly variable, that size-frequency data are not reliable criteria for distinguishing life and death assemblages.

Articulated: disarticulated shells, and differential sorting of valves:

The ratios of articulated to disarticulated shells, and pedicle (PV) and brachial (BV) valves, were used by Boucot, Brace and DeMar ('58)

to assess the amount of transport that had taken place. Of the three brachiopod genera studied, two had PV:BV ratios very close to 1, while the third value was greater than 10. From this, they concluded that the latter had undergone extensive transport, but that the former had not. Of the two local forms, one was more frequently found articulated, indicating a differential between genera in tendency for the valves to become separated. From the results, it was suggested that this type of study could be used to "contour" distributions, and hence identify the source areas for the various animals.

The hydrodynamic responses of differently shaped valves has been well-documented in the literature, particularly the right-left sorting of bivalve shells along beaches (eg. Lever ('58), Craig ('67)). A similar effect is seen in brachiopod shells; Worsley and Broadhurst ('75) noted that there were fewer BVs among the smaller disarticulated shells of Atrypa, and concluded that these lighter valves had been removed selectively by currents; in older individuals, there was little difference in the numbers of disarticulated pedicle and brachial valves, showing that both were now too heavy to be winnowed away.

Shell orientations:

Flume experiments carried out by Brenchley and Newall ('70) indicated that the long axes of models controlled their orientation during transport, with a dominantly cross-current lineation resulting. However, modifying this for shells are the effects of loading (which produces an eccentric centre of gravity) - for example, by thickening of the umbones which is a feature of many brachiopods. The experiments showed that the load lay preferentially up-current of the long axis after transport. Nagle ('67) carried out flume trials which indicated that, for spiriferids, the direction of the apices depended upon the strength of the depositing current, with upstream orientations produced by low flow regimes, and downstream ones from high flow regimes. Further to this is the finding that the degree of orientation of an assemblage depends upon whether the shells have been moved, rotated, or transported, and if impedence occurs (Brenchley and Newall ('70)). To interpret assemblages showing preferred orientations of shells, the conditions of their deposition must also be evaluated.

The final orientations of shells in flume experiments are commonly approximately unidirectional, but their relation to the current direction varies, from current-parallel to cross-current. Brenchley and Newall

('70), and Nagle ('67), recorded Turritella aligned current-parallel and apices-upstream, but Kelling and Williams ('67) found that another spired gastropod - Nucella lapillus - although similarly aligned, had the apices downstream. Results obtained for other shells - bivalves and gastropods - in this latter study frequently showed a bimodal orientation with peaks in cross-current and current-parallel directions. Flume experiments show that shell shape is only one factor influencing final current orientations, and others, such as buoyancy distribution and current strength, may account for the very different results obtained for similarly constructed shells.

A parameter not yet considered, but integral to transport of shells, is the substrate type. Brenchley and Newall ('70) found that shells "flipped" from concave-up to the stable convex-up orientation more readily on muddy sediments than on sand, and that once this had occurred, there was very little further transport. They concluded that assemblages composed dominantly of convex-up shells, although drifted, may only have travelled a few inches on muddy substrates from their source area, although on sand the distance could be considerable. The ease of burial of shells also depends upon the particle size; current scour leading to partial burial of shells commonly occurred in sand, leaving the shells inclined across the bedding, but was rare in fine sediment.

Shell fragmentation:

Experiments into breakage of bivalve shells were carried out by Trewin and Welsh ('72). They found that the size of the shell was significant, with small valves being damaged more quickly in turbulent conditions than large ones. Also, small shells tended to smash completely into numerous fragments, whereas larger valves broke into a few pieces many of which then proved resistant to further damage. This supports Hallam's ('67) suggestion that small bivalves may suffer selective destruction during transportation. "Old" shells which had deteriorated during burial prior to transportation broke more readily than fresh ones, and thick shells were more resistant to damage than thinner, lighter valves. Therefore the degree of shell fragmentation depends on several factors besides the amount of current sorting.

Summary:

1. Size-frequency data cannot be used to distinguish life and death assemblages of fossils. Rarity of small individuals typifies many living populations and may be explained by several mechanisms

besides size-sorting by currents.

2. The ratio of articulated to disarticulated shells will depend both on the extent of transport and on the fossils involved, since there is a species differential in tendency for the valves to become separated.
3. The ratio of opposing valves of a species may indicate that shell transport has taken place. Sorting results from the different hydrodynamic responses of dissimilarly-shaped shells. However, selective destruction of lighter thinner shells may also produce a differential.
4. The ratio of convex- to concave-surface upwards provides evidence of current action. On muddy sediment, shells may have suffered less movement than on hard substrates, because valves "flip" more readily to the stable, convex-side up, attitude on soft sediment. Current scour leading to partial burial of shells happens more easily in coarser sediments than fine ones; it is rare in the latter.
5. Current orientations of shells commonly show current-parallel and cross-current directions, but in closely-packed assemblages impedence may have a strong modifying influence. The flow regime, the shell shape and buoyancy distribution, and whether the shells have been transported or merely rotated, are other controlling factors in the final alignments.
6. Shell fragmentation results from wear and tear during current sorting and transport, but shell size and thickness, and whether the shells are fresh, are all important factors.

SIZE-FREQUENCY ANALYSES:

Surveys of size-frequency distributions, together with other related ecological parameters, were carried out for the brachiopods D. navicula, S. wilsoni, S. ornatella, I. orbicularis and S. lunata.

1. D. navicula:

Length of the shell was taken as a representative measure of shell size. Ontogenetic studies show a progressive relative increase in elongation with age (Tucker '68, p 614). However, small shells were not common in the assemblages studied, and it is these which show a marked difference in the ratios of length: width: depth from the mature forms. The relative scarcity of small individuals may be explained in a number of ways (- see p 333). For Davia the ecological strategy may

be a major explanation. The young stages have a fairly large foramen, suggesting that they were pedically attached, but progressive incurving of the umbo during ontogeny to impair the opening indicates that the pedicle atrophied to leave larger forms lying free on the sediment. Accompanying the incurvature of the umbo is rapid relative increase in the depth of the shell - similar development is recorded for A. reticularis by Worsley and Broadhurst ('75). This greatly increases the internal volume of the shell, presumably to accommodate the soft parts while also allowing space for the secondary thickening of the ventral floor in the umbonal region. The selective addition to the shell is a weighting device to stabilise unattached individuals. Such an adaptation for a free-living existence is seen in many brachiopods (Rudwick '65).

The samples examined were taken from two localities in the shelf edge region of Leintwardine - Lawnwell Dingle (SO.416.768, section LD-) and Shelderton (SO.416.778, SH/1-), and from sections in the Ludlow anticline. The shelf edge strata were basal LLB, the Mocktree or Dayia Shales of Elles and Slater (1906). In this area, there are 10-13 m of strata containing a profusion of D. navicula (frequently to the exclusion of other types), which overlie massive, nodular UBB limestones with conspicuous K. knightii bands. The Dayia beds are so calcareous in the lower part as to form the top of the Aymestry Limestone facies. The proportion of silt increases upwards, where the lithology is dominantly calcareous siltstone flags, with thin subordinate shelly limestone bands. The Dayia assemblages studied in the Ludlow anticline were taken from the lower 10 m of the LLB. In this area, Dayia is very common in many assemblages, but the fauna is more diverse and several different species (such as S. ludloviensis, and I. orbicularis) are numerically dominant in other, interbedded assemblages (see the quadrat surveys at MF33, p363 ff.). The sediments are calcareous siltstones, interbedded with shelly limestone bands and lenses; some of the siltstone flags are well-laminated.

E. Shelderton:

The samples from Shelderton were taken from one shell band with a lateral separation between adjacent quadrat sites of one metre. The shells were concentrated onto one level, with the majority orientated convex-up. It was not possible to quantify articulation ratios; the concave-up pedicle valves in the assemblages were disarticulated, but

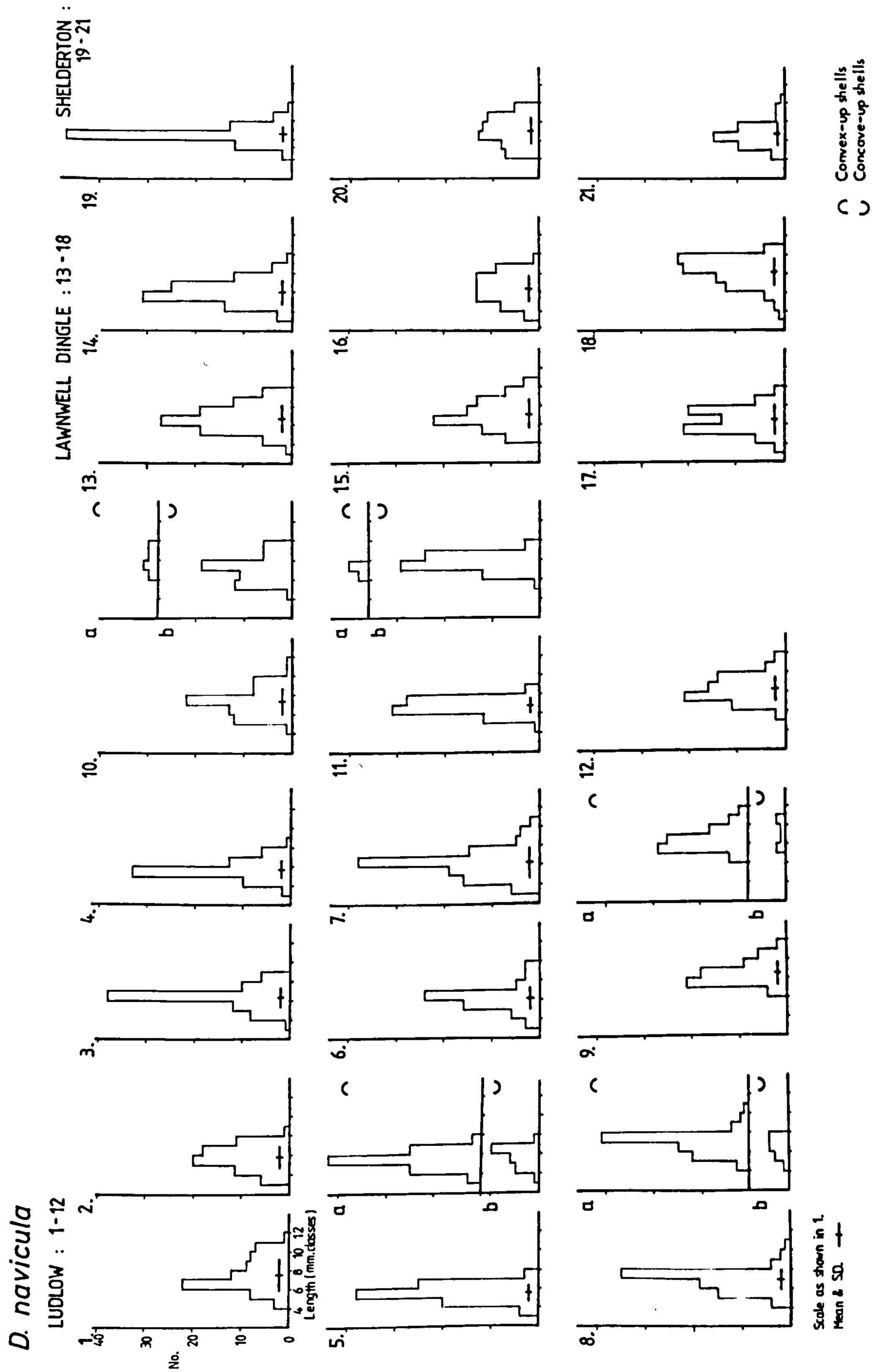


Fig. 6.13 : D. navicula size-frequency graphs.

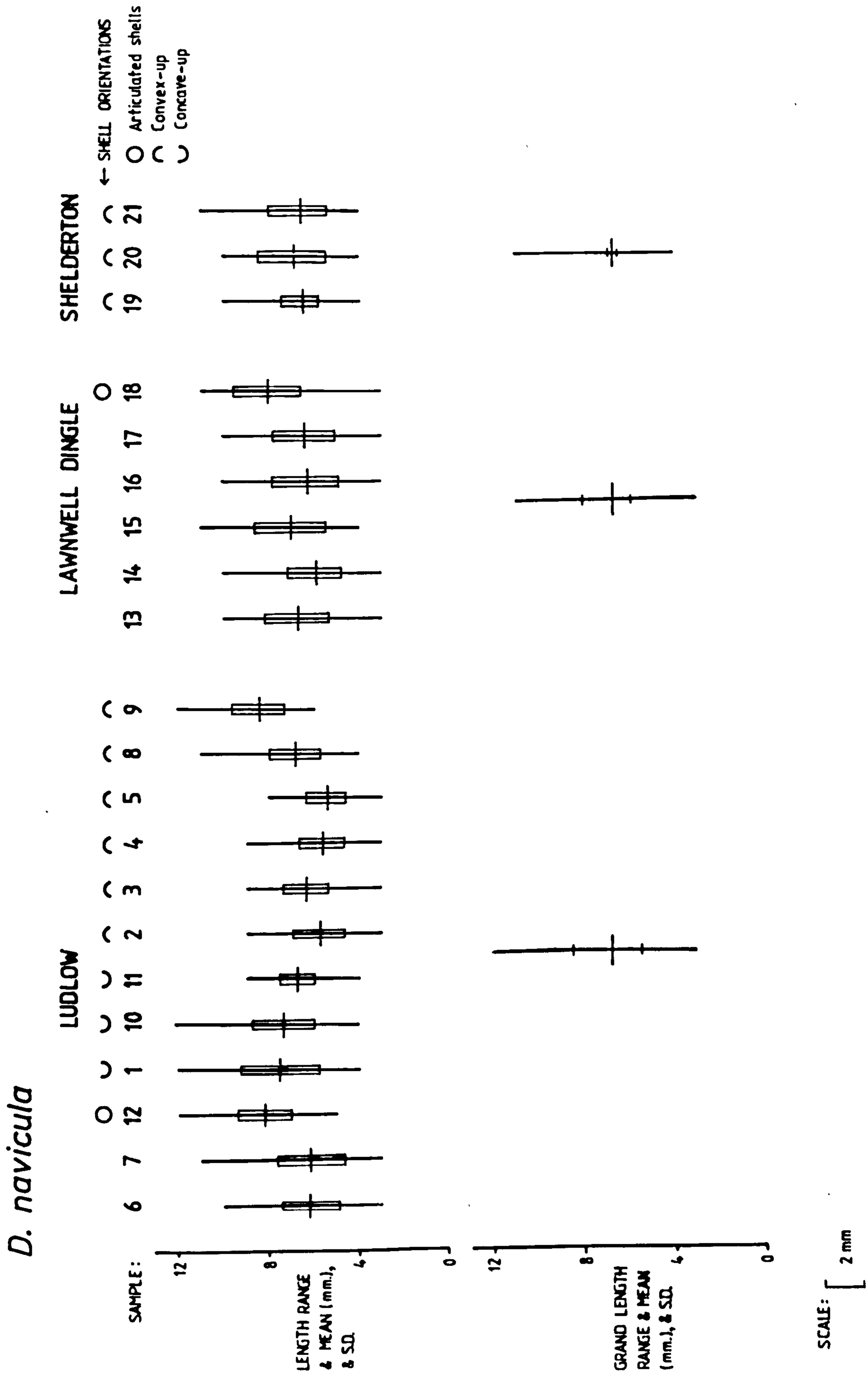


Fig. 6.14 : D. navicula populations - size range, mean and S.D.

the hinge region of pedicle valves with convex surface up was obscured beneath the shells. However, a number of these which had damaged portions of the shell could be seen to be disarticulated. Very few articulated specimens were observed in any part of the horizon. The fauna was composed almost entirely of Davia, with very few brachial valves (PV:BV ratios 9:1) observed in the assemblages. The proportion of damaged and broken shells was moderately high, with about 65% of the valves in the three samples showing chips or cracks; the quantity of fine debris associated with the shells varied from area to area of the band.

The results are plotted in Fig 6.13p339 nos. 19-21. The size-frequency graphs, though all normal distributions with similar means (5.6-7.0 mm) and the same modal class (6-7 mm), show very different profiles. The high proportion of individuals in a narrow size-range in 19 is indicated by its low S.D. of 0.86, compared with the wider general spread of size in the other two assemblages. The dissimilarity of all three graphs, however, is confirmed by χ^2 rank tests which indicate probabilities of less than 0.1% for any pair having equivalent distributions. The sample means do not differ significantly (Table 1, Appx). Hence, the assemblages may belong to the same population, and reflect the inherent variability in its composition at one level. The heterogeneity is also described by the density differences observed in the three quadrat areas.

2. Lawnwell Dingle (LD-):

The samples from Lawnwell Dingle were taken from slightly higher in the succession, the base of the LLB not being exposed in this section. The strata here were irregularly-bedded, calcareous siltstones and shelly limestones, in which Davia was numerous through the 7 m section. The fossils were commonly evenly distributed throughout beds, as well as occurring abundantly on planes. These latter populations were generally single valves, often very closely packed. There was frequently a high proportion of damaged shells in such assemblages (eg. 14). Beds in which Davia was more evenly distributed appeared to have a higher proportion of articulated individuals. Although difficult to determine because of the close packing of the shells in these beds, minimum articulation ratios were estimated for 13 to be 35%, 15 as 65%, and 18

as 70%, where for a plane assemblage in LD-F the ratio was approximately 15%. There were noticeably more articulated and unbroken individuals in some of the shelly limestone bands (eg. 15 and 16); others, however, consisted largely of shell debris. The nature of assemblages in the siltstones was found to be highly variable, with some patches consisting largely of entire individuals while laterally adjacent areas had dominantly disarticulated specimens. The orientation of the shells was mostly random except in the plane assemblages, which tended to have convex-up pedicle valves more commonly. As at Shelderton, single brachial valves were relatively scarce among the populations, and those present were usually fairly large. Damage was more characteristic of shells in highly concentrated assemblages (eg. estimated as 50% in 14, cf. 25% in 16).

The results of samples from Lawnwell Dingle are shown in Fig 6.13 nos. 13-18. The mean size of individuals lies between 6.0 and 7.1 for 13-17, but is noticeably larger for 18 at 8.1 mm. This last graph also shows a negative skew and large S.D. The sample was taken from a band where shells were frequently articulated, and quite a number were orientated umbo-down in the sediment with the commissure steeply inclined. This assemblage may represent a mature, <u>in situ</u> population; similar distribution characteristics have been ascribed to a single spat-fall by Paine ('69), and Neall ('70). In such an instance, the lack of small individuals is a primary feature. Of the other graphs, samples 15 and 16 are comparable, both coming from shelly limestone bands in which complete unbroken individuals were common. Their size-frequency profiles appear flatter than those for the siltstone assemblages, with correspondingly higher S.D.s. However, representative χ^2 rank tests (Table 2) for 16 against 13, 14, 15 and SH/1-20 show only 14 to differ significantly in distribution at the 95% confidence level, and the comparison of 16 with 20 indicates that apparent similarity of the two limestone populations may only reflect chance in sampling. The variability suggested by the Shelderton samples is confirmed by the histograms for Lawnwell Dingle populations. The bimodal distribution in 17 may represent mixed populations - for example, successive generations living in the same area.

3. Ludlow:

The assemblages 1-12 come from LLB in the Ludlow anticline. Here, D. navicula is less common in the lowermost strata, particularly in the eastern part of the region (eg. Sunnyhill Quarry, the stratotype section). It increases in abundance upwards, forming one of the prevalent fossils in many assemblages from the middle part of the LLB (eg. MF/F-), but does not occur in comparable density, dominance, or vertical persistence to its distribution in the shelf edge areas. Except for no. 1, which was from Sunnyhill Quarry, the assemblages measured were from locality 33 of Lawson ('73) (Fig. 2.1p13; SO.4895.7240), from section MF/F-. The fossils were found randomly-orientated throughout some beds, whereas others displayed a concentration one or two shell layers thick at certain levels. The thin bands were usually laterally impersistent over more than a few metres. The samples 1-12 may be divided into those from beds with homogeneous fossil distribution, and those from the discrete shell layers. The second group can be further split according to degree of articulation and to the dominant orientation of the shells.

Samples 6 and 7 belong to the first category. Both were composed largely of isolated pedicle valves, and only occasional brachial valves, although no. 7 had some articulated specimens (min. 15%). Slight damage to valves was common, particularly in individuals associated with patches of shell debris in 6. There appeared to be no preferred orientation of shells within the sediment. The size-frequency histograms are normally-distributed, with similar means and modes; no. 7 has a high S.D.

Of the assemblages from concentrated shell bands, no. 12 had mainly articulated (75%), unbroken specimens, variably orientated in a layer one-shell thick. Their density was fairly consistent within the area studied (45 shells per 10 cm quadrat). The population had a high mean size (8.2 mm) and a slight positive skew to the frequency histogram. This association may, like LD-18, be representative of a life community.

Samples 1, 10 and 11 came from assemblages where the shells were mostly concave-surface up. All were composed very largely of single pedicle valves, often stacked one inside the other in dense accumulations

(1 = 105/quadrat, 10 = 66/quadrat, 11 = 80/quadrat). The smaller specimens were frequently damaged but most of the large shells were unbroken. However, a slightly higher level in the calcareous lens than 11 had abundant shell debris. The histograms for these assemblages differ considerably in profile, from positively-skewed with a high S.D. in 1, to a tall-peaked normal distribution with low S.D. in 11.

The remaining assemblages from the Ludlow area were dominated by detached pedicle valves (very few articulated shells were seen), orientated with the convex surface upwards (ie. overturned). Nos. 2-5 were taken from the same shell horizon, 2 and 3 representing adjacent quadrat sites, 4 and 5 lying respectively 0.7 m and 1.7 m away (Sample 6 was taken from immediately above this band). All the samples show normal distributions, with means from 5.5-6.4 mm, and relatively low variance. The shells were fairly evenly distributed on the bedding plane, although more closely arranged in site 5 (90 individuals/quadrat cf. an average of 67/quadrat for 2-4). In contrast, assemblage 9 was a tightly-packed concentration of large individuals (mean size 8.5 mm, and density of shells of 120/quadrat), while assemblage 8 was taken from a plane rich in convex-up S. ludloviensis valves over which single Davia ventral valves were commonly scattered (shell density of 40/quadrat). Graph 9 shows an appreciable positive skew to the distribution. The proportion of broken shells in the assemblages was not high, and damage was often to the smaller individuals. An exception to this was the dense accumulation in 9, in which many of the valves had small chips and cracks.

The differences between the means of samples 2-5 were compared against their mean standard errors to evaluate the probability that they belonged to the same population. (If the observed difference μ_0 is greater than twice the combined standard error μ_e, the means may be taken to deviate significantly). The results (Table 3, Appx) show that assemblage 3 differs significantly from the rest. The distinction between even the adjacent quadrat sites 2 and 3 may result from extensive current sorting during the deposition of the fauna.

Summary:

The characteristics of the samples from D. navicula assemblages are shown in Table 4 (Appx) which discriminates between features more and less likely to result from sorting and transport. The obvious

scarcity of the brachial valves among disarticulated shells, and the general rarity of small forms in these populations, indicate that all have been affected to some degree by current action.

The groups, in order of decreasing evidence of strong or extensive current activity, are:-

1. D, F: Convex-up valves in plane assemblages.
   These typically show features associated with current sorting. Ludlow samples (D) have a lower proportion of broken and damaged shells than the Shelderton ones (F).
2. C: Concave-up valves in plane assemblages.
   Relatively less frequent. Again, accumulations formed by current transport.
3. A, E: Shells randomly orientated, evenly distributed through beds.
   Heterogeneous, generally with a wider population variance. Complete specimens common in some assemblages (cf. rare in plane faunas), together with disarticulated valves. Lawnwell Dingle samples (E) have a higher proportion of articulated specimens.
4. B, B': Assemblages of articulated shells.
   Large mean size, and skewed population distribution. Apparently not transported far.

Conclusions:

At both Ludlow and Leintwardine, plane assemblages of single valves interdigitate with beds of evenly distributed fossils and occasional bands of articulated shells. The latter may represent life assemblages; they do not appear to have moved far, which indicates that D. navicula was indigenous to these areas. The transported assemblages can be explained by periodic current disturbances, for example by storms, causing reworking of the surface sediments in which shells were irregularly disposed. Then, the sequences may reflect fluctuating current action upon the local benthos.

However, more considerable current transport can be ruled out for the plane assemblages of pedicle valves. Reineck and Singh ('73) described shell transport (without great mechanical destruction) over several kilometres in Recent storm deposits of the North Sea. At Leintwardine, the basal LLB have an abundant fauna almost exclusively composed of D. navicula. Fossils occur in plane assemblages and are more evenly distributed in other beds. Thus the clearly transported and little disturbed assemblages have the same composition. This

indicates either than D. navicula had a very wide distribution in monospecific populations so that shell transport has not introduced other fauna in the plane assemblages, or that the amount of transport has not been extensive. At Ludlow, the prevalent species in assemblages change frequently. Most faunas are in transported plane assemblages or lenticular coquinas, but beds in which faunas of similar species composition are more evenly distributed are also found. Here, again, it is necessary to postulate either wide zones with consistent faunas or only local transport.

Particularly at Lawnwell Dingle, the intimate association, vertically and laterally, of clearly transported and indigenous assemblages suggests that disturbances have not been extensive. Heterogeneity of population structure probably reflects an original feature of the settlement pattern. The great abundance of the fossils in all beds suggests that the free-lying D. navicula individuals lived in close proximity, deriving stability among surrounding shells. Limited dispersion of the species, typical of living articulate brachiopods (Rudwick '62(a)), resulting in clusters of single spat-falls would produce the "patchy" population structure observed.

2. S. wilsoni:

The measurement taken as proportional to size was the length of the shell. Assemblages from three sections in the shelf inliers - Perton Quarry (SO.596.400), Chances Pitch (SO.748.403) and Woodbury Quarry (SO.743.637) - were examined.

a. Woodbury Quarry:

S. wilsoni occurs abundantly at horizons throughout the LLB in this section. Frequently it is found comprising monospecific accumulations in laterally extensive bands, as well as in impersistent coquinas and small clusters of shells. M. nucula has a similar distribution and mode of occurrence in these beds, and typically, associations dominated by one of the two rhynchonellids include subordinate numbers of the other type. The vertical thickness of individual bands rarely exceeds 15 cm, and many are less than 5 cm. The assemblages occur in both siltstone and limestone beds. Above the top of the Aymestry Limestone facies, which in this area extends up into the LLB, many of the limestones contain dense fossil accumulations and are probably biogenic in origin; commonly, siltstone assemblages

show relative carbonate enrichment of the sediment surrounding shells (caused by migration of ions out into the adjacent matrix), so that the central portions of close-packed concentrations often comprise limestones, but the top and bottom parts are noticeably less calcareous.

Populations taken from six monospecific assemblages were measured, and the results plotted in the histograms 7-12, Fig 6.15 p348 . There are two types of distribution - those with wide variance and those with a much narrower spread of size. The first group includes 7, 8, 10 and 12: all have similar means (12.4-12.8 mm) and high standard deviations (>1.5 mm). Their distributions are normal to slightly negatively skewed. χ^2 rank tests showed pairs 7 and 10, 8 and 12 not to differ significantly in distribution; all other sample pairs rejected the null hypothesis at a 99.9% confidence level (Table 5, Appx). The second type of size-frequency histogram is shown by assemblages 9 and 11. These differ markedly in mean size both from each other and from the consistent average for the rest of the samples. The mean standard errors were compared to assess the probability of samples belonging to the same population - Table 6 (Appx) The table indicates that 9 and 11 differ sufficiently to make their derivation from a single population improbable.

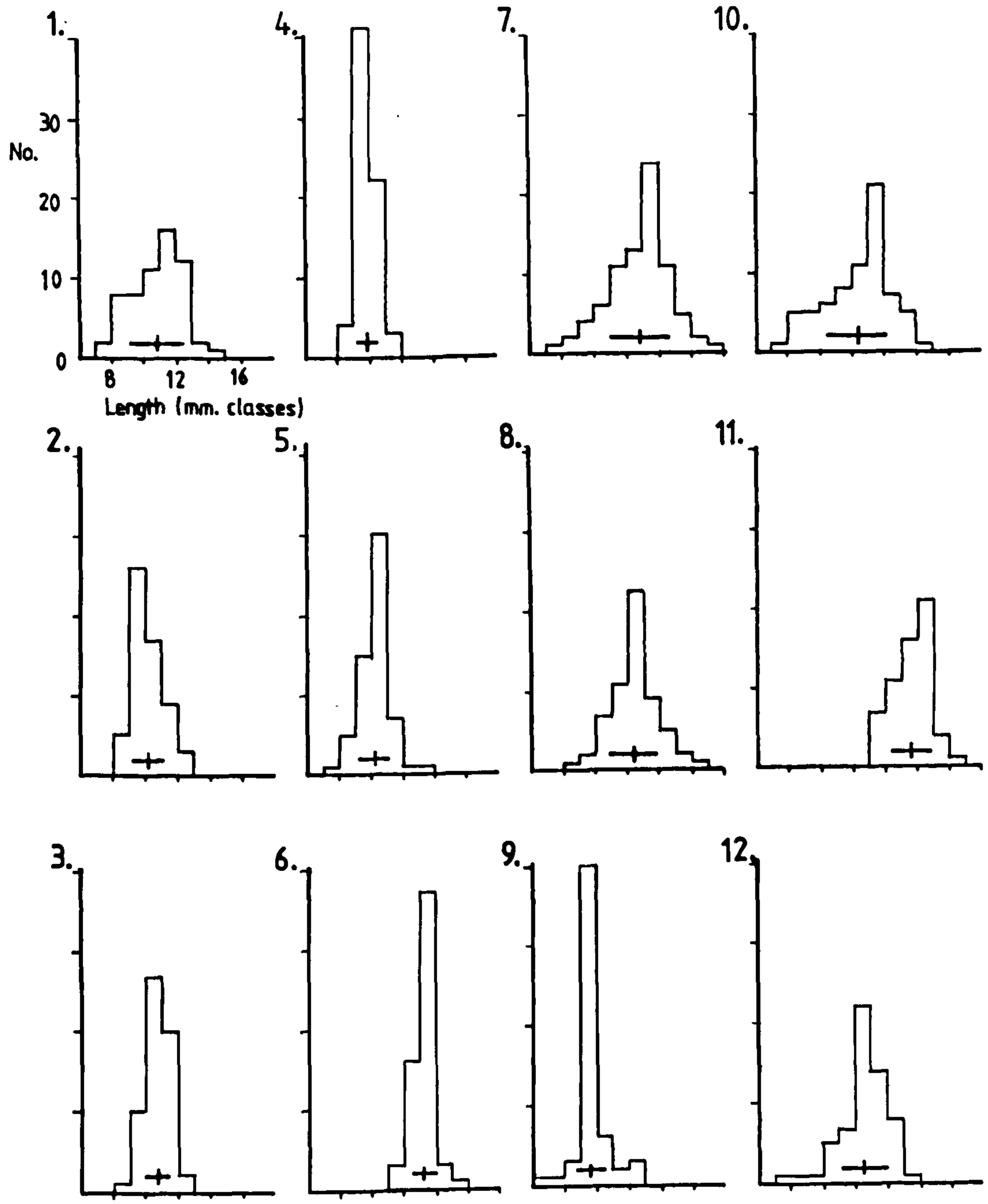
b. Perton Quarry and Chances Pitch:

At Perton Quarry and Chances Pitch, in the middle part of the LLB, S. wilsoni commonly composes monospecific concentrations in thin shell limestone bands. These beds are found among flaggy siltstones in which debris-layers are not infrequent, and where successive plane assemblages are dominated by different members of the fauna. Other limestone horizons in these sequences contain a more diverse fauna. Some are conglomeratic, some consist of accumulations of bioclastic debris, and there are also unfossiliferous limestone beds.

From Perton Quarry, three monospecific limestone assemblages were sampled, each one from three different sites along the band (Fig6.16p349). In addition, one sample was taken from a richly fossiliferous limestone (PL/B-B), in which several species were very common (see also S. ornatella - 9, Fig 6.18p356). At Chances Pitch, two monospecific bands were considered.

The results are shown in Figs 6.15, 6.16, 6.17 . It can be seen that all the bands containing S. wilsoni exclusively are characterised by normal distributions having low standard deviations, while the mixed fauna in PL/B-B - graph 1 - has a negatively-skewed profile, and

S. wilsoni



Scale as shown in 1.
Mean & SD. —+—

1-4 Perton
5,6 Chances Pitch
7-12 Woodbury

Fig. 6.15 : S. wilsoni size-frequency graphs.

S. wilsoni - LATERAL VARIATION

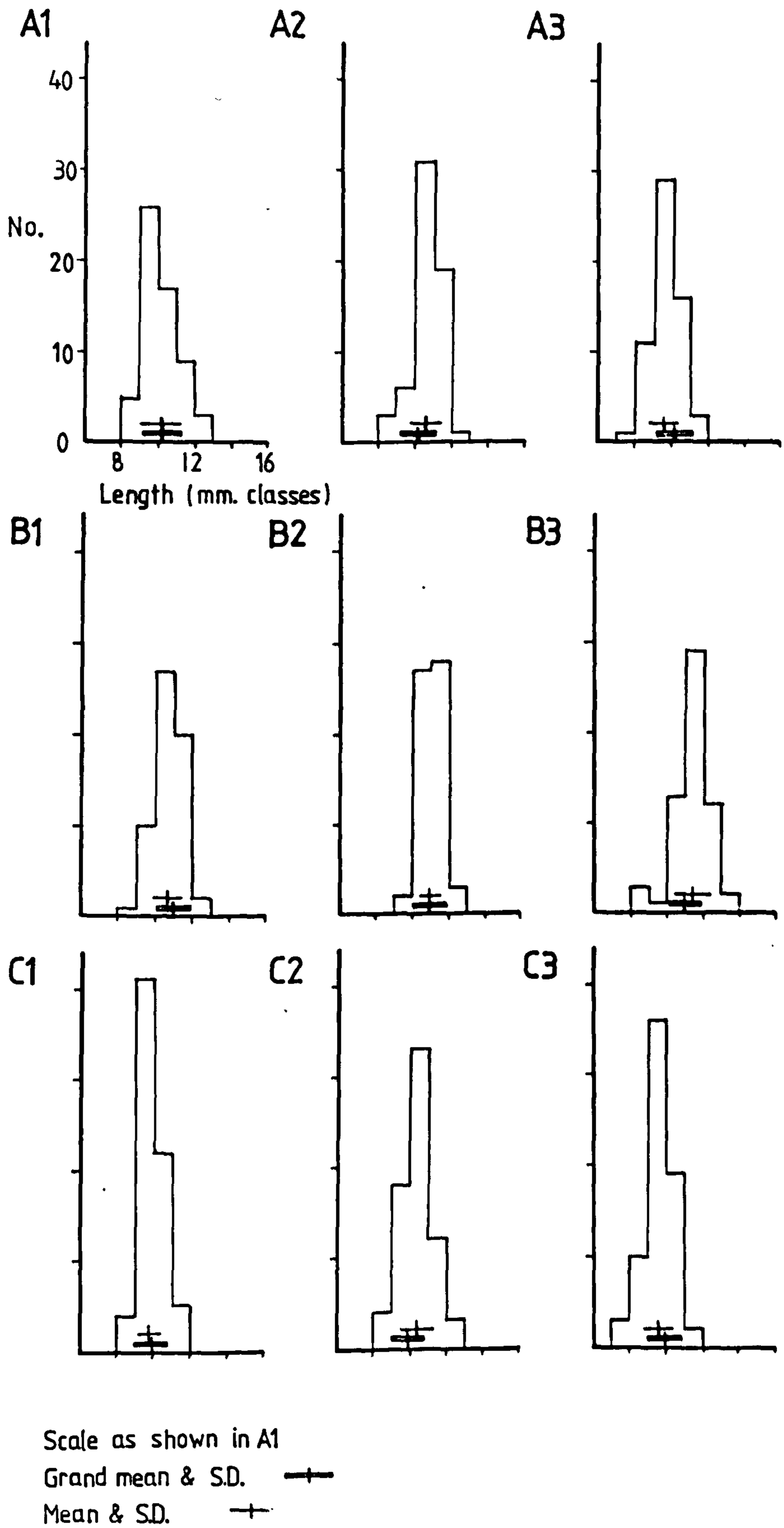


Fig. 6.16 : S. wilsoni - Lateral variation, Perton Quarry.

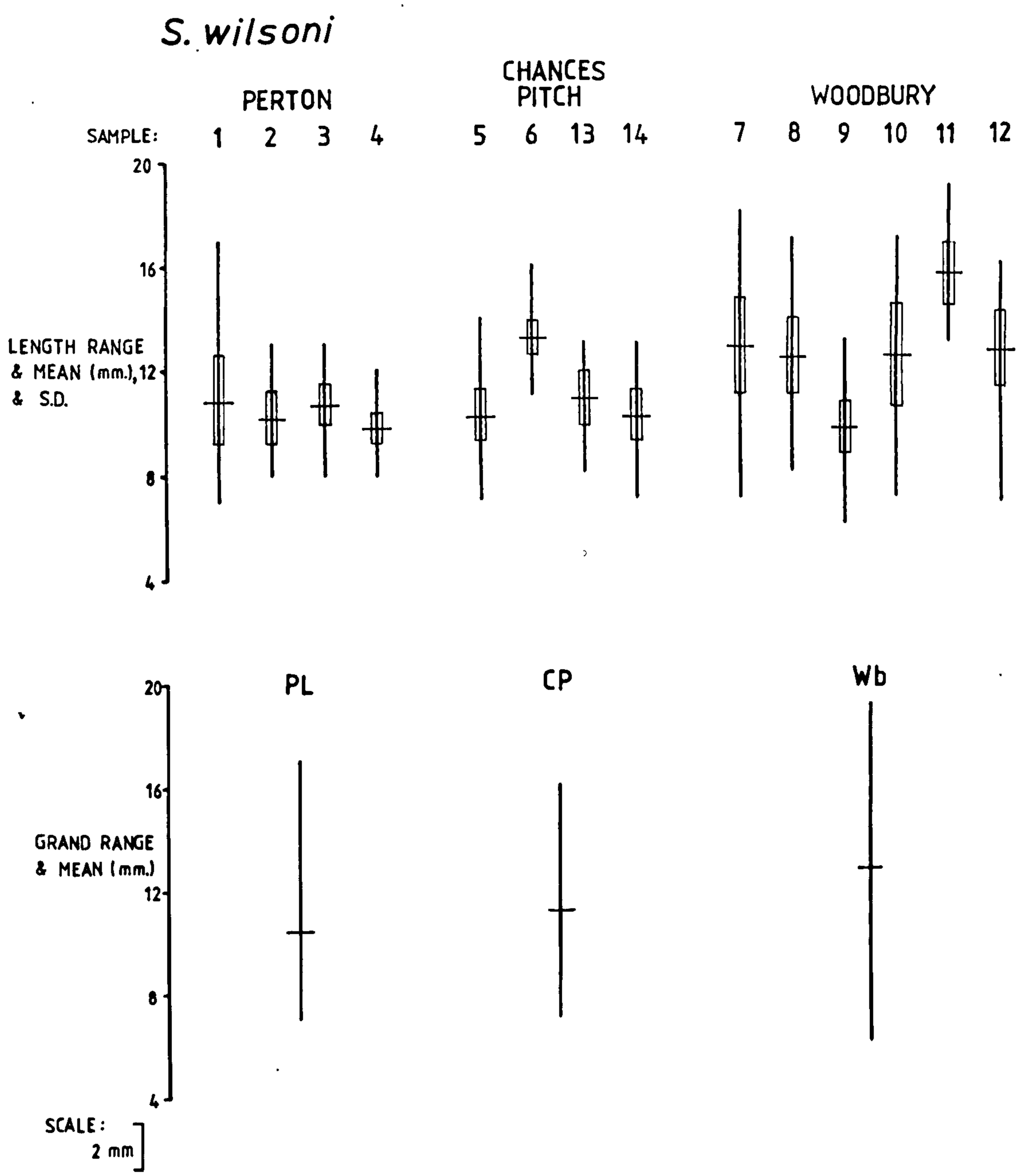


Fig. 6.17 : S. wilsoni populations - Size range, mean and S.D.

wide size-spread (ie. high S.D.). χ^2 rank tests matching the profiles of the left-hand skewed graphs for 7, 10 and 11 against 1 showed a significant difference only for the last pair (Table 7, Appx). It is interesting to note that these comparisons are between monospecific samples from Woodbury Quarry, and the varied fauna in the Perton assemblage.

Graphs 2-6 all show standard deviations of less than 1 mm indicating the closely similar dimensions of the majority of individuals in each assemblage. Fairly consistent values of mean size for the samples from Perton Quarry, average 10.4 mm, compare with a grand mean of 12.6 mm for the Woodbury faunas. This mean size discrepancy appears significant in view of the relatively constant values obtained within each locality. The two Chances Pitch assemblages differed by 3 mm in the average size; results from two further, though smaller, assemblages of shells (13-40 individuals, and 14-35 individuals) were therefore included in order to estimate a representative mean value. This was calculated as 11.1 mm, which lies slightly closer to the Perton average, although occupying an intermediate position between the other two.

For the Perton Quarry assemblages 2, 3 and 4, two more sites in the same horizons were also examined, with lateral separations of approximately 1 m and 3 m from the first samples. The results are shown in Fig6.16p349. Within each level, equal numbers of specimens were used for all the samples. Concentration of the specimens varied to some extent, but remained generally high. The graphs show the consistently small size spreads within any of the associations, which is emphasized by the low estimates for the probability that these lateral assemblages are samples from one population. In spite of the overall mean size deviating by a maximum of only 0.5 mm from the sample means, the mean standard errors are small enough to indicate that the difference is significant for many of the samples (Table 8, Appx). The comparisons of means of the horizons showed comparable distinction (Table 9, Appx) although it should be noted that some individual samples from the three bands show a close similarity in distribution eg. A2 and B1, A3 and C3.

The mean size for the three sites in each level alters directionally only in B. In the other cases, the mean increases to the second sample, then is smaller again in the third.

To account for the difference between the samples from Woodbury and those from Perton and Chances Pitch, the conditions of deposition must be considered. These brachiopods are generally articulated and little abraded - this may be explained by relative strength of articulation and the spherical shape rather than because of lack of transport of the shells. In the more diversely fossiliferous limestone bands, many of the other types, eg. Isorthis, P. ludloviensis, occur as single and broken valves, while the rhynchonellids are largely complete. At Perton, the thin shell limestones typically have sharp bases and there is a high frequency of intercalated bands of shell debris in the succession. Some of the more concentrated S. wilsoni assemblages contain considerable numbers of disarticulated shells as well as undamaged specimens; other bands appear to have mainly complete individuals. Similar facies are found at Chances Pitch, but here the shell limestones are often thinner, with most less than 5 cm thick. At Woodbury, many of the rhynchonellid horizons contain largely unbroken shells (in siltstones, often compressionally distorted). Some limestones show a higher proportion of disarticulated shells; these bands also frequently have clearly distinct lower boundaries though more transitional upper limits.

The monospecific assemblages at Perton and Chances Pitch, with their low-variance, normal distributions, are found in beds with sharply-defined bases, typical of current accumulations. The high degree of size-sorting is analogous to that found in many Recent shell banks as a result of current sorting in transport (eg. Lever and Thijssen '68), as is the lateral variation in size along one horizon. The characteristic pattern of shell beds or debris-covered planes occurring at levels within the sedimentary sequence indicates the occurrence of periodic catastrophic events. Beds containing one species exclusively may be regarded either as products of extreme current sorting or as indicative of an original distribution feature. The faunas in this part of the succession are commonly dominated by a few different elements alternately. This suggests a mosaic distribution of species such as is typical of Recent marine environments (Thorson '57). Frequent fluctuations in the relative species proportions and abundances with time are caused by the interaction of various environmental parameters, and species areal distributions change

correspondingly. The monospecific S. wilsoni assemblages may represent size-sorted products from populations which themselves were largely exclusive. The reworking involved in formation of these shell bands appears more extensive than that creating the thin, impersistent plane faunas.

This original colonisation pattern is confirmed by the monospecific Woodbury assemblages, which include both highly-sorted samples (9 and 11) and populations with a wider variance of size. The latter examples cannot be regarded as products of extreme current sorting. The common occurrence of populations with a broad size variance indicates less rigorous current activity in their formation than the conditions prevailing during the deposition of most of the Perton (except population 1) and the Chances Pitch assemblages.

The greater mean size of individuals in the Woodbury succession is interesting, especially in view of the great abundance of rhynchonellids, numerically and relative to other faunas, in these strata. Such characters may indicate more optimal ecological conditions in this region, compared with other areas (Ager '65).

Conclusions:

The spherical shape of S. wilsoni, and its resistance to disarticulation and breakage, make it susceptible, after detachment, to extensive current sorting. At Perton, uniformly-sized individuals are accumulated together in some bands along which there is a gradual lateral shift in the mean size. These shell limestones are clearly current-swept deposits. The interbedded calcareous siltstones have frequent plane faunas that are dominated by various species in turn. The bedding-plane assemblages, often laterally impersistent, represent periodic current disturbances. From the limited lateral and vertical extent of many faunas, it is inferred that transport of shells was frequently not extensive, and the fluctuating faunal composition results from a mosaic pattern of sea-floor settlement. The monospecific limestones could show primarily the dominance of S. wilsoni in the source area, but do appear to have been extensively reworked.

At Woodbury, well-sorted and more heterogeneous, monospecific, S. wilsoni populations are interbedded. The latter, which have many large, individuals associated with relatively low amounts of shell debris, have not been subjected to such severe current action as the

former. The exclusive composition of both faunas suggests that this was a feature of the original distribution.

The S. wilsoni assemblages examined include more and less extensively transported monospecific associations. This indicates that in the original distribution of S. wilsoni there were areas in which the brachiopod was virtually exclusive.

3. S. ornatella:

The width of the hinge (than is, the max. width of shell) was measured for the size-frequency histograms. Assemblages from the Ludlow anticline, and from several of the shelf inliers, were examined. The sediments included calcareous siltstones and shelly limestones. This brachiopod species is characteristically abundant in the ULB of the shelf, where the acme is taken to indicate this stratigraphical division (eg. Phipps and Reeve '67, Lawson '55). However, it occurs very commonly at intervals through the LLB, and becomes increasingly numerous in the upper 10 m of this division in the Ludlow anticline.

Typically, assemblages rich in S. ornatella are composed of single valves. In some cases, the fossils are concentrated onto planes; specimens are often little broken or abraded, and occur both concave and convex surfaces upwards (nos. 3, 4, 7). In other bands, the shells are more obliquely directed into the sediment, in small clustered groups, or "stacked", as well as lying parallel to the bedding (Nos. 1, 5, 8). Again the shells are commonly undamaged, though disarticulated. In shelly limestones, the species is found in both monospecific (5, 6, 8) and more diverse (2, 9) faunas. The proportion of broken individuals associated with the complete valves varies considerably among assemblages.

Five samples were studied from the upper 10 m of the LLB at Ludlow - 1-4 from Sunnyhill Quarry section SY/B-, and 5 from the beds below the ULB stratotype on the Whitcliffe (Wh-). The sediments from SY/B- are largely decalcified alternations of well-laminated and more homogeneous siltstones and shell limestones. Fossils in the laminated beds are restricted largely to bedding-parallel assemblages in thin bands and planes, while the unlaminated flags may show an even distribution of randomly-orientated fossils. The Whitcliffe sequence has very calcareous siltstones, both laminated and more massive, intercalated with shelly limestones, in which the faunal distributions

are comparable to those of the Sunnyhill succession further to the W.

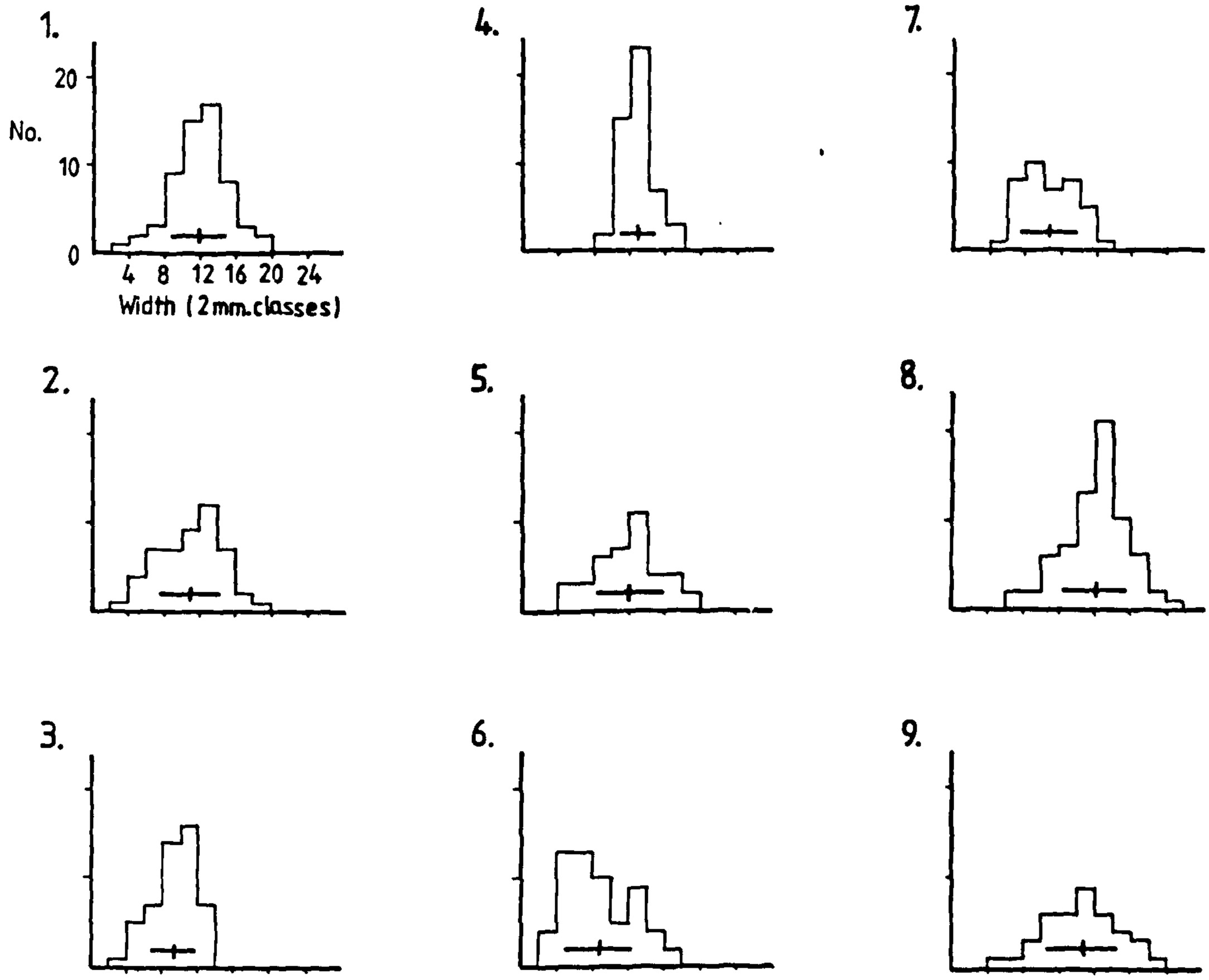
The other four examples were taken from sequences in the shelf inliers, from Perton Quarry, Woodbury Quarry and Chances Pitch. At Perton, assemblage 9 came from the same horizon as S. wilsoni sample 1 - Fig 6.15 - a diverse and richly fossiliferous, middle LLB limestone bed (PL/B-B). The Woodbury samples were at the LLB-ULB boundary level, from a monospecific limestone band (Wb/B-z) and a shell plane in the overlying siltstones (Wb/B-α). Assemblage 8 was from a monospecific bioclastic limestone in the central part of the LLB at Chances Pitch.

The results are shown in Fig 6.18p356. The graphs are mostly normal to slightly negatively skewed except for the Woodbury samples, which both show a tendency to bimodality in their distributions. The standard deviations are noticeably less for the plane assemblages: <3.0 cf. 3.2 for sample 1, and cf. >3.6 for the other samples. The profiles of selected pairs of histograms were compared using χ^2 tests, the results of which are shown in Table 10 (Appx) . The failure to reject the hypothesis of similarity of distributions, for several pairs, indicates some relatively consistent population profiles.

The faunas from Ludlow (monospecific, except for 2) were tested, by comparison of their respective means and standard errors, for the probability that they might be samples from the same population. The results are shown in Table 11 (Appx) . Only assemblage 3 can be separated from all the rest, possessing a significantly lower mean size. This implies that sample 4 could derive from winnowing on the population of 1 - they came from the same horizon - by the selective removal of the smaller individuals. The mean of 11.8 mm for 1 compared with 12.8 for 4, and smallest class of 3 mm cf. 9 mm accords with such a mechanism. That assemblage 3 was a "plane" concentration, with low variance and a normal distribution, suggests that it may itself be a sorted population from which the smaller sizes have been preferentially lost. Its low mean size then, may be due to general immaturity of its members. Alternatively, the sample could represent a current accumulation of small specimens.

The two Woodbury assemblages, 6 and 7, show comparable bimodal histogram profiles. However, they differ significantly in mean size

S. ornatella



Scale as shown in 1.
Mean & S.D. —+—

1-4	SY/B
5	Wh
6,7	Woodbury
8	Chances Pitch
9	Perton

Fig. 6.18 : S. ornatella size-frequency graphs.

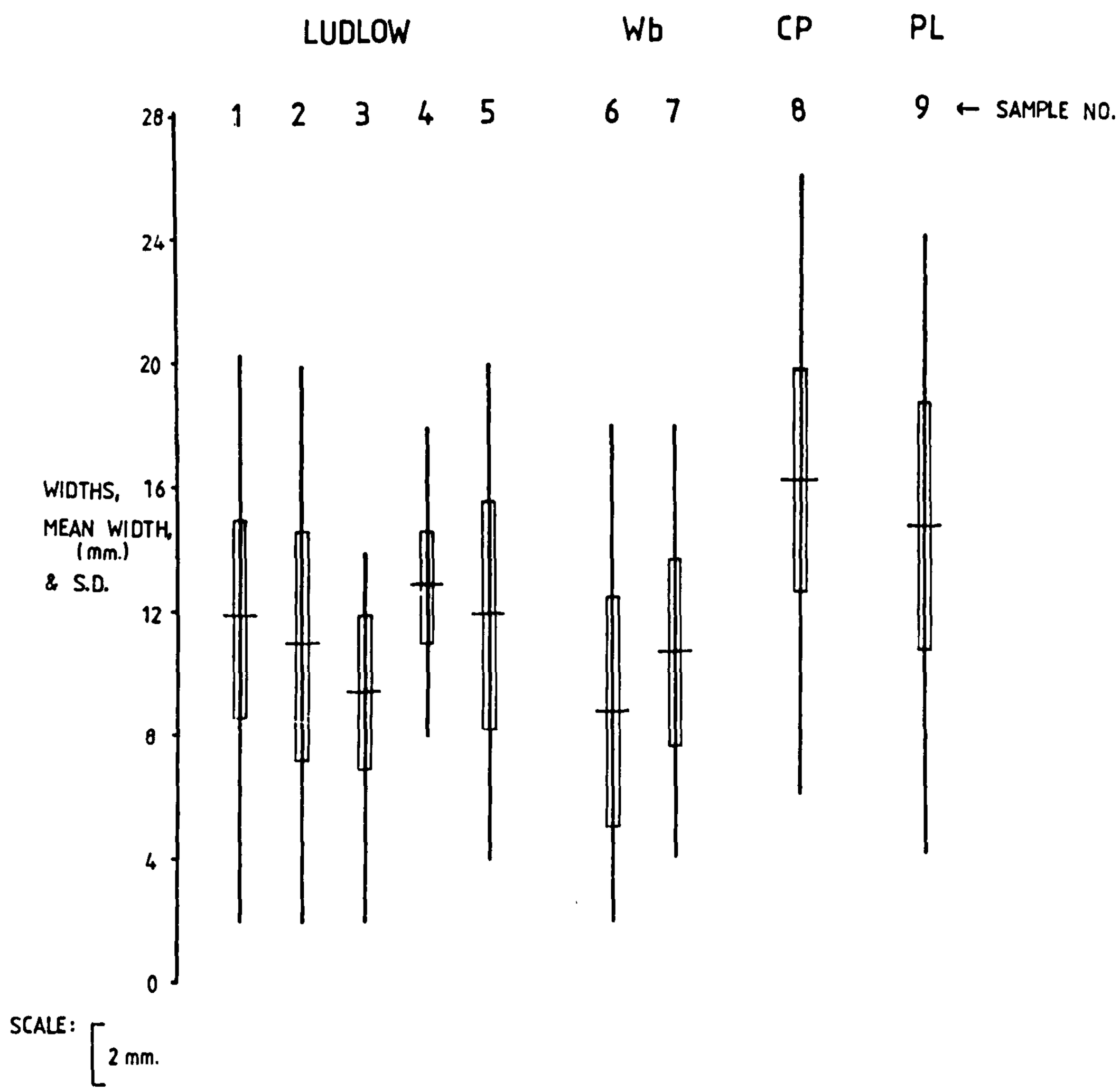


Fig. 6.19 : S. ornatella populations - Size range, mean and S.D.

(μ_o 1.87: μ_e 0.76) and in actual distributions ($\chi^2 < 0.001$, Table 10(Appx)). However, sample 7 is a plane concentration, with greater mean size and lower S.D. than 6, and with a higher smallest-size class. As with 4 and 1, therefore it is possible that the former assemblage may represent a current-modified product of a population like 6. The bimodality of their profiles is unique among the graphs; it may result from the growth of successive spatfalls living in the same area.

The assemblages 5 and 8, 2 and 9 all come from bioclastic limestones - two with monospecific (5 and 8), and two having diverse (2 and 9), faunas. They have broadly similar size-frequency distributions; the generally high S.D.s even in the monospecific faunas argue against their restricted faunas being the result of extreme current action on previously more varied associations. Rather, the prevalence of one species must be considered an original feature of the community.

Sample 8 had a very close-packed accumulation of valves, some lying parallel to the bedding and others "stacked" obliquely. The carbonate cement decreased outwards from the highest density areas, demonstrating the biogenic origin of the limestone. There was a relatively high proportion of broken shells associated with this deposit. The large mean size of the population (16.1 mm) could be partly a product of the selective destruction of smaller shells, but may also reflect favourable conditions in the source area for S. ornatella.

The other limestone assemblages (5, 2, 9) are characterized by concentrations of variously-orientated shells, together with shell debris, in beds which rest with sharp contact upon those beneath. They appear to be current accumulations, possibly resulting from storm disturbances. The random attitudes of the faunas, and wide size variances, suggest rapid deposition of these beds.

Summary:

1. The normally-distributed, plane assemblages 3, 4 and 7 (cf. 6) have small standard deviations and low size spreads, which suggests that they have been current-sorted. However, the degree of breakage was generally not high.
2. Assemblage 1 was partly plane-concentrated, but other valves were variably disposed in the sediment. Breakage was again not high. Distributions with this alternating character could result from

periodic reworking of the top sediment layers to produce the shell planes.

3. The S. ornatella limestones represent current accumulations of shells. There is a higher amount of breakage, and less ordered orientation of the fauna, than in the plane faunas. This suggests that formation was rapid. The size-frequency histograms have normal distributions with wide variance.

Conclusions:

S. ornatella rested unattached on the sediment, and so was evidently susceptible to current scour and transport. The flat, broad shell would disarticulate readily on death of the individual (because the valves are largely held together by muscles), and valves are light and buoyant. "Stacking" of stropheodontid valves was considered by Williams ('53) to be a result of current action, as was "flipping" of the valves to an oblique position with the anterior edge directed into the substrate.

The S. ornatella assemblages all appear transported. However, those in which breakage was not high are unlikely to have been moved by turbulent currents. The shell limestones appear to be formed in more agitated conditions. The extent of transport is difficult to determine. S. ornatella is uncommon in fine muddy sediments (eg. the shelf edge region) where the valves would tend to "flip" quickly to a stable, convex-up position. Neither are the shelf facies coarse, when current scour leading to rapid partial burial of valves in the sediment might prevent much transport taking place (Brenchley and Newall '70). The strength of currents involved will be the controlling factor, and fairly extensive shell transport cannot be discounted. The monospecificity of the shell bands could be an original distributional feature or the result of current accumulation; the high proportion of unbroken valves in some associations would favour the former explanation.

The LLB appearances of S. ornatella (and L. filosa) in the lower part of the division are typically in sudden abundance in monospecific bands, before disappearing from the fauna equally rapidly (for example, Chances Pitch CP-Ra, Perton PL-S). This could indicate that fairly extensive transport has introduced S. ornatella into these areas periodically, but could also indicate spasmodic opportunistic colonisation (Levinton '70). The detailed section for MF/E-S to Z

(Fig 2.17p46) shows such a vertical distribution, with strophomenids S. ornatella and L. filosa largely restricted to debris-rich shelly limestones, which are interbedded with calcareous siltstones with plane faunas. This suggests that the stropheodontids have been introduced into the area rather than being indigenous to it.

4. I. orbicularis and S. lunata:

The size-frequency distributions (Fig 6.20p361), valve ratios and attitudes of a number of LLB populations from shelf sections were studied. The maximum width of the shell was taken as a representative measure of size. Of the assemblages, two were from Frith Wood (SO.723.404) in the Malverns - numbers 10 and 11, one (no. 9) came from Wood Green Quarry (SO.694.197), and the rest from sequences in the Ludlow anticline. A few of the samples (1, 2, 3, 11) included both species together, but most of the assemblages had only one of the two. Discrimination of the enteletacean species is readily made only from internal moulds, so that field identifications of limestone populations were problematic. However, typically, the two species occurred in separate assemblages.

I. orbicularis is found in great abundance throughout the LLB, whereas S. lunata becomes increasingly common in the upper half of the succession. Monospecific accumulations of close-packed valves, often comprising shell limestones, occur at many levels, as well as more scattered and diverse assemblages. The proportion of disarticulated valves is generally high, although some limestone populations (eg. 5, 6) contain a higher proportion of complete individuals. The amounts of damaged and broken shells are very variable, but are generally high in the assemblages from MF33 (12, 15, 16).

The samples may be divided into those from shelly limestone beds (4, 5, 6, 10) and the rest from plane assemblages largely of disarticulated valves. The former have relatively large standard deviations (> 2.7 mm) in normally-distributed populations. 4 and 10 had shells orientated mainly convex-surface, and pedicle valve, upwards, but 5 and 6 had similar proportions of each valve uppermost in a convex-up attitude. These last two beds contained more articulated shells, and less bioclastic debris, and may represent quieter conditions of formation.

Several of the plane assemblages have bimodal distributions, indicating that they are composed of mixed populations. As well as the Isorthis and Salopina assemblages found together in 1, 2, 3 and 11, sample 9 contained two discrete populations of I. orbicularis of very different sizes. The histograms for separate valves in 1 and 9 show that their distributions have different modal peaks; in 1, the brachial valves of both species are generally wider whereas in 9, their pedicle valves are larger. The equivalent patterns shown by the two species suggest that this is a hydrodynamic effect on the dissimilar valve shapes. The remaining distinction of the populations suggests that current reworking, whichhas aligned the valves consistently convex-side up, has not been extensive.

In the remaining plane assemblages (7, 8, 12-16), all of which come from the Ludlow anticline, the populations have tall-peaked, normal distributions of very dominantly convex-up valves. The difference between PV and BV histograms, comparable to that observed in the mixed populations, is shown in 15 and 16. 7, 13, and 14 are composed of one valve only - the PV in the former, but the BV in the other two. Only 8 and 12 comprise equal numbers of the same-sized valves. All these faunas show characteristics of transported associations. Current sorting has produced accumulations of fossils differing little in size, and frequently showing a concentration of one valve. This indicates that extensive post-mortem transport may have taken place in the formation of many of the plane faunas.

Conclusions:

The predominance of disarticulated, convex-up valves in the enteletacean assemblages shows that all have been affected by currents. It also indicates the ease with which the shell becomes disarticulated after death, because it is only in a few limestones which appear less reworked (eg. 5, 6: high S.D., less associated bioclastic debris) that conjoined shells are fairly common. These latter populations cannot have been moved far.

The mixed plane populations of S. lunata and I. orbicularis, and of I. orbicularis alone, where each component has a normal distribution, and some differential transport of the valves is seen, have been separately derived. The absence of an overall normal distribution for the assemblages shows that the combined populations have not been extensively winnowed.

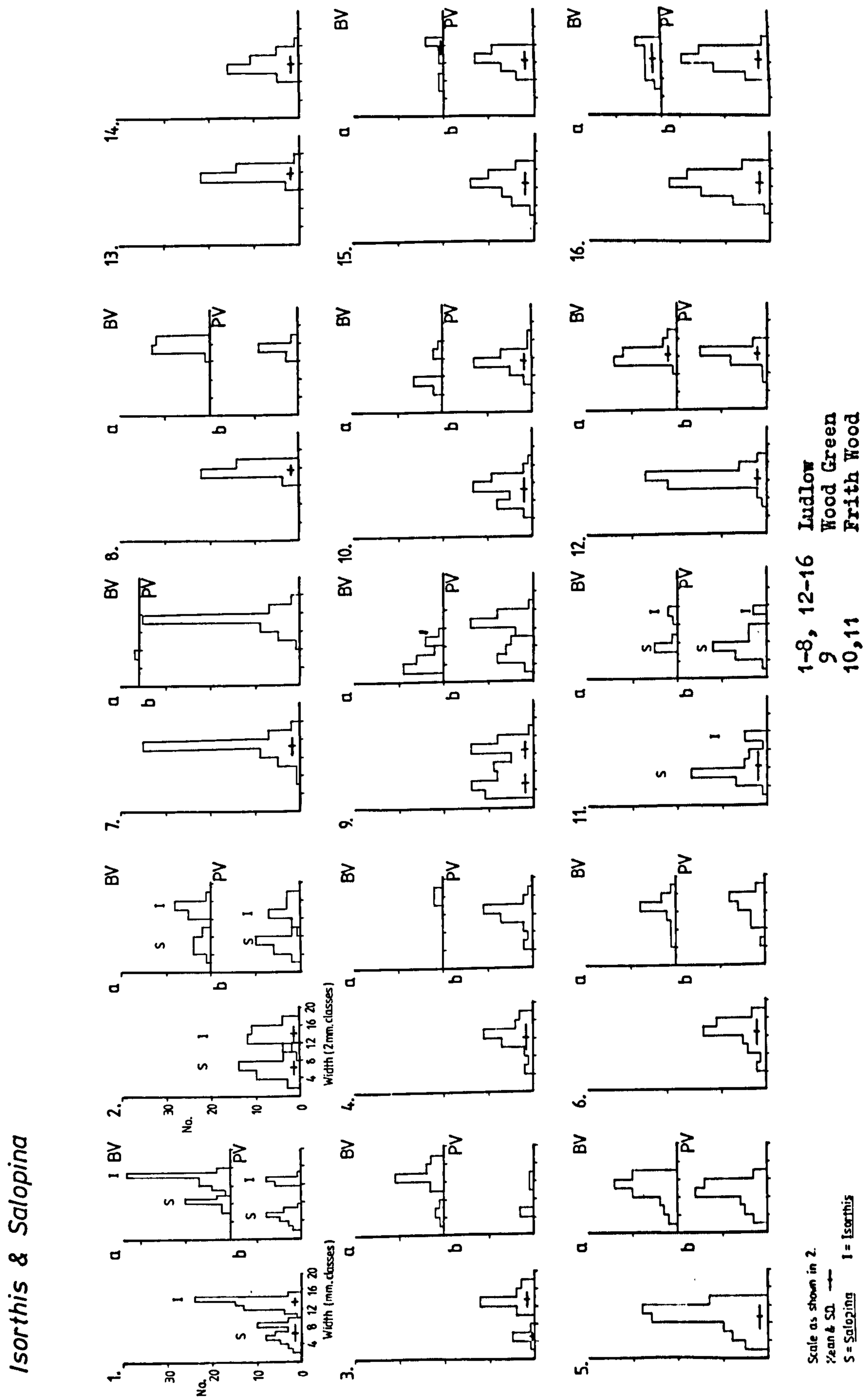


Fig. 6.20 : Isorthis and Salopina size-frequency graphs.

Several of the plane assemblages have bimodal distributions, indicating that they are composed of mixed populations. As well as the Isorthis and Salopina assemblages found together in 1, 2, 3 and 11, sample 9 contained two discrete populations of I. orbicularis of very different sizes. The histograms for separate valves in 1 and 9 show that their distributions have different modal peaks; in 1, the brachial valves of both species are generally wider whereas in 9, their pedicle valves are larger. The equivalent patterns shown by the two species suggest that this is a hydrodynamic effect on the dissimilar valve shapes. The remaining distinction of the populations suggests that current reworking, whichhas aligned the valves consistently convex-side up, has not been extensive.

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Single plane populations from Ludlow appear to have resulted from considerable current action. The high amount of broken shell debris associated with 12, 15, and 16 supports this conclusion. At MF/E, limestone populations 5 and 6, which appear locally derived, are interbedded with well-sorted plane faunas (eg. 8). This indicates either that the species were abundant over a wide area of the sea-floor or that transport has not been extensive in the formation of the plane assemblages. It is not possible to discriminate here between the two explanations.

PALAEOECOLOGICAL SURVEYS OF CALCAREOUS SILTSTONE FACIES:

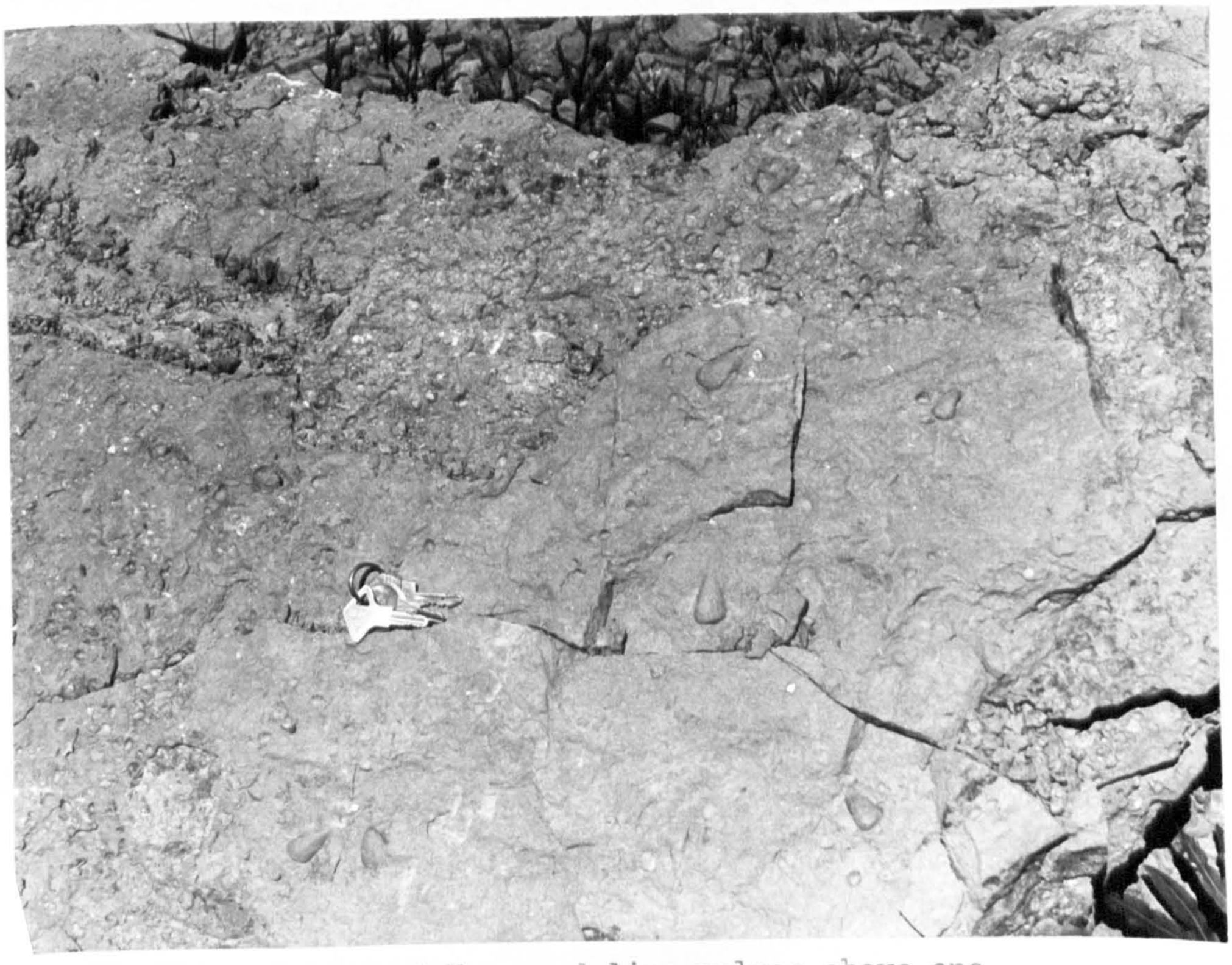
A. VERTICAL VARIATION IN FAUNAL COMPOSITION:

1. Ludlow: MF33: (SO.4895.7240)

The strata exposed immediately west of the quarry are nodular UBB limestones, containing compound and solitary corals, *S. euglypha*, *A. reticularis*, and abundant crinoid debris. The basal units of the overlying LLB are not well exposed in this section, but the higher flaggier strata can be examined both in the quarry walls and in the large blocks lying loose on the quarry floor. Despite the blocks not being *in situ*, their stratigraphical position can be fairly accurately assessed by reference to the base of the LLB, and to the strata slightly higher in the succession (MF/F-) which are exposed in the eastern wall. The weathered surfaces of the large blocks show bedding planes which are excellent for palaeoecological studies.

The sediments of this part of the succession are flaggy calcareous siltstones, well-bedded, in which fossils are concentrated into bands, and relatively few individuals occur in the intervening layers. The shelly bands are typically dominated by one or two species, with the prevalent types changing frequently. The interval between the shelly planes varies: commonly it is only 1-2 cm. Some of the siltstones show a patchy lamination of more and less calcareous layers. Burrows are evident in many of the flags, so it is possible that biogenic reworking of the sediments may have destroyed more extensive original lamination (Moore and Scruton '57); however, the shell-covered planes show no marked signs of disturbance by bioturbation.

MF33 : Siltstone plane with numerous l. orbicularis.



MF33 : Plane of F. amygdalina valves above one with abundant D. navicula.

D. navicula, I. orbicularis, S. wilsoni and F. amygdalina all occur in great abundance, each dominating the assemblages of many fossiliferous horizons. Sometimes one species is found in great profusion and concentration, almost to the exclusion of other types: in other cases the assemblage is more diverse, with several common species. Figs. 6.21 1-14 p365 show the results obtained from studies (using a 20 cm square quadrat) on different bedding plane surfaces.

For each set of data, the minimum number of individuals has been noted - valves of disarticulated specimens were recorded separately, and only the greater of the two abundances added to the total. Disarticulation ratios were not calculated, neither for whole planes nor for individual species. Generally, rhynchonellids were found articulated, whereas other types were very largely disarticulated, so that in an assemblage containing abundant S. wilsoni the ratio would be very low, while Dayia - or Isorthis - dominated faunas would show a high value for disarticulated: articulated shells. Also, the fossils were mostly decalcified and weathered, so that the preservation was not good enough to be able to distinguish consistently between separate valves and complete specimens. Orientations of shells were noted so that the ratio of convex-up to concave-up shells could be found. Where Isorthis shells were common, the relative proportions of pedicle and brachial valves were recorded, for consideration of differential sorting effects.

Fig 6.21 p365 illustrates the great variation in the relative proportions of the common species, which is typical of the assemblages in this lower part of the succession. 14 representative analyses are shown, in which D. navicula and I. orbicularis are most often numerically dominant, and can be seen to exhibit an inverse relationship in their abundances, while other planes - such as 12 and 9 - show a paucity of both, correlated with dominance by another species (S. wilsoni in 12, and F. amygdalina in 9). The data does not attempt to give an objective estimation of the relative frequencies of planes dominated by each species, but to indicate the heterogeneity of the assemblages. Indeed, other species which commonly occur prevalently in assemblages include M. nucula, S. ludloviensis, S. lunata and P. ludloviensis.

As well as the quantitative proportions of the species comprising the assemblages, the absolute numbers (max. T) of individuals found

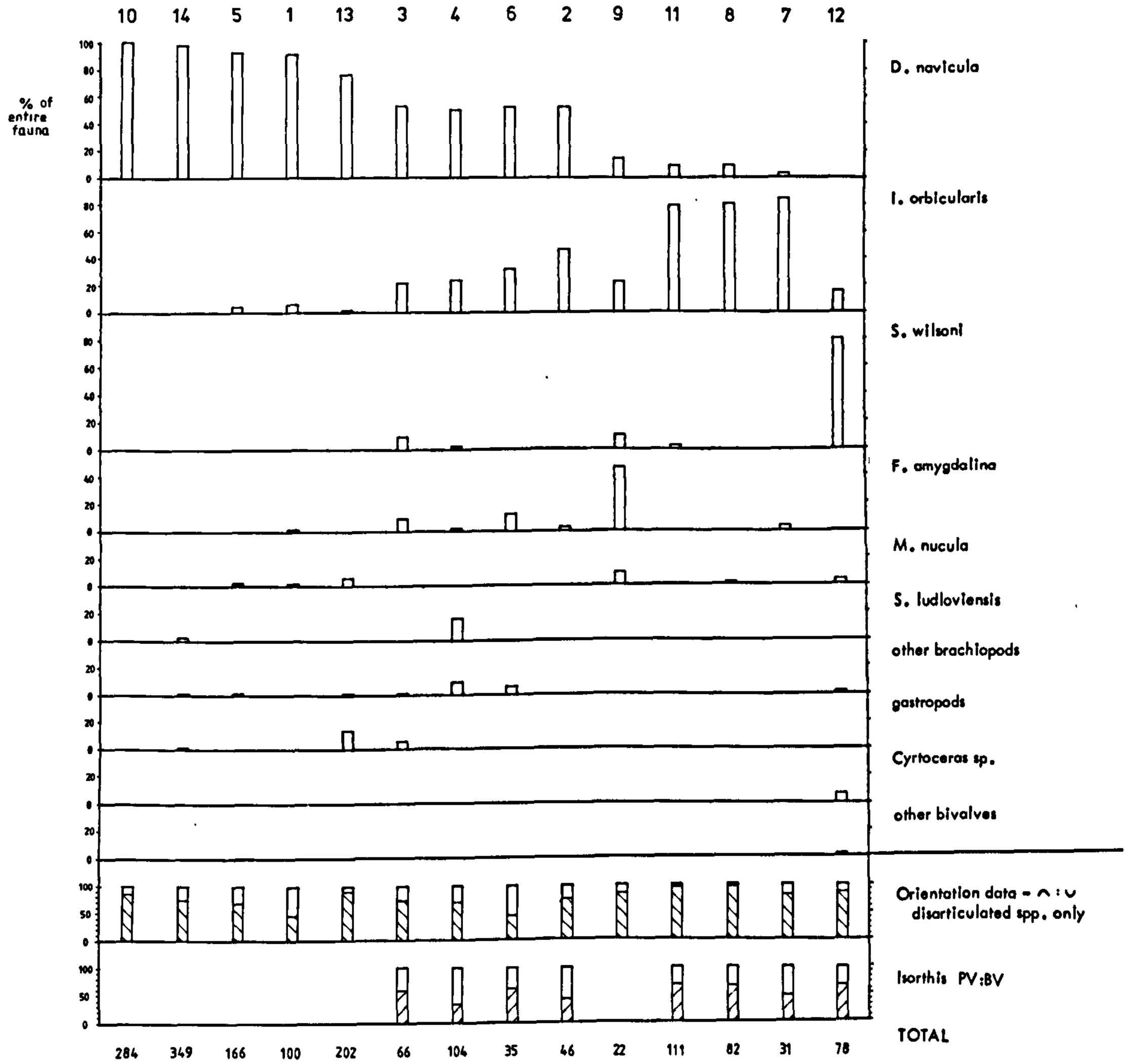


Fig. 6.21 : MF33 - Vertical variation of faunal composition.

within a 20 cm-square quadrat can be seen to vary considerably (Table 21), up to several hundred specimens in some cases (eg. 14, 10). Such great concentrations of shells tend to be characteristic of areas with virtually monospecific assemblages, such as the Davia-band sampled in 14, and the Isorthis-rich plane 11.

The ratio of convex-up to concave-up shells was plotted (Fig 6.21) for disarticulated valves - ie. excluding rhynchonellids, gastropods, and cephalopods. In all but two instances (1 and 6), this gave results of over 2:1. The χ^2 Null hypothesis (of a 1:1 ratio) gave probabilities of less than 0.1% in the other 12 cases (Table 12(Appx)). The preponderance of convex-up valves suggests transport by currents, this attitude being the more stable. In the two cases where the ratio approximated to the hypothesis - data sets 1 and 6 - and in set 4, it is interesting to compare the figures obtained for Davia with those of the rest of the single valves in the fauna (Table13(Appx)). These are the only example where, for Davia, the number of pedicle valves found lying convex-up did not greatly exceed the concave-up fraction.

In all three instances the rest of the fauna shows the average result, with the convex-up valves significantly outnumbering the other orientation. The Davia results for 1 and 6 show the converse, with probability again significant (within 95% confidence limits), while the specimens in 4 have the 1:1 ratio proposed for a random orientation of shells. These opposite trends may indicate that the Davia component of these fauna had been derived separately from the other constituents in these assemblages, but possibly the hydrodynamic properties of the various shell shapes were sufficiently different to produce the observed distributions.

The relative numbers of pedicle and brachial valves, and right and left valves (for bivalves), may indicate differential sorting. χ^2 tests were carried out on Isorthis data where the numbers involved were high enough. The results are shown in Table 14 (Appx).

Three of the analyses, numbers 4, 8, and 11, show a significant result for a divergence (within 95% confidence level) from the expected ratio. Examination of the valve orientations, where five of the six probabilities indicate depositional bias towards the convex-up attitude which is a characteristic of current transport, supports the proposition that the PV:BV ratios in 4, 8, and 11 result from differential sorting effects.

The numbers of F. amygdalina valves found within a single quadrat area were not sufficient to be valid in statistical tests. It can be seen in Table 21 (Appx), however, that their orientation was consistently convex-up, and that the difference in numbers of right and left valves may reflect some selective valve transport (eg. in 9, and 3).

The results for Davia do not include any figures for BVs, because very few were found in these bedding-plane assemblages. This could be explained by several different mechanisms. Tucker ('64) considered the flat shape of the brachial valve to be more conducive to transport by currents so that these could have been winnowed out from the assemblages. Selective destruction of the lighter, thinner valves (Driscoll '70) might also explain their rarity, especially in faunas where the degree of shell breakage is relatively high, and in the concentrated shell accumulations. Alternative explanations might include sorting produced by differential transport of the two valves (although no assemblages composed mainly of brachial valves were recorded), or collection bias from the less conspicuous specimens being overlooked. It is unlikely, however, that this latter mechanism could account for the virtual absence of records of brachial valves (see discussion of Davia ecology p 344.

It is important to establish whether any of the faunas represent in situ populations. This is very difficult to ascertain, much of the evidence being equivocal, as is discussed in the preceding literature review of palaeoecological analyses (p 332-337). It is necessary to assess several different criteria for considering transport together with the sedimentological evidence.

Summary:

1. The qualitative and quantitative compositions of the assemblages vary from plane to plane, and the prevalent species change frequently.
2. Fossil density of assemblages is similarly variable, often highest in monospecific associations.
3. Generally, the convex-up shell attitude is significantly predominant. In the exceptions, the D. navicula fraction of the fauna had a high proportion of concave-up pedicle valves, but the rest of the assemblage had mostly convex-up orientations.
4. Differential sorting of the two valves was noted in some Isorthis populations, and appears typical of D. navicula, where the

brachial valves occur only rarely. Selective destruction of the lighter, thinner valves in Davia may also explain their scarcity.

5. The characteristics are consistent with transported assemblages, but evaluation of the extent of movement requires a consideration of the sedimentological regime and the lateral faunal distribution patterns.

2. Frith Wood (SO.723.404) and Wood Green Railway Cutting (SO.694.197)

Palaeoecological surveys were carried out on bedding-plane assemblages at these localities, where weathered surfaces are well-exposed. At Frith Wood, the samples came from 4 m of sequence in the upper part of the LLB succession, while at Wood Green, the faunas were from 3 m of strata in the middle LLB, in the U. Blaisdon Beds of Lawson ('55). The sediments were alternating calcareous siltstones and thin, fossiliferous limestones. There were frequent planes of shells, but few fossils in the intervening beds. Quadrat studies and records of the first 50 benthonic fossils counted were used for analysis of the vertical variation in faunal composition.

Fig 6.22p369 shows the results obtained from the latter method. The assemblages differ considerably in relative species abundances, and also in faunal content. Commonly, one or two types dominate the fauna, but the prevalent species change repeatedly. For example, FW 8-10 are successive plane faunas; the first has several prevalent species, the second is dominated by S. lunata, the third by M. nucula. In some cases, the fauna is almost monospecific - for instance, FW1, with I. orbicularis. The fossils are mostly separate valves, except for the rhynchonellids and some H. elegans individuals. This may relate more to differential resistances to disarticulation than directly to the extent of transport (Boucot, Brace and DeMar '58). The species which tend to remain articulated have plicated commissures which interlock to prevent sideways movement of the valves, whereas many other shells (for example, strophomenids) rely mainly on muscular action to keep the two valves together. Therefore, as at Ludlow (MF 33), disarticulation ratios were not calculated. Ratios of shell orientations (convex- to concave-surface upwards) were found for valves of various species in assemblages (Table 15) and show a general preponderance of the convex-up, stable, attitude. The concentration of fossils onto bedding-planes, and the

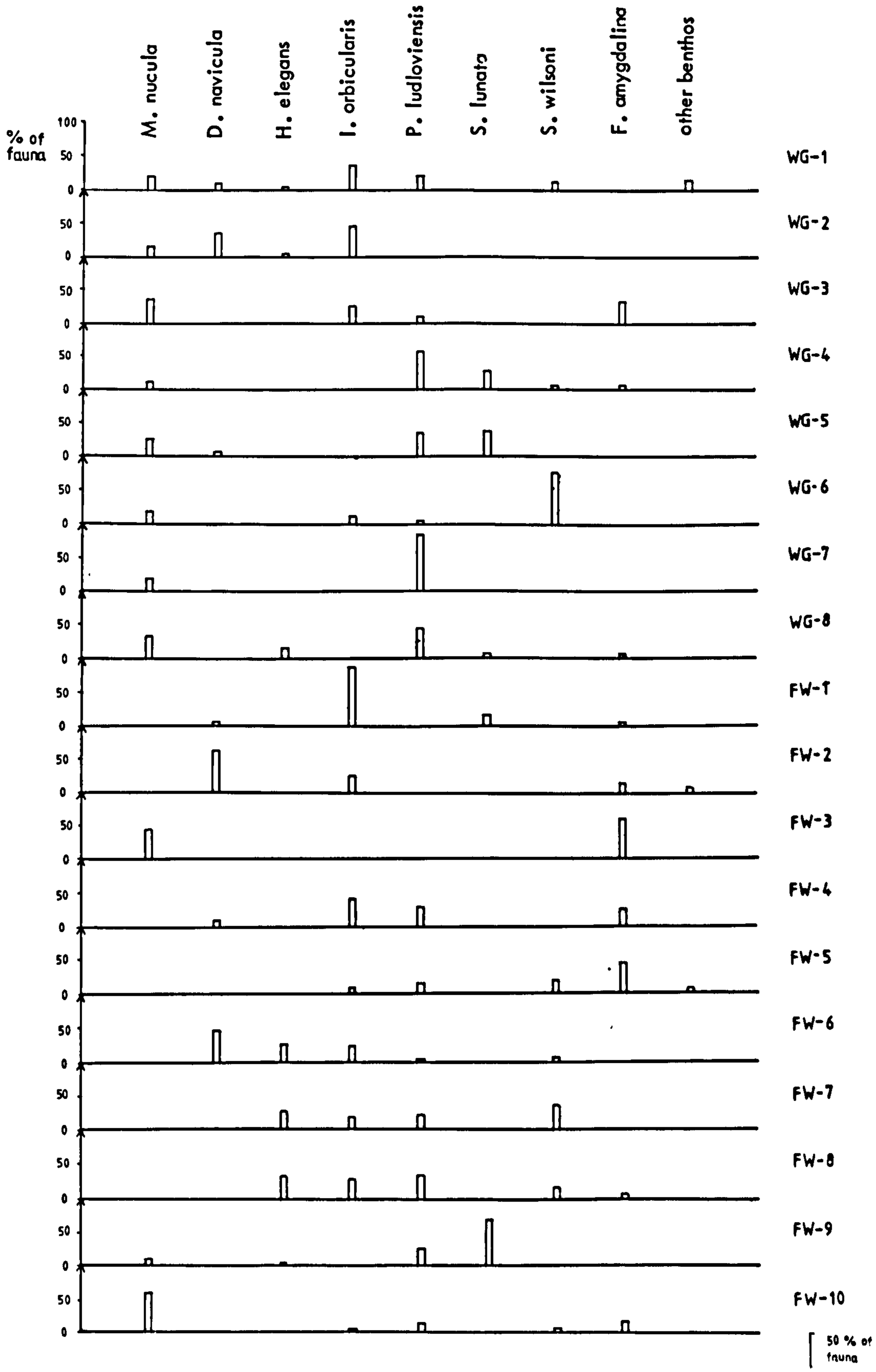


Fig. 6.22 : Wood Green and Frith Wood - Vertical variation in faunal composition.

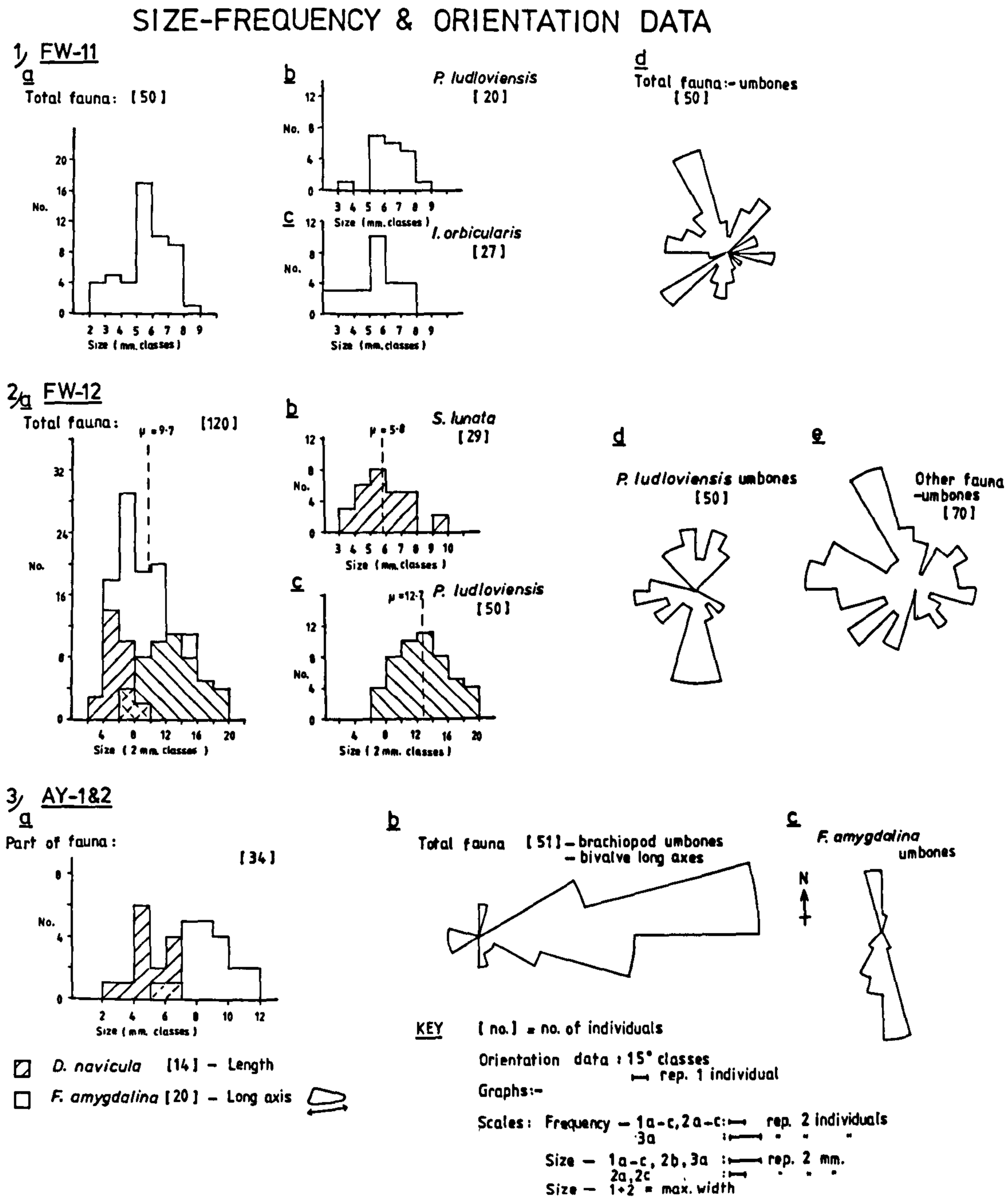


Fig. 6.23 : Size-frequency graphs and orientation diagrams.
1 - FW-11, 2 - FW-12, 3 - AY-1+2.

population characteristics, indicate that the assemblages are transported.

Most assemblages are dominated by epifaunal benthos, but planes with many shallow-burrowing or semi-infaunal bivalves (F. amygdalina, G. cymbaeformis) are found at intervals. The rarity of infauna among the assemblages, except for certain horizons, indicates that often only the surface of the sediment was affected by the currents which accumulated the shells.

A few assemblages were analysed for preferential alignment of shells. Sample results are shown in Fig 6.23 p370 . FW 11 was the top surface of a limestone bed, where convex-up P. ludloviensis and I. orbicularis valves were very common. The size-frequency histograms do not distinguish whether the assemblage comprises mixed populations or a single entity, although the similar modes suggest the latter (cf. FW 12, below). The umbo-orientation diagram for the assemblage has slight emphasis on NNW and NE-SW directions. The perpendicular trends may be comparable to the along-current and cross-current components found by Brenchley and Newall ('70) for transported shells.

FW 12 was a richly-fossiliferous calcareous siltstone plane, dominated by P. ludloviensis but with several other species also fairly common. In Fig 6.23-2(c), the P. ludloviensis population was considered separately, as well as integrally in the assemblage. Size-frequency plots for S. lunata and P. ludloviensis show that they each have normally-distributed populations of widely different means, suggesting that they were derived independently. The overall assemblage, although clearly of transported fossils (disarticulated, convex-up valves), therefore contains mixed populations. The rose diagrams show some alignment of P. ludloviensis in a southerly-facing direction, which is in contrast to the W and NNW trends displayed by the rest of the fauna. This again indicates that the assemblage is made up of several populations.

The degree of alignment of shells in these assemblages is small compared with that displayed in many plane assemblages of the laminated siltstones at Aymestrey. Fig 6.23-3 shows one such association dominated by F. amygdalina and D. navicula. The size-frequency histogram has a wide size range, with the two species overlapping little. Shells were disarticulated, and mainly convex-surface up (3.2:1). Rose diagrams for the brachiopod umbo and bivalve long axis orientations, and

for F. amygdalina umbones, were plotted (Fig 6.23-3). The former shows a pronounced assemblage alignment eastwards, indicating strong currents. The uniformity of alignment of F. amygdalina is demonstrated also in the umbo orientations, which reflect the preponderance of right valves over left (3:1), another effect of current action (eg. Lever '58). At Aymestrey, Newall ('66) commented on the consistent evidence of currents flowing westwards shown by the aligned shell assemblages and erosional scour channels. However, in the plane assemblages of Frith Wood, the presence of current alignment is often equivocal (as in FW 11 and 12). The inference that rigorous reworking was not involved in the formation of the associations is supported by the preservation of the delicate spines on many P. ludloviensis valves.

The fluctuating composition of the shell assemblages is characteristic of the calcareous siltstone facies of the shelf. Although the fossils generally appear transported, the assemblages are laterally heterogeneous (see next section p 374). The amount of bioclastic debris associated with the fossils varies greatly from one horizon to another, and so does the density of shells in the assemblages. For instance, FW 9 had 78 fossils in a 20 cm quadrat site, where the next plane, FW 10, had only 22 in the same area - a ratio of 3.5:1. Further density estimates are shown in Table 15 (Appx).

Conclusions:

The analyses suggest that extensive transport has not controlled the formation of many bedding-plane assemblages. They do, however, represent current accumulations, from disturbances which frequently affected only the epifauna. Vertical heterogeneity of the associations is probably representative of both original "patchiness" in the species distribution, and the temporal fluctuations brought about by environmental and ecological controls.

B. LATERAL VARIATION OF FAUNAL COMPOSITION

Among the palaeoecological analyses of bedding-plane assemblages from Frith Wood (SO.723.404) and Wood Green Railway cutting (SO.694.197), the lateral variation along several calcareous siltstone beds was investigated. The first 50 benthonic fossils were recorded from each of three sites of the same horizon. The percentage composition of the assemblages at the lateral sites is shown in Fig 6.24 p373.

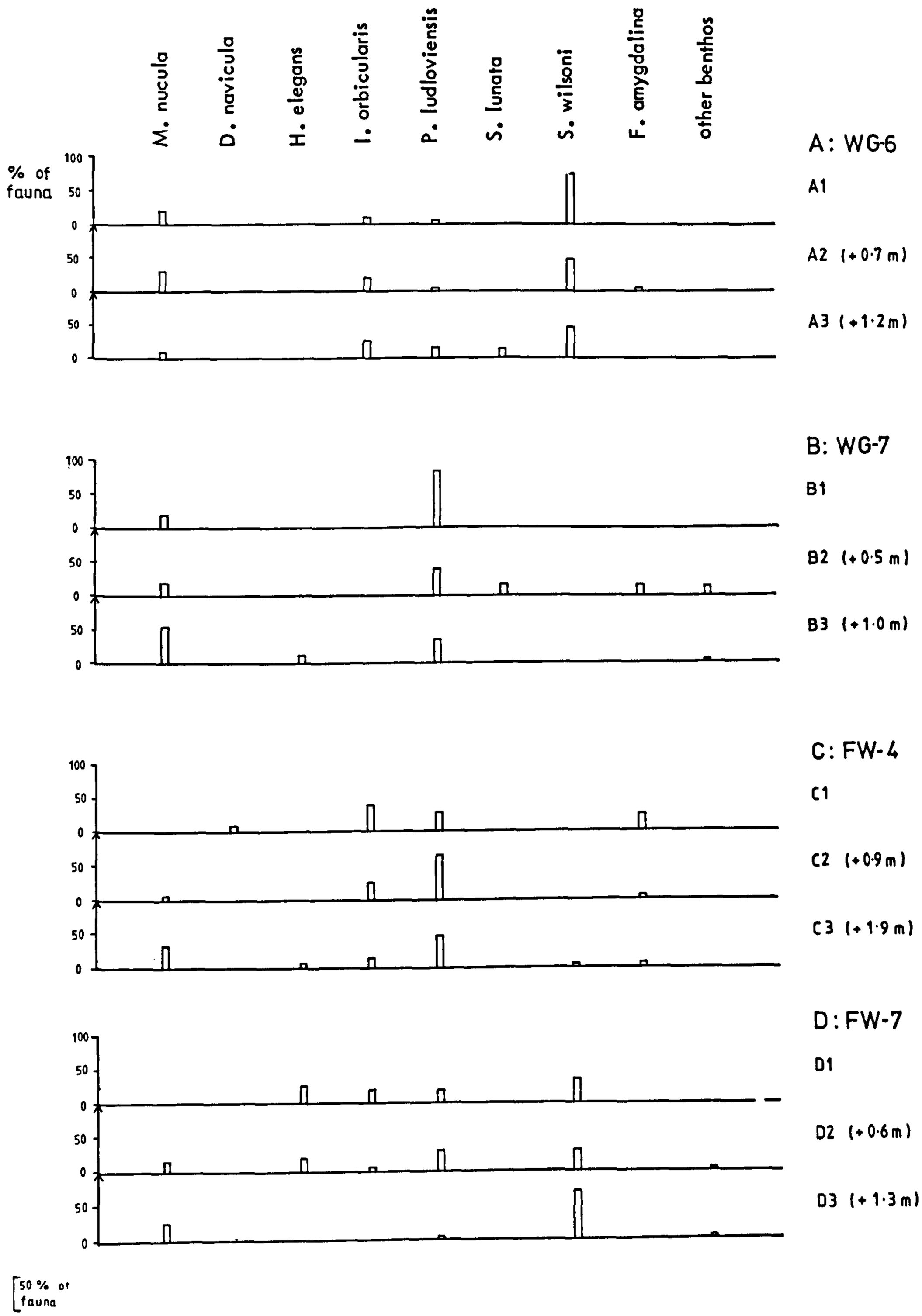


Fig. 6.24 : Wood Green and Frith Wood - Lateral variation in faunal composition.

The diagrams show the variation in both the relative abundances of the common species, and in the qualitative composition of the fauna. For example, in assemblage D (FW-7), D3 has a nearly exclusively rhynchonellid fauna of S. wilsoni and M. nucula, but 1.3 m laterally away, D1 has four common brachiopod species yet no M. nucula. Similarly, in C, F. amygdalina is prominent among the C1 assemblage, but is infrequent in C2, 0.9 m away, and absent from C3, another metre away.

The results indicate a mosaic distribution of species in these assemblages. As was discussed in the consideration of vertical variation (p 368), valves of most brachiopods (- except rhynchonellids) and bivalves are generally found disarticulated and orientated with the convex surfaces upwards. The plane faunas are evidently transported. However, the "patch" composition of assemblages suggests that current disturbance was not extensive. The local variations in the fauna, as with the vertical changes, are indicative of heterogeneity in the original distributions. The colonisation pattern is analogous to that described by Petersen ('13) and Thorson ('57); a dynamic equilibrium in which local relative abundances of species alter frequently in response to environmental factors. The relative successes of the pelagic larval stages was considered by Blegvad ('25, '28) to be responsible for fluctuations in the faunal distribution without environmental changes.

The lateral variation along some S. wilsoni limestone bands at Perton Quarry (SO.489.724), and in D. navicula beds at Shelderton (SO.416.778) and Ludlow (SO.596.400), was examined. The assemblages were monospecific, in bands laterally persistent over many metres.

The S. wilsoni beds (see p 352) had sharply-defined bases, and were composed of closely-packed individuals and broken shells. The lateral samples were all normally-distributed populations with a small size-spread, whose mean size differed significantly between samples. These beds represent well-sorted current accumulations. Interbedded in the same sequence are less extensive S. wilsoni coquinas, "dominated" plane-assemblages of fossils where the species composition varies laterally and vertically, and more diverse, shelly and fragmental limestones. The "scale" of the assemblages must reflect the strength of the disturbance which created them. Then, the laterally persistent S. wilsoni faunas are the result of extensive reworking, while the

thin, plane-assemblages, which still retain the heterogeneity of the original faunal distribution, are formed by less severe current action upon the benthos. Therefore, the degree of lateral variation found in beds is itself irregular, depending upon the conditions of formation of the assemblages as well as the faunal settlement patterns.

The D. navicula faunas studied (see p337-346) were dominantly of convex-up, pedicle valves, associated with amounts of broken shell debris. The assemblages were closely-packed (although variable in density). The population characteristics indicate that these are current-accumulations. However, they are much less uniform than the S. wilsoni beds. The different reactions of the two shells to currents may account for this. D. navicula typically occurs disarticulated, and in soft sediment. Brenchley and Newall ('70) noted the ease with which shells on soft sediment were "flipped" to a convex-up attitude, which is very stable and resists further transport. Therefore, D. navicula valves may not be extensively moved, so that original population heterogeneity remains. In contrast, the spherical S. wilsoni shells do not disarticulate readily and will be susceptible to prolonged rolling about and sorting by currents. The D. navicula strata of the basal LLB at Leintwardine are virtually monospecific over several metres of the vertical succession, so the lack of lateral variation in the species composition here relates to an original feature of the faunal distribution.

Therefore, the degree of lateral variation found within shell horizons is controlled by the initial configuration of the fauna, and also by the conditions of formation of the assemblage.

LLB SHEET-LAMINATED SILTSTONES:

The LLB sequence at MF/F- includes numerous shell lenses and bands that have sharp or erosive bases, and grade up into parallel-laminated siltstones. These fining-up units alternate with calcareous siltstones containing similar fossils, sometimes evenly-distributed in beds, but more usually concentrated into plane assemblages. The fauna is dominated by D. navicula, S. ludloviensis and I. orbicularis. A few steeply-inclined burrows were observed to extend upwards through the laminated sediments above the basal shell beds. Discrete burrows are fairly infrequent in the unlaminated and poorly-banded siltstones, but a mottled bioturbate texture is seen in some beds indicating extensive

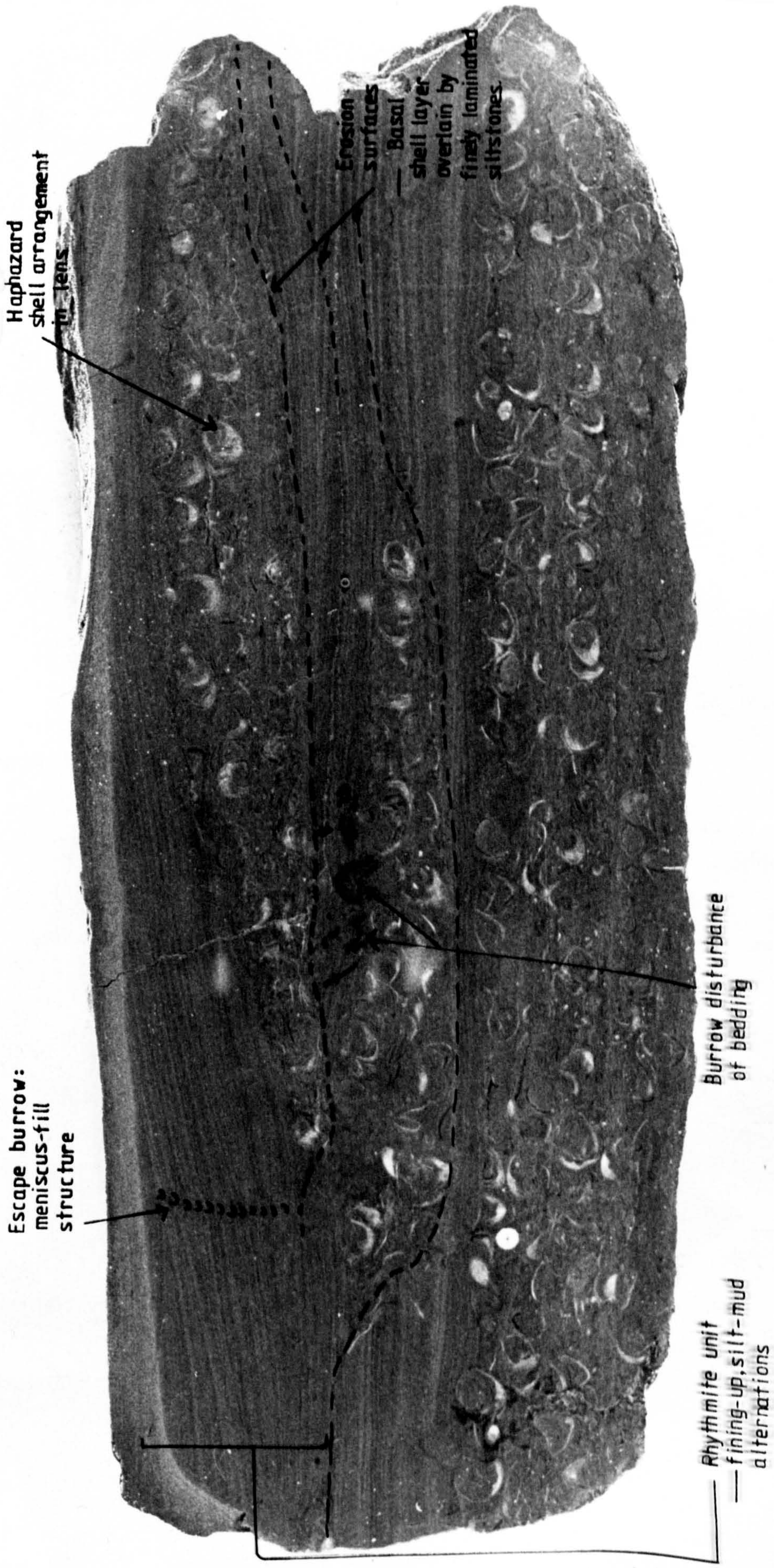
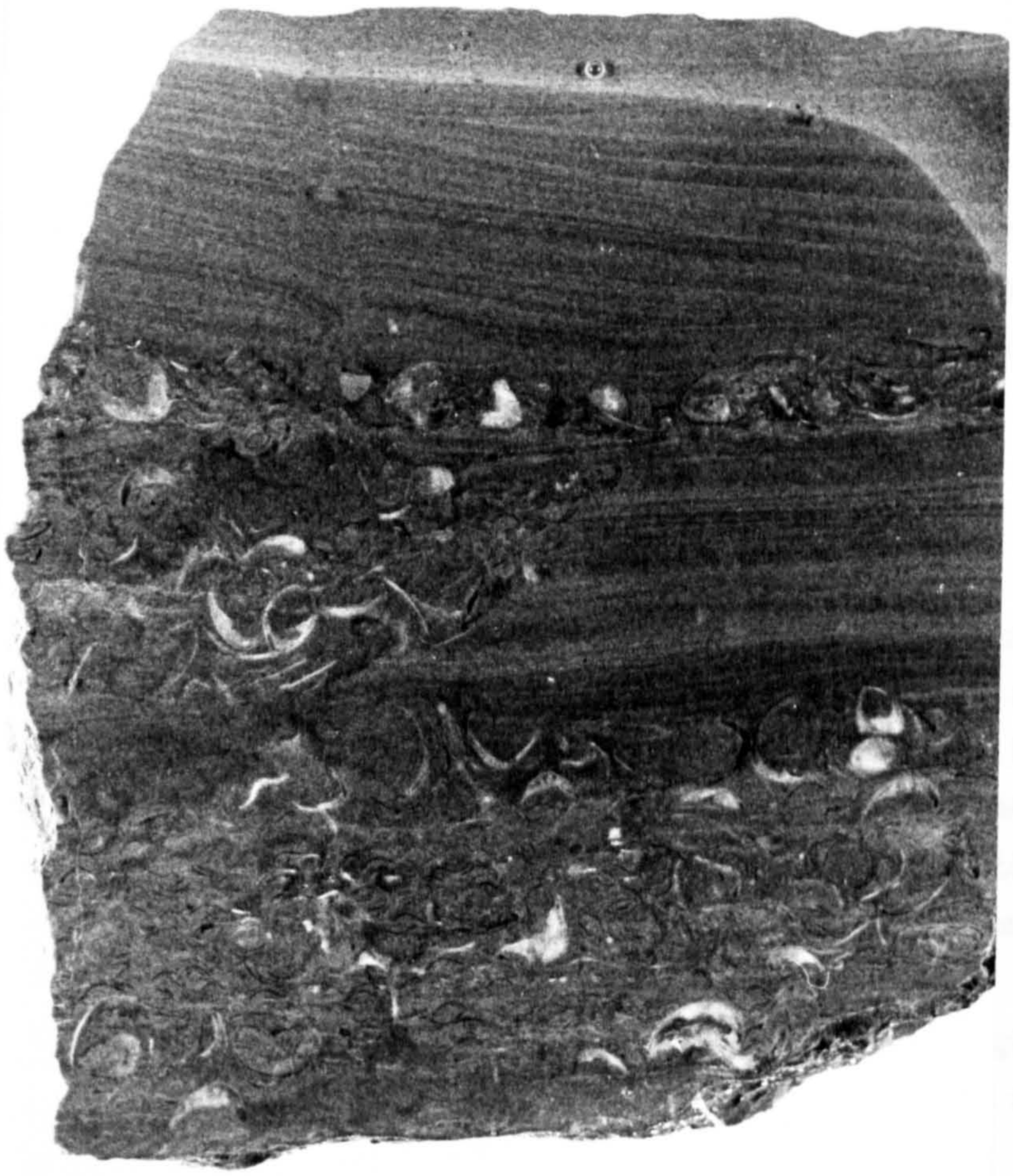
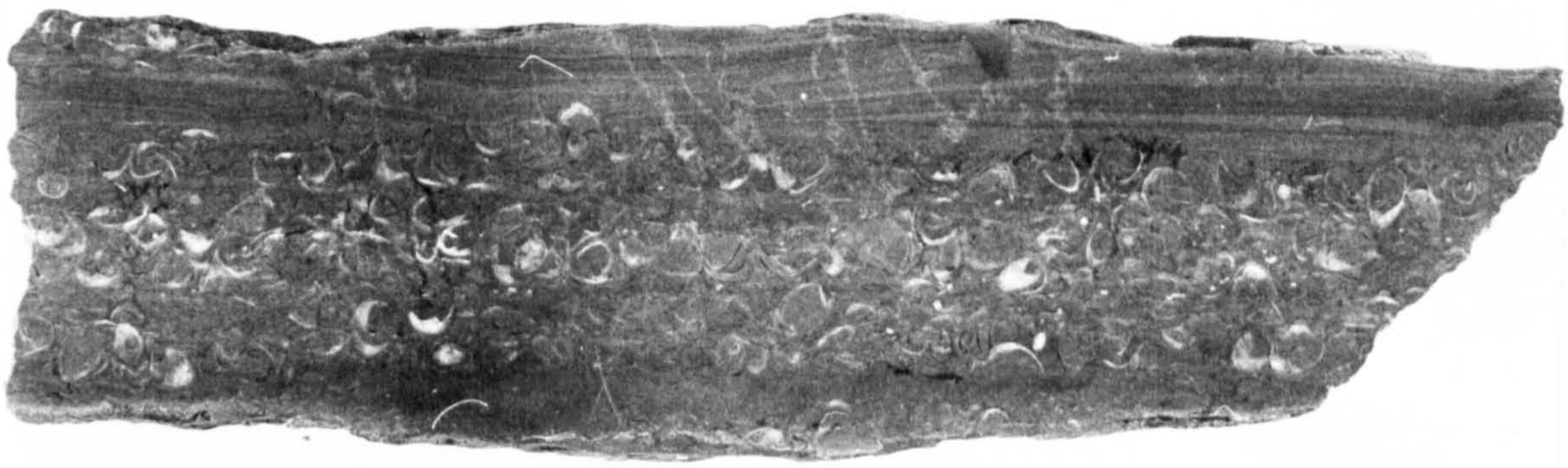


Fig. 6.25 : Sheet-laminated siltstones, Ludlow (MF/F). (x 1)



a : Detail from Fig. 6.25 showing escape burrow trace through finely-laminated siltstones, and erosive base to shell lens. (x 1.25)



b : Shell band with fairly haphazard arrangement of fossils - mainly D. navicula and S. ludloviensis - above bioturbated siltstone and overlain by well-laminated siltstones. (x 0.67)

Fig. 6.26 : Sheet-laminated siltstones, Ludlow (MF/F).

reworking. The thickness of the laminated units is very variable, up to 15 cm yet often less, and changing rapidly laterally. Many shell lenses are less than 1 m across, although some extend a few metres before thinning out. There are also laterally-extensive shell horizons at the bases of laminated units. Some bedding-planes appeared ripple-marked, but the siltstones were not clearly cross-bedded. Minor undulations in the lamination are common.

Similar sequences are found in the other Ludlow sections in the middle LLB (ie. SY/B-, MF/A-).

Interpretation:

Units of finely-laminated sediment (silts and sands) from the North Sea were interpreted by Reineck and Singh ('72, '73) as the result of the settling of the suspended sediment load produced by storms. With the decrease in energy of the storm, sediments carried out from the coast to the open shelf are deposited as parallel-bedded sand layers. Towards the shelf mud, finer sediment forms thinner units which are not rippled or ripple-bedded.

Deposition of the storm sediment in offshore regions is mostly preceded by slight erosion. The coarse basal layers of units can include both autochthonous and allochthonous shells. Transport of shells without much mechanical destruction, as sediment load, over several kilometres is documented for the Recent North Sea deposits. The overlying evenly-laminated rhythmite beds are sometimes graded - that is, individual lower layers are thicker and coarser than their higher equivalents. The top, muddier beds grade up into well-bioturbated, normal, shelf mud deposits. Occasional escape burrows seen in the rhythmite units indicate the rapid deposition of these layers.

Although they preferred storms as causal agents, Reineck and Singh conceded that turbidity currents could account for transport of sediment to the outer shelf (Hayes '67) and for the deposition of parallel-laminated sedimentary units (Kuenen '66). They argued that the depositional slope of the North Sea (2°-3°) is too low to generate turbidites, but that clouds of suspended sediment are frequently observed offshore after storms. Therefore, ebb currents are effective as a transporting medium for sediment, and it is not necessary to invoke the flow of turbidity currents to explain this offshore movement.

Goldring and Bridges ('73) described Palaeozoic and Mesozoic examples of laminated sheet sandstones interbedded with fossiliferous marine shales and siltstones. They commented upon the difficulty of distinguishing storm-deposited layers from turbidite beds, but considered that evidence of penecontemporaneous erosion provided by scoured, bioturbated tops of units is against a turbiditic origin. The open shelf sediments described were cross-bedded, parallel-laminated, fine sandstone units, commonly with basal shell lenses or bands. Llandovery examples from the Welsh Borderlands were recognised. These had varied shell assemblages largely of fragmental material, but also with some fossils on which delicate structures were preserved. Shells clusters in the interbedded muddy sediments, which were low in diversity, were interpreted as in situ assemblages. The fauna of the laminated units was thought to be allochthonous.

The LLB examples are very comparable with distal shelf deposits of the North Sea. The occasional burrows in the laminated beds may be interpreted as escape traces because of fairly rapid deposition. Fine sediment need not relate directly to an offshore environment, since it depends upon the provenance, but the absence of cross-bedding confirms this position.

The similarity of the faunas (and sediment type) of the laminated units and interbedded flags is interesting. It poses the alternatives that extensive transport of shells has not occurred or that faunal belts were wide. There is no means of discriminating certainly. The offshore environment, and relatively small scale of many shell lenses, make extensive transport less probable than in more proximal shelf areas where storm energy would be higher. However, as neither explanation can be discounted, and some of the basal shell beds are much more extensive, the proposition of wide faunal zones appears reasonable.

LLB FAUNAL VARIATION

Detailed range charts of parts of the vertical succession illustrate the nature of the LLB faunas.

The concentration of epifauna in the transported assemblages of the basal conglomeratic limestone beds (discussed in Chapter Three p67), compared with the greater proportion of infauna and limited epifauna in

the intervening siltstones is shown in Figs. 3.5,3.9A, &3.12. Fig. 3.12 p89 shows the greater species diversity of these limestones than is usual in the plane faunas of the interbedded sediments. The conglomeratic limestones are commonly very fossiliferous. The large amounts of bioclastic debris and distinct lower boundaries are indications that these deposits are current-accumulations. The dominance of epifauna shows that only the surface of the sediment was affected. The higher diversity of species compared with individual interbedded plane assemblages suggests that the limestone populations result from more widespread shell transport, mixing laterally adjacent "patches" of epifauna.

Figs. 3.6, 3.9B, 2.13, 2.15 and 2.16 (Chs.2+3) all show the rapid fluctuation in species abundance and composition found in successive plane-assemblages of the calcareous siltstone facies. In addition, Fig. 3.9B illustrates the interbedded fossiliferous limestones which are considered to reflect stronger current disturbances (eg. PL-Ja).

Alternative sampling method:

Figs. 4.8(p123)+3.14(p96) show the fauna recorded by counting the first 50 macrofossils in each band. Results have been plotted as percentages of the fauna. The diagrams illustrate well the quantitative variations in relative species abundance found from bed to bed. The major differences from the charts for the standard method of describing the fauna are in the lower diversities (because less individuals were observed) and absence of ostracodes. The latter would be a serious objection to using this system of recording in sequences such as the top LLB at Shelderton (SR/2-), because there ostracodes often form a numerically important faunal element. However, in shelf sequences, ostracodes are generally minor constituents of assemblages, or are absent. Standard quantitative samples are useful for direct comparisons of faunal diversity. The lower diversity for some faunas recorded in the charts for the first 50 fossils shows that this sample size is not high enough. Calef and Hancock's ('74 - p 803) rarefaction graphs for May Hill Ludlow brachiopods show that the rate of addition of new species has decreased by this sample size, however.

Shell transport:

The plane assemblages of MF 33, Wood Green and Frith Wood used for palaeoecological analyses are transported fossil associations that do not appear to have suffered extensive movement. The original colonisation

heterogeneity is reflected in their fluctuating composition. The concentration of fossils onto bedding-planes, while few shells are dispersed in the intervening sediments, shows that the assemblages resulted from periodic current disturbances. This pattern of faunal distribution is characteristic of the calcareous siltstone facies of the shelf.

Intercalated among the sequences with plane faunas are sharply-based shell limestones containing much bioclastic debris, and fragmental limestones. The faunas may be monospecific like the S. wilsoni beds investigated at Perton (p351), or more diverse, as, for example, in bed PL/B-B used in the S. ornatella (p 355) and S. wilsoni (p 347) population studies. The former associations have undergone rigorous reworking while the latter bed has a rather haphazard arrangement of shells and debris indicative of rapid accumulation. The assemblages reflect more disruptive events than were involved in formation of the plane faunas.

The sheet-laminated siltstone facies (p 375 ff.), developed most fully at Ludlow, has lenticular, fossiliferous horizons at the base of finely-laminated siltstone units. The dominantly epibenthonic fauna is associated with much shell debris. It is similar in species composition to faunas in interbedded unlaminated units which have alternating plane assemblages and beds with more evenly-distributed fossils. The facies is interpreted as resulting from major storm events or turbidity current flows, analogous to Recent deposits of the North Sea (Reineck and Singh '72, '73). Clouds of sediment thrown into suspension during storms, or in turbidity currents, are carried offshore, incorporating shells as traction load before settling. Transport of shells over several kilometres is documented for the North Sea.

All the types of fossil assemblage described are composed mainly of epifaunal benthos, except for some planes of bivalves that are thought to have been infaunal or burrowing forms (eg. F. amygdalina). Therefore, stronger bottom currents resulting, for instance, from storm disturbances generally only affected the surface of the sediment, acting to accumulate the epifauna. The comparable nature of the assemblages suggests that all resulted from periodic current disturbances of various strengths. Shell transport may range from distances of only metres to

several kilometres, depending on the nature of the bottom currents.

However, shell transport, even in the sheet-laminated siltstones, has not introduced different faunas into the sequences. (Some stropheodontid horizons such as in MF/E:R to Z - Fig. 2.17 p46 could be exceptions to this - see p359). The quantitative compositions of the extensively transported faunas more frequently tend towards being monospecific, but they are qualitatively like the interbedded "local" plane assemblages. Therefore, it is necessary to postulate either that similar faunas contemporaneously existed across wide areas, or that the distances over which shells were moved by currents were not large. In view of the comparison made with Recent storm-influenced sedimentation, the latter explanation is unsatisfactory. Also the faunal distribution maps show that the main lateral distinction in the LLB is between "shelf" and "basin" environments, and then between proximal and distal shelf. It seems likely that the width of faunal belts was sufficiently great even for considerable transport not to bring in qualitatively different assemblages.

COMMUNITIES

Ziegler ('65) and Ziegler et al. ('68) defined five, level-bottom, benthonic communities for the Llandovery. In order of increasing distance from shore, these were the Lingula, Eocoelia, Pentamerus, Costistricklandia and Clorinda communities. It was proposed that the associations were of species that responded similarly to the physical environment, in which depth was the controlling factor. All except the Lingula community (where inarticulate brachiopods and molluscs were important faunal elements) had at least 85% of the fauna composed of articulate brachiopods. Although shells were commonly concentrated into lenses at the bases of beds, post-mortem transport was not thought to distort the original distribution pattern. This conclusion was based upon population analyses, the rare occurrence of similar, in situ assemblages, and because of the large zonal widths occupied by communities. The relative abundances of species in the recurrent associations were important, since many types were present in several communities. In spite of the tendency for the deeper associations to occur in finer sediments (Ziegler '65), the nature of the substrate was not considered a controlling factor. The communities were stated to be completely intergrading in composition, so that their definition was arbitrary.

Following the Llandovery work, statistically-defined brachiopod communities were described by Calef and Hancock ('74) for the Wenlock and Ludlow clastic sediments. Four communities, drawn from "an environmental continuum with no natural breaks" (Calef and Hancock '74 p 805), were recognised in the Ludlow rocks: the Salopina, Sphaerirhynchia, Isorthis and Dicoelosia communities. These were considered, on the basis of diversity and density, to compare closely with the Llandovery Eocoelia to Clorinda community spectrum, and thus to be correlated with depth. A sequence of the communities from "deep" to "shallow" through the Ludlow was used to postulate continuous regression for the period.

Calef and Hancock ('74) used the Llandovery pattern as a template for their study. Lawson ('75) pointed out the omission of separate evidence that the Ludlow assemblages are representative of original distributions. No in situ associations were described, and the extent of the community belts was not established. Lawson (p 512) described the four, successive, major benthonic assemblages which characterise the Ludlow stages in the shelf sequences, in lists of species abundance compiled from the range charts for eight areas. His faunas include non-brachiopod benthos, which are frequently numerically important - in contrast to Calef and Hancock's contention that "brachiopods generally make up at least 90% of the total fauna" (p 783). For example, in the Protochonetes-Salopina assemblage (Whitcliffe Beds fauna), six out of the ten most common species are not brachiopods (Lawson '75 p 515).

Lawson's assemblages compare in brachiopod content with Calef and Hancock's communities, although there are some important differences. Uneven sampling of the succession by Calef and Hancock, for instance with over a quarter of the localities taken from the atypical facies of the Sawdde Gorge, and questionable stratigraphical assignments of some collections (Lawson '75 p 517), are partly responsible. A maximum of only 3.4% of the vertical succession was calculated by Lawson to have been sampled by Calef and Hancock. In contrast to the brachiopod communities, which are stated to intergrade completely in composition, three of Lawson's major assemblages change abruptly in faunal content. A close correlation between the nature of the substrate and the community in Ludlow clastic sediments (Calef and Hancock '74 p 797) was noted by Lawson, who cited the informal use of names such as Dayia shales, and strophomenid siltstones. A depth decrease from the Elton Beds to the

Whitcliffe Beds was not disputed by Lawson, but the regional pattern of two transgressions and regressions proposed by Phipps and Reeve ('67) for the Ludlow was considered to have sufficient sedimentary and faunal support.

The Leintwardine Beds fauna of the shelf comprises the Davia-Isorthis assemblage of Lawson ('75), and corresponds most closely to the Sphaerirhynchia community of Calef and Hancock ('74). The stratigraphical division is characterised by lateral and vertical, faunal and facies changes. It corresponds to the second period of maximum transgression postulated by Phipps and Reeve ('67) to take place above the Aymestry Limestone, but for Calef and Hancock's continuous regression, should be shallower than the Bringewood Beds. The detailed palaeoecological study carried out on the LLB enables a critical evaluation to be made of the Ludlow brachiopod depth-related communities, and of the significance of various species distributions. In addition, the significance of the major faunal assemblage can be related to the evolving palaeogeography.

LLB FAUNAL ASSOCIATIONS:

In this study, sequences were examined bed-by-bed, and the faunas for each unit were recorded both qualitatively and semi-quantitatively (see section on Methods - p 10). The characteristic occurrence of fossils is in bedding-plane assemblages and shell bands, with relatively few in the beds between fossiliferous horizons. This distribution is contrary to Calef and Hancock's ('74 - p 780) statement that fossils are usually found throughout beds.

The palaeoecological analyses carried out (p 363 ff.) indicate that there is considerable lateral and vertical variation in the composition even of closely-spaced plane assemblages, particularly in the relative abundances of the common species. The prevalent species change repeatedly/ and frequently. Many associations are virtually monospecific, for example, the basal LLB Davia beds of Leintwardine, and the S. wilsoni limestone bands of Perton and Woodbury. The shell assemblages commonly consist dominantly of epifaunal benthos, and are considered to have been accumulated by currents which usually affected only the sediment surface. Planes on which bivalves that are thought to have been infaunal or burrowing types (eg. F. amygdalina) are common are intercalated with the other, brachiopod-rich assemblages. The bivalves were probably exhumed by occasional, more extensive reworking.

The distance of transport of shells in many of the plane faunas of the calcareous siltstone facies was concluded, from the palaeoecological surveys, not to have been large. However, the fossils in the sheet-laminated siltstone facies could have suffered extensive transport, and some lenticular, debris-rich, limestones that alternate with plane faunas (eg. S. wilsoni deposits at Perton) show signs of prolonged current sorting. Transport of shells, except in the slumped beds of the basinal areas (eg. Lyepole Bridge) has not caused mixing of qualitatively different faunas. Therefore, it was deduced that, because shell movement over large distances appears probable for some LLB deposits, the belts occupied contemporaneously by similar associations of species were wide.

"Communities"?

The nature of the LLB fossil distributions means that bulk sampling from a single horizon, as practised by Calef and Hancock ('74), will tend to neglect the infauna, and is likely to reflect a very local faunal pattern. Commonly, LLB assemblages are composed of only a few species. Heterogeneity of the species associations is sufficiently marked to mean that successive planes, and even adjacent areas of one bedding plane must be assigned to different "communities" as defined by Calef and Hancock.

A rapid vertical alternation of Salopina, Sphaerirhynchia and Isorthis "communities" over a very limited vertical thickness of strata is shown in Fig.6.27p386. In this sequence, L. lewisii also occurs very commonly, in bands in which many specimens lie perpendicular to the bedding, apparently in life position. Calef and Hancock (p 796) related monospecific Lingula assemblages to the "restricted" Lingula community of Ziegler et al. ('69): that is to the shallowest conditions.

Fig. 6.24 shows an example of different communities on the same bedding plane from Frith Wood. Here, C1 has a fauna dominated by I. orbicularis, with P. ludloviensis and F. amygdalina, and less common D. navicula. It could be assigned to the Isorthis community, when the other two common species would be unusually numerous, or the Sphaerirhynchia community without either of the 100% present rhynchonellid species appearing. However, 0.9 m laterally away (C2), the prevalent species is P. ludloviensis, with I. orbicularis, and some M. nucula and F. amygdalina. This assemblage most closely resembles the Salopina community (although with more I. orbicularis).

Calef and Hancock ('74) postulated that communities were depth-related. Hancock, Hurst and Fursich ('74) proposed that the Silurian

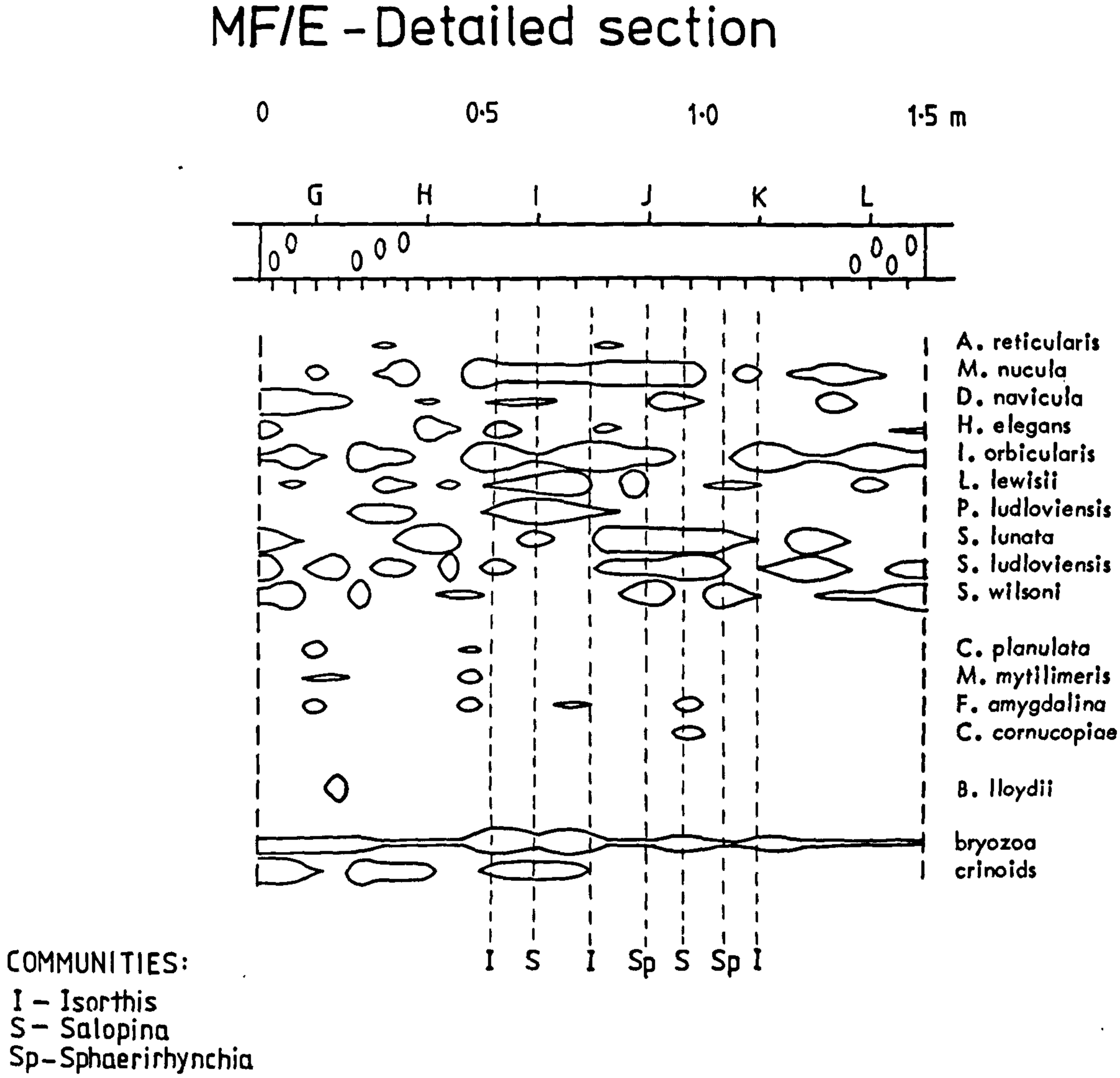


Fig. 6.27 : MF/E - Detailed section G-L showing the rapid alternation of Calef and Hancock's ('74) brachiopod communities. L. lewisii, perpendicular to the bedding, is very common through this sequence.

community spectrum of Lingula to Visbyella occupied areas down to 1000-1500 m depth. The lower limit was fixed by a comparison of depth gradients in brachiopod size, density, "biomass" and species diversity with modern analogues. From stratigraphical considerations, the greater part of the total depth range was attributed to the deeper, Dicoelosia and Visbyella communities. However, this still suggests that the Salopina to Isorthis depth range was several hundred metres. Although it is difficult to envisage such environmental changes for successive assemblages, it is impossible to do so for a single plane only up to a few metres across, particularly when "post-mortem transport capable of obscuring the community distribution and composition did not affect the collections" (Calef and Hancock '74 p 781).

A curious anomaly for the depth-related communities is the graptolite - L. lata fauna which is widespread in the basinal areas. Rare specimens of L. lata perpendicular to the bedding of the laminated siltstones (see p179) indicate that the species was indigenous here. Epibenthonic fossils are scarce in these sequences. The associated fauna includes graptolites and other pelagic forms such as orthocones. The assemblage is best developed at Lyepole Bridge, where bedding-planes of abundant L. lata, of graptolites, and of the two together, alternate, in the undisturbed units of laminated siltstones between slumps. Assemblages exclusively of closely-packed L. lata should presumably be in the "restricted" Lingula community. Yet, where L. lata is found together with graptolites, orthocones, C. cornucopiae and small pterineids, but other brachiopods or benthos are rare, the fauna is more comparable with the deep-water 'Marginal' Clorinda community of the Llandovery (Cocks and Rickards '69) or the Visbyella community recognised for the Wenlock (Calef and Hancock '74, Hancock, Hurst, and Fursich '74). The apparent combination of the two extreme communities is interesting, especially in respect of the considerable environmental separation in depth proposed by Hancock, Hurst and Fursich.

Criticisms:

The objections to the Ludlow brachiopod communities are on two levels: the first conceptual, the second interpretative.

That recurrent intergrading species associations do occur in the LLB can be seen by examination of the vertical range charts. For example, D. navicula, S. ludloviensis and I. orbicularis are found

commonly, in various relative abundances, at Ludlow and Leintwardine. But the significance of individual assemblages of fluctuating species composition is not the same as that of the major faunal grouping which indicates the Leintwardine Beds in the shelf. The former indicate species which were locally ecologically associated at one time, while the latter combines numerous minor assemblages which are vertically and laterally separate, but which characterise a suite of rocks. The distinction of the Leintwardine Beds fauna from the vertically-adjacent, major, faunal divisions of the shelf - the Bringewood and Whitcliffe Beds - coincides with the widespread development of conglomeratic limestones at the UBB-LLB boundary (see Map A - p 167), and with phosphatised fragment beds that occur in several areas at the ULB-LWB junction. These levels probably represent depositional breaks. In addition, the UBB fossils of the Aymestry Limestone are largely a facies fauna; for example, compound and solitary corals, and the large brachiopod K. knightii, none of which is common in siltier lithologies. The changes in major faunas probably relate to palaeogeographical and environmental differences (Lawson '75). These assemblages are not completely intergrading, but rather, are fairly distinct in composition.

The vertical range charts for the LLB succession at different localities show the great lateral and vertical variation in fauna and facies within the division. The graptolite-L. lata fauna of the laminated siltstones of the basin correlates with the largely benthonic shelly fauna of the LLB on the shelf. In view of the complexity found within this one division, it must be an oversimplification to think that a maximum of 12 LLB samples taken by Calef and Hancock from 4 localities can be representative. 2 of these are from the L. lata Beds of Builth (UBB-LLB), where Davia associations were collected. Benthonic fossils here are concentrated into discrete bands among thick sequences of poorly-fossiliferous siltstones with a graptolite-lingulid fauna (Straw '37), so that the question of post-mortem transport of shells must be considered. Another 2 samples are of Davia associations from the LLB at Ludlow, leaving 8 LLB collections which were assigned to three "depth" communities.

The 8 LLB samples show a puzzling degree of deviance from the standard community definitions given by Calef and Hancock - as shown in Table 18(Appx). They differ also from the faunal distributions described

for the LLB in this study. At a sample size of 60 individuals (which Calef and Hancock's Text-fig 2 (p 781) shows to be below the sample size for flattening of the rarefaction curve, but in text-fig 6 (p 803) is above the levelling-off point - that is, the diversity figures are minimum estimates), species diversity is consistently greater than community species density (no. of species per collection) at 100-200 specimens. In the case of the Salopina community of Usk 1, a species diversity of 15.3 at 60 individuals compares with an average density in larger collections of 7.2. The allocation of this collection to the low diversity, numerically-rich, Salopina community is surprising. But the average brachiopod species diversity for the 8 LLB collections of 12.9 is far greater than was noted in most LLB plane assemblages, even at larger sample sizes (eg. Fig. 6.21p365). Presumably, Calef and Hancock's collections frequently mixed several different fossil assemblages together to produce such results. The difficulty in assigning individual LLB faunas to a community often follows from the restricted diversity of these "dominated" assemblages.

The relation between depth and brachiopod distributions was discussed by Lawson ('75), who commented that several, potentially controlling, environmental factors which normally vary with depth, such as substrate, turbulence, and food supply, are not directly controlled by it. For example, sediment size will depend upon provenance, and not necessarily upon offshore conditions. Although brachiopods are most often the dominant faunal group in the LLB, it is frequently other groups, and associated sedimentological evidence that are more useful for environmental interpretation. For instance, lingulids associated with a restricted largely molluscan assemblage, in sediments which display features typical of shallow water conditions (as in the Downton Castle Sandstone - Holland, Lawson and Walmsley '63, and Lingula community of Ziegler et al. ('68)), may be confidently assigned to a near-shore environment. But the monospecific L. lata assemblages found in finely-laminated siltstones with a restricted, but mainly pelagic fauna, and the L. lewisii bands which are intercalated among richly-fossiliferous beds of the shelf sequences, cannot be similarly interpreted. Indeed, the former association suggests an offshore environment.

The frequent alternation, and even co-existence, of communities in the LLB of the shelf, without accompanying sedimentological evidence of

greatly changing conditions, means that the concept of a depth correlation must be re-examined. Shabica and Boucot ('76) recently criticised the theoretical basis for the absolute depth range of up to 1500 m deduced for the Silurian brachiopod communities (Hancock, Hurst and Fursich '74). They argued that several of the analogies drawn between Silurian and Recent communities were invalid (for example, the extrapolation of biomass gradients for plankton to benthos), that depth alone was not controlling, and that the Visbyella community was not proved to be in situ. Their estimate for the community depth range of 200 m differs from a minimum of 600 m proposed by Johnson and Potter ('76) from distributions of Recent brachiopods (eg. Foster '74). Even for the lowest figure, if assemblages relate to depth, it still requires numerous, considerable changes in depth to accommodate the vertical LLB faunal distributions - and lateral community differences along a bedding-plane remain unexplained.

The alternative hypothesis is that Calef and Hancock's statistically-defined communities are not indicative of depth. The distinction between minor assemblages and the major faunal divisions is important here. The depth-related Llandovery communities are analogous to the latter, being vertically and laterally extensive. For example, in the Whitcliffe Beds, where the association of P. ludloviensis, S. lunata and M. nucula is characteristic, proximal shelf conditions are inferred before the transition to non-marine beds in the Downtonian. This same combination of species, when it first appears in the LLB of the shelf inliers (eg. May Hill), commonly occurs prevalently in many assemblages. However, these species are, at this level, found associated with other fossils which do not persist up into the Whitcliffe Beds, but which are abundant in these sequences (eg. S. wilsoni, I. orbicularis). Palaeoecological analyses indicate a local derivation for fossils, from a mosaic, faunal settlement pattern in a shelf environment. This particular species association is not diagnostic of Whitcliffe-type conditions here, but of an environment within the ranges of tolerance of the individual species. The controls on brachiopod distributions discussed earlier (p 233 ff.), and the LLB species distributions, show that each species responds differently to interacting ecological parameters. The associated fauna (and facies) are essential for environmental interpretation.

The nature of LLB faunal assemblages means that individual associations are not widely representative. Dominated, and monospecific, faunas are especially typical of the calcareous siltstone facies. Calef and Hancock seem not to have recognised this, regarding collections with a high dominance of one or two species as atypical. Thus, though the prevalent species of the Sphaerirhyrinchia community compare most closely with the LLB fauna, individual assemblages must frequently be assigned to other communities. Therefore, the statistically-defined communities, in the LLB, often describe minor distributional patterns. Community changes do not indicate large environmental changes.

Continuous regression ?:

Newall ('66) recognised three environmentally-controlled units in the UB Aymestry Limestone of the Main outcrop. Atrypa-Strophonella faunas, which are in silty, less fossiliferous beds, represent the calmest conditions. Coral units containing numerous tabulate coral colonies, many in position of growth or little disturbed, indicate fairly turbulent conditions in the shallow photic zone. High energy conditions are shown by Kirkidium units, which consist of accumulations of disarticulated, mainly pedicle, valves that are not unduly worn. They are considered to have moved far, probably from an area within wave-base. Algae from the UBB at Aymestrey (Elliott '71) indicate a water depth of less than 30 m. The Kirkidium banks, which are concentrated along the shelf edge region from Aymestrey to View Edge (SO.426.807), were interpreted by Alexander ('36) as accumulating on a shallow, offshore ridge.

The overlying thinly-bedded LLB siltstones at Aymestrey have an abundance of the distal shelf species D. navicula. Unidirectional currents (E-W) are indicated by small erosional scours (Fig 4.10), and assemblages of aligned shells (eg. Fig 6.23-3). Graptolites and L. lata are fairly common among the benthonic fossils. There seems ample evidence to show that deposition was below wave-base, and hence deepening had occurred here. In some shelf inliers, conglomeratic limestones are developed at the UBB-LLB junction, and in the LLB more thinly-bedded, siltier flags replace the Aymestry Limestone facies (eg. Phipps and Reeve '67 - Malverns). Further SE, as at May Hill (Lawson '55), the Aymestry Limestone is not developed. Well-developed conglomeratic limestones in the basal LLB here suggest unstable, shallow conditions before the development of thinly-bedded shelly

siltstones in the U. Blaisdon Beds (see p309 ff.).

Calef and Hancock ('74) did not consider the calcareous, Aymestry Limestone facies and fauna. Evidence for a second transgression above this unit, and not a continuous regression through the Ludlow, is shown both in the faunal (especially non-brachiopod) and facies changes.

LLB RECURRENT SPECIES ASSOCIATIONS

Intergrading, recurrent species associations within the LLB, which relate to the palaeoecological and palaeogeographical conditions, can be used to assess the environmental changes taking place through the period. It has been deduced that faunal belts on the shelf were wide, so that even possibly extensive transport of shells has not significantly mixed the faunas. Diachronism of sessile benthonic organisms, which are mainly controlled by the physical environment, can be seen against the distribution of groups which are stratigraphically more useful, such as the neobeyrichiids. Because each species responds individually to the environment, though, it means that diachronism can also be recognised by comparing different members of one group; for example, in the articulate brachiopods, S. lunata appears earlier in SE shelf inliers, but S. wilsoni dies out lower in the succession in the N of the shelf.

Five sub-faunas can conveniently be recognised from the LLB. Three are dominated by sessile, suspension-feeding, benthonic fossils. These approximate to Petersen's ('13) concept of animal communities; that is, of a combination of species inhabiting large areas of the sea-floor, a few of which are conspicuously abundant, and having a "patch" distribution. This means that quantitative composition of samples varies more than the qualitative faunal list. The species distributions change temporally and laterally in response to fluctuating local environmental and ecological parameters, for example, differential larval success, and variations in turbulence and sedimentation rates. Progressive environmental changes influence qualitative changes as conditions become limiting for individual species, or replacements of species by others better adapted to the environment takes place. The majority of Ludlow species are long-ranging forms, so that their acmes are considered to be important for both stratigraphical and ecological considerations.

Three of the environmentally-influenced faunas include benthonic articulate brachiopods as major constituents. Fig. 5.32 which relates shell form, feeding structure and habit of articulate brachiopods

illustrates this control. The sub-faunas intergrade with one another, so that descriptions are general. No form of inter-dependence is assumed within communities.

1. Inner shelf, brachiopod-dominated assemblages:

This fauna is dominated by ribbed, pedically-attached brachiopods - ie. by epifaunal suspension-feeders. It composes the fauna of the shelf inliers. The association is firstly dominated by the strongly-ribbed, thick-shelled forms in the basal conglomeratic facies - A. reticularis, M. nucula, S. wilsoni, H. elegans - all well-adapted to withstand turbulent, turbid conditions. The more finely-ribbed, orthids and P. ludloviensis increase in the calcareous siltstone facies at the expense of the two spiriferids, suggesting some decrease in agitation of the environment. Filter-feeding bivalves such as F. amygdalina are common in bands. Particulate food is assumed to be dominantly in suspension because of the scarcity of fossils of deposit-feeders, but bioturbation in the sediment indicates that an unpreserved, deposit-feeding component was associated in this environment.

2. Outer shelf, brachiopod-dominated assemblages:

Small, smooth, unattached brachiopods predominate in monospecific assemblages. D. navicula and S. ludloviensis are most typical, the former composing the fauna virtually exclusively through several metres of succession in the basal LLB of the shelf edge at Shelderton. The finely-ribbed orthid, I. orbicularis, becomes increasingly common towards the inner shelf. The fossil assemblages are again dominantly of suspension feeders, but found in bioturbated sediments so that a deposit-feeding component can be assumed. The association, which grades laterally and vertically into association 1, contains forms more adapted for quiet conditions, and soft substrates.

3. Top LLB, large brachiopod - trilobite association:

This fauna can be recognised over many areas of the shelf at the top of the LLB. It represents a change in morphotype of the brachiopod fauna, with large, unattached species - A. reticularis, L. depressa and S. ornatella - entering the fauna. There are marked increases in the non-brachiopod component of the fauna, especially trilobites, but also other deposit-feeding forms such as gastropods and ostracodes. The non-brachiopod groups increase in importance towards the shelf edge region. The brachiopod forms are considered to be adapted for resting on soft substrates, in conditions of low turbidity and sedimentation rate.

4. Beyrichiacean - A. gravi association:

This association is widespread at the top of the LLB in the outer shelf and basin, but is most typical of these areas in the ULB. Its ecological significance is shown by its persistence in spite of compositional changes in the ostracode component, and by the generally separate occurrence from assemblages of benthonic fossils. The basinal distribution of the association in plane assemblages among sequences with pelagic faunas (eg. Kerry) could be explained by transport among detached algal vegetation (see faunal distribution sections); the deposit-feeding ostracodes and possibly epiplanktonic brachiopod are unlikely to be indigenous here. Both constituents of the fauna also occur exclusively in assemblages. They are most common in the outer shelf region among a fauna dominated by deposit-feeders of association 3 and with members of association 5.

5. L. lata - S. leintwardinensis association:

This association characterises the basinal sequences, where other benthonic forms are rare, and the infrequent associated forms are dominantly pelagic. The association also spreads commonly onto the outer shelf region among benthonic forms. The environmental significance of indigenous specimens of the infaunal, suspension-feeding L. lata without other benthos has been proposed to indicate low concentrations of dissolved oxygen in the water. Graptolites, as planktonic organisms, are deposited on the bottom after death, so that the chance association only occurs after death of the organisms. However, in its exclusive form, the association represents conditions inimical to other benthos; such an environment cannot be assumed where the association is found in sequences together with benthonic fossils, as at the shelf edge.

These sub-faunas are not discrete nor uniform entities, and each includes many minor recurrent species associations. They are useful for a general environmental consideration, however. The five faunal units recognised here for the LLB compare with Calef and Hancock's('74) classification of the Leintwardine Beds fauna into a single brachiopod community - the Sphaerirhynchia community.

DIACHRONOUS FAUNAS AND FACIES:

Recognition of diachronism in major lithological units relies largely upon faunal evidence, but fossils, particularly benthonic forms, may themselves be facies-controlled and diachronous. It is necessary to

consider the ecological requirements of various groups and species in order to assess their relative stratigraphical usefulness, and also the time significance of the Ludlow faunal units.

A. PELAGIC FORMS

1. Graptolites:

Ideally a zonal index fossil should be common, have a wide, facies-independent distribution, and a short time range. Pelagic groups are potentially most useful, and in particular, graptolites. However, although the Ludlow basinal sequences may be zoned using graptolites, their scarcity in the shelf areas is reflected by the classification (Holland, Lawson and Walmsley '63). The stages are indicated on the shelf by biostratigraphical divisions based on shelly faunas, and defined at standard sections at Ludlow. Correlation of basinal and shelf sequences relies upon the interdigitation of shelly and graptolitic faunas in intermediate regions. Selective destruction of the graptolite rhabdosomes in the more agitated environments of the shelf may explain their general rarity in these sequences, or this could be an original distributional feature.

In this study, the correlation of the LLB and leintwardinensis zone was confirmed by the occurrence of the species in most shelf sequences. S. incipiens was not identified from the LLB of the shelf. It probably represents a lower zone in the succession, as is recognised for graptolitic sequences in other areas of Britain (Rickards '67, Palmer '72, Warren '71). The fine correlation with the lower beds remains somewhat equivocal because the lowest S. leintwardinensis identified (RBR) at the stratotype was from about 10 m above the base, although the species was found in the basal beds at Leintwardine. In the inliers, only rare graptolite fragments were recorded from the basal conglomeratic facies. At the top of the LLB, S. leintwardinensis primus was found with S. leintwardinensis in several sections. Graptolites are still rare in the inliers, but they are fairly common at the type section for the base of the ULB. This enables precise correlation of the top of the LLB with the leintwardinensis zone. (- also true for ULB, because S. cf. leintwardinensis was reported within the top metre of ULB by Holland, Lawson and Walmsley '63 p 145).

It could be argued that the paucity of graptolites on the shelf is related to facies-control, and that first and last appearances of a

species are not necessarily synchronous with the basinal zonation. However, the graptolite evidence from the LLB confirms a correlation of the shelly fauna with the leintwardinensis zone (and higher than the incipiens zone), and does not indicate diachronism within the LLB.

2. Orthocones:

Orthocones are nektonic forms, with a wide, relatively facies-independent distribution. However, they are generally badly-preserved moulds, and the group is poorly-known taxonomically. Therefore, they are not useful for stratigraphical correlation.

B. VAGILE BENTHOS

3. Ostracodes:

Beyrichiaceans:

The two main points arising from the distribution of beyrichiaceans are firstly, the marked increases in diversity and abundance at the top of the LLB, and then, the vertical restriction of the geographically extensive neobeyrichiid fauna. The LLB species are less well documented, but the few common species are only locally common and are relatively long-ranging.

It was concluded in Chapter 5 (p 250-5) that the beyrichiaceans were probably benthonic forms. The characteristic top LLB association with A. gravi in thin fossiliferous seams, separate from assemblages of other fossils, and their wide distribution in basinal and shelf edge sequences, can be explained if the ostracodes lived among algal vegetation. The rarity of ostracode - A. gravi faunas in the shelf sequences could reflect selective destruction of the shells, but probably represents an original ecological feature of the distribution. In the ULB, the N. lauensis - A. gravi fauna is characteristic of the more thickly-bedded siltstones of the "C" gravi Beds, although not restricted to this facies.

The N. lauensis - N. scissa - N. confluens fauna is confined, in the Welsh Borderlands, to the ULB. Although the former species is used as a faunal index for this division (Holland, Lawson and Walmsley '63), no neobeyrichiids have been found at the stratotype, and only very rare individuals are recorded from the shelf inliers. The fine correlation with the S. ornatella fauna of the shelf is therefore problematic. N. nutans, which precedes N. lauensis in the Gotland succession (Siveter '74), is found in an equivalent position in the topmost LLB of several

localities, including Chances Pitch in the shelf inliers. In the Lake District, Shaw ('71) recorded N. nutans with N. lauensis and N. scissa in his ULB, which have characteristic assemblages of these ostracodes with A. gravi. N. confluens here is typical of Shaw's Whitcliffe Beds, but its range overlaps with N. lauensis in beds designated as LWB on the basis of the loss of A. gravi, N. nutans, N. scissa and other characteristic Leintwardinian species from the fauna (Shaw '71). The absence of S. ornatella (and S. leintwardinensis) from the ULB fauna of the Kendal District means that the question remains of correlation of the ostracode assemblages with the shelly fauna.

The distribution of the N. lauensis fauna appears largely linked to facies. The beyrichiacean - A. gravi assemblages represent a recurrent ecological association, and indicate the similar mode of life of various genera and species of ostracodes. The limited vertical range of the neobeyrichiids, their wide distribution in the basinal and shelf edge ULB (and topmost LLB: N. nutans) sequences of the Welsh Borderlands, and on a broader scale, in the Lake District, Gotland, Latvia, and Scania (Siveter '74), make them stratigraphically useful. However, the coeval occurrence of N. lauensis and N. confluens in the Welsh Borderlands contrasts with their different, but partly overlapping, ranges in the Lake District (Shaw '71), so it is important not to assume synchroneity of different species. Neobeyrichiid faunas and graptolites seem often mutually exclusive (eg. in this study, at Shelderton, Kerry, Ludlow MF/A; Holland and Palmer '74, Shaw '71). This is reflected by their different facies distributions, the former in thick siltstone flags but the latter in the thin laminated siltstones, and it means that a detailed correlation with the graptolites cannot be made.

In view of the short time-range of the neobeyrichiid fauna, it is considered a stratigraphically useful horizon. Basal diachronism must be relatively shall, because the N. lauensis - A. gravi fauna is usually preceded by the ecologically-equivalent beyrichiacean assemblages, which indicate that the environment was suitable. Then, the appearance of the neobeyrichiids has a time significance.

4. Trilobites:

Trilobites are vagile benthos, limited in the LLB to areas of the shelf and shelf edge. Their abundance and diversity increase at the top of the LLB. The distribution patterns of calymenids, and to a

lesser extent of encrinurids, cut across those of other shelly members of the Leintwardine Beds fauna, for example, the neobeyrichiids and brachiopods. This is important because C. puellaris and E. stubblefieldi are taken as faunal indices for the ULB (Holland, Lawson and Walmsley '63), and the stratigraphical significance of the trilobite fauna needs evaluation in relation to the other groups.

The two encrinurid species, E. stubblefieldi and E. rosensteinae, are coeval and sympatric, commonly occurring together in beds, and therefore presumably with similar modes of life. The distribution shows a definite facies preference for siltier beds. E. stubblefieldi is most common in the "C" gravi beds lithology. The acme for the encrinurids precedes the appearance of neobeyrichiid fauna at Shelderton (SR/2-), where they are associated with beyrichiacean - A. gravi assemblages, graptolites and proetids, in a diverse fauna. In other areas, this level corresponds to the N. lauensis horizon, and some encrinurids appear in the S. ornatella fauna of the ULB of the shelf inliers (Map D p167). At the ULB stratotype, Encrinurus sp. was reported from the basal bed and occurred fairly commonly throughout the division (Holland, Lawson and Walmsley '63 p 117). In other Ludlow sections, the acme is close to the level where N. lauensis appears and hence to the lithological change to more thickly-bedded siltstones. (N. lauensis is not recorded from the type section). E. stubblefieldi parallels the beyrichiacean - A. gravi fauna in its distribution, but also links the S. ornatella and graptolite faunas. Its widespread distribution in the ULB compared with the beds below shows the rapid spread of suitable environments at this level. Although facies-controlled, the vertical restriction of the range and the extensive ULB distribution of encrinurids make them useful stratigraphically. There is a slight difference in the distribution pattern from that of the neobeyrichiid fauna.

The calymenids C. puellaris and C. lawsoni, which appear mutually exclusive, do not appear at a consistent level in the succession according to the brachiopod fauna. Both species are found lower in the LLB in the SE inliers, and migrate progressively north and west. The two species, where their ranges overlap at Leintwardine, are found separately. C. lawsoni is very common only in the channel-fill deposits. This could indicate different ecological preferences for the two species. That their modes of life were probably similar is shown by the comparable areal distribution patterns. C. puellaris is also found in

the Lake District, Gotland and Scania, with a limited vertical range from high in the Leintwardine Beds to the LWB (Siveter '73).

At the stratotype for the base of the ULB, C. puellaris was recorded from the basal bed (Holland, Lawson and Walmsley '63 p 118), and it becomes common at this level in other sections at Ludlow. The species enters the fauna and/or increases in abundance, in many sequences further west at the N. lauensis horizon. However, in the SE inliers the acme starts at a lower level, in the LLB (eg. May Hill, Chances Pitch) well below the S. ornatella beds. The distribution is therefore parallel with the N. lauensis-A. gravi fauna in sections west of Ludlow, but not to the east. This suggests that, in the LLB, calymenids migrated in response to a relatively gradual environmental change, but that suitable conditions developed contemporaneously over a large area to the west in the ULB with the calymenid distribution extending accordingly. In this case, C. puellaris is only useful as a ULB faunal index in these areas west of Ludlow.

The proetids P. obconicus and W. ludlowensis are found throughout the LLB, and are not therefore stratigraphically important for detailed correlation. However, they become much more common in the top LLB in many areas of the shelf, but especially at Ludlow and Leintwardine. In the shelf inliers, this level is shortly below the S. ornatella acme. At Ludlow, proetids occur with abundant S. ornatella in the eastern sections, but with beyrichiacean - A. gravi assemblages in the west (MF/A-) and at Leintwardine. Thus, the proetid acme is not parallel to that of S. ornatella, but correlates with the pre-lauensis, ostracode - A. gravi fauna at Ludlow and further west. In the ULB, there is a comparable westward extension in distribution to the calymenids and encrinurids, but proetids are less common at this level.

5. Bivalves:

The morphology of bivalves is adapted to their ecological requirements. The majority of LLB species are suspension-feeding types, either byssate or shallow-burrowers, and are confined to the shelf and shelf edge regions. However, P. tenuistriata and C. cornucopiae are also found, fairly infrequently, in the basinal sequences of thinly-bedded, laminated siltstones. The former is interpreted as an epibyssate species (p 263), the latter either free-living or byssate, but not infaunal (p 266). LLB bivalves are long-ranging, and most are facies-

controlled; they are not therefore stratigraphically valuable.

Bivalves increase in abundance at the top of the LLB, when several distributions also extend further westwards. These changes suggest an environmental change at this level. A deposit-feeding species, N. antiquus, becomes common in the ULB.

6. Gastropods:

Gastropods are vagile benthos which form a minor component of the LLB fauna. The common species, thought to be herbivores, are confined to the shelf and shelf edge regions, and appear facies-controlled. They are also long-ranging, and thus not useful stratigraphically.

Gastropods increase in abundance in the ULB. The distribution shows a westward spread at the top of the LLB and ULB.

C. SESSILE BENTHOS

7. Brachiopods:

The success of sessile benthos is related to the ability to maintain their position. Various ecological strategies have been adopted for this purpose, and these largely control the species distributions. Thus, facies control must be anticipated, and with it, diachronism. For articulate brachiopods, the adaptations of various morphotypes have been interpreted in Fig 5.32 . Most of the Ludlow species are long-ranging, and so it is faunal acmes which are considered to have correlative value (Holland, Lawson and Walmsley '63).

A. gravi and L. lata are the only brachiopods with common distributions in the LLB basinal sequences. The latter is infaunal, and apparently adapted to the basinal environment (see p184). The former, which is characteristically associated in assemblages with beyrichiaceans, is interpreted as an epiplanktonic species which probably attached to algal vegetation. Although it is often taken as a faunal index for the ULB, A. gravi occurs below the N. lauensis level west of Ludlow, mostly in the ecologically equivalent, ostracode assemblages (eg. Shelderton SR/2-) of the LLB.

The other LLB species have distributions centred on the shelf and shelf edge areas, and all are epifaunal apart from the larger lingulid species, L. lewisii. The vertical and lateral faunal variations depend upon environmental conditions. For example, D. navicula remains concentrated in the more distal areas of the shelf, while S. lunata, which enters the fauna earlier in the SE inliers, appears to prefer more proximal shelf conditions. The migration north and west of the

typical Whitcliffe Beds assemblages of P. ludloviensis, M. nucula, and S. lunata during the Leintwardinian suggests that there was a progressive environmental change across the shelf. However, the opposite trend for S. wilsoni, which dies out lower in the succession in the shelf edge and Ludlow areas, to be replaced by S. ornatella, shows that each species responded individually and differently to the evolving palaeogeography. The top LLB and ULB shelf fauna has an abundance of the large strophomenids S. ornatella, L. depressa and A. reticularis all of which appear adapted for resting freely on a substrate, in fairly quiet conditions and with little sedimentation. In contrast, the middle LLB shelly limestones of Perton have a concentration of ribbed, plicated, pedically-attached forms - S. wilsoni, M. nucula, H. elegans - which are well-adapted for more turbulent conditions. Hence, the distributions of the brachiopod species in the LLB are thought to be of ecological, rather than stratigraphical, significance.

It was concluded from the palaeoecological studies and environmental interpretations in this chapter that shelf faunal belts were wide. This means that the amount of diachronism may not be great. For example, the acme of S. ornatella, although basally diachronous, nevertheless appears to occupy a wide expanse of the shelf contemporaneously in the ULB. Similarly, the disappearance of S. wilsoni in the shelf takes place at different levels against the trilobite, ostracode, and other brachiopod evidence, but the species is ubiquitous and very common throughout much of the LLB. Therefore, the limits of individual species' ranges have less correlative value than the main distribution.

The fauna of the basal LLB is dominated by brachiopods, and initially consists of a "remnant" assemblage left after the loss of the diagnostic UBB fossils. The Aymestry Limestone has a demonstrably diachronous top, using the faunal changes for correlation (Fig 5.3 p168), but some diachronism of the fauna would also be expected. The effect of the latter may be ignored because of the widespread development of conglomeratic beds, and disconformable or unconformable junctions, at the level of the UBB-LLB boundary in many sequences. These horizons represent pauses in deposition, and erosion (p 309-29), which result in accentuated faunal distinction of the UBB and LLB assemblages.

Many of the LLB epifaunal brachiopods show some diachronism across the shelf in relation to the biostratigraphical unit, and have

distribution patterns which cut across those of the trilobite and ostracode fauna, and of other brachiopod species. This is mostly seen in the limits of the ranges, rather than in the main distribution. Therefore, it is not serious for the broad, shelf correlation of the Ludlow classification, but restricts more detailed correlation within the shelf in the Leintwardine Beds.

D. PALYNOLOGICAL ASSEMBLAGES:

(Results from K.J. Dorning)

A number of samples from the basal and topmost LLB of various areas were sent to K.J. Dorning for palynological analysis. Some of the correlations for the basal beds are interesting in relation to the sedimentary discontinuities inferred at this level over much of the shelf. It should be pointed out, though, that results for several samples did not correlate well with the macrofossil evidence, and so any conclusions are very tentative.

The standard sample from the stratotype at Sunnyhill Quarry (taken directly beneath the basal bed) correlated closely with samples from:-

1. the basal LLB siltstones at Aymestrey (above the eroded surface of Aymestry Limestone)
2. the basal LLB siltstones at Bow Bridge (sharp contact of siltstones with the limestone)
3. the basal LLB siltstones at Hocktree Quarries (sharp contact of siltstones with the limestone)
   - Of two samples laterally 6-7 m apart, one was indicated as basal LLB, the other as ? uppermost Bringewoodian.
4. the basal conglomeratic beds at Chances Pitch
5. beds 3-4 m above the base at MF/E- (J to L) in the Ludlow anticline.

Also, from IGS material:-

6. beds above the bored conglomerate of the Dean borehole, Wenlock Edge.

Stratigraphical gaps were noted by Dorning within the L. Blaisdon Beds at Wood Green. The conglomerates here (KJD collection) and those at Titos Point (IGS Brookend borehole) were considered "older" than the stratotype sample.

These results suggest that a period of erosion at Aymestrey, as suggested by Lawson ('73(a) p 262), and that indicated in the Dean borehole (p 324), took place at the end of U. Bringewood times, before

LLB sedimentation began. The Wood Green and Tites Point conglomerates may include derived pebbles from older rocks, but could represent discontinuities at this same, top Bringewoodian, level. The stratigraphical "gaps" predicted agree well with the conclusions reached in the discussion of the basal conglomerates (p309-29).

At the top of the LLB, samples from the channel-fill beds in the main quarry at Aymestrey, the equivalent beds on the Bengry Track at Aymestrey (JDL collection: AY 223), and the topmost LLB at Shelderton (SR/2-) correlated well, and were comparable to the topmost LLB, or ULB, at the type section at Ludlow. N. nutans is present in the Aymestrey quarry beds and at Shelderton. The palynological evidence confirms the presumed equivalence of the basinal N. lauensis fauna and the ULB assemblage of the stratotype.

CONCLUSIONS FOR LLB BIOSTRATIGRAPHY:

A. PELAGIC

1. Graptolites: Confirm the leintwardinensis - LLB correlation.

2. Orthocones: Poorly known taxonomically.

B. VAGILE BENTHOS

3. Ostracodes:

a. Beyrichiaceans: The appearance of N. lauensis in sequences with beyrichiacean-A. gravi assemblages is particularly stratigraphically useful. The distribution is facies - controlled though, and comparison with the graptolite zonation and S. ornatella fauna is somewhat uncertain.

b. Smooth ostracodes: Poorly known taxonomically.

4. Trilobites:

a. Encrinurids: Facies-controlled, but vertically restricted and widespread in ULB. Their appearance does not correspond exactly with the N. lauensis horizon, but is often associated with beyrichiacean-A. gravi fauna.

b. Calymenids: The distribution cuts across that of the brachiopod fauna. Parallel with N. lauensis fauna west of Ludlow though, and widespread, suggesting rapid environmental change over this area in the ULB.

c. Proetids: Long-ranging, therefore not index fossils. However, the top LLB acme is not parallel to that of S. ornatella, but parallels the beyrichiacean-A. gravi fauna at Ludlow and Leintwardine.

5. Bivalves: Ecologically-controlled distributions, and long-ranging species. Not stratigraphically useful.

6. Gastropods: Ecologically-controlled distributions, and long-ranging species. Not stratigraphically useful.

C. SESSILE BENTHOS:

7. Brachiopods: Within the LLB, faunal changes occur in response to the environment. However, wide faunal belts mean that the degree of diachronism is often small; only the limits of species ranges are usually affected. This does not therefore cause serious stratigraphical difficulties for correlation of the major Ludlow assemblages, but restricts lateral correlation within the Leintwardine Beds.

D. PALYNOLOGICAL ASSEMBLAGES:

Potentially stratigraphically useful, but not researched extensively yet. (Used tentatively as supporting evidence).

LLB ECOLOGY AND ENVIRONMENT Fig. 6.29 p406

The palaeogeography inferred from facies and thickness variations, and general faunal evidence, is of a wide, gently sloping, shelf area, which is bounded by a steep marginal zone down into a narrow, SW-NE elongated basin. The abundant LLB benthonic fauna of the shelf contrasts with the generally sparse, and mainly pelagic, fauna of the basin. At the top of the LLB, benthonic assemblages enter the fauna of many of the Brecon sequences in the SW of the basinal area (eg. Ysgwydd Hwch YH1-), where the N. lauensis-A. gravi beds show a further enrichment of the benthonic fraction of the fauna. There is generally an associated facies transition to more thickly-bedded, calcareous siltstones (Facies Maps C and D, p167). The areas of the basin affected by these changes are the more proximal parts of the axial palaeoslope deduced from thickness considerations.

Bioturbation:

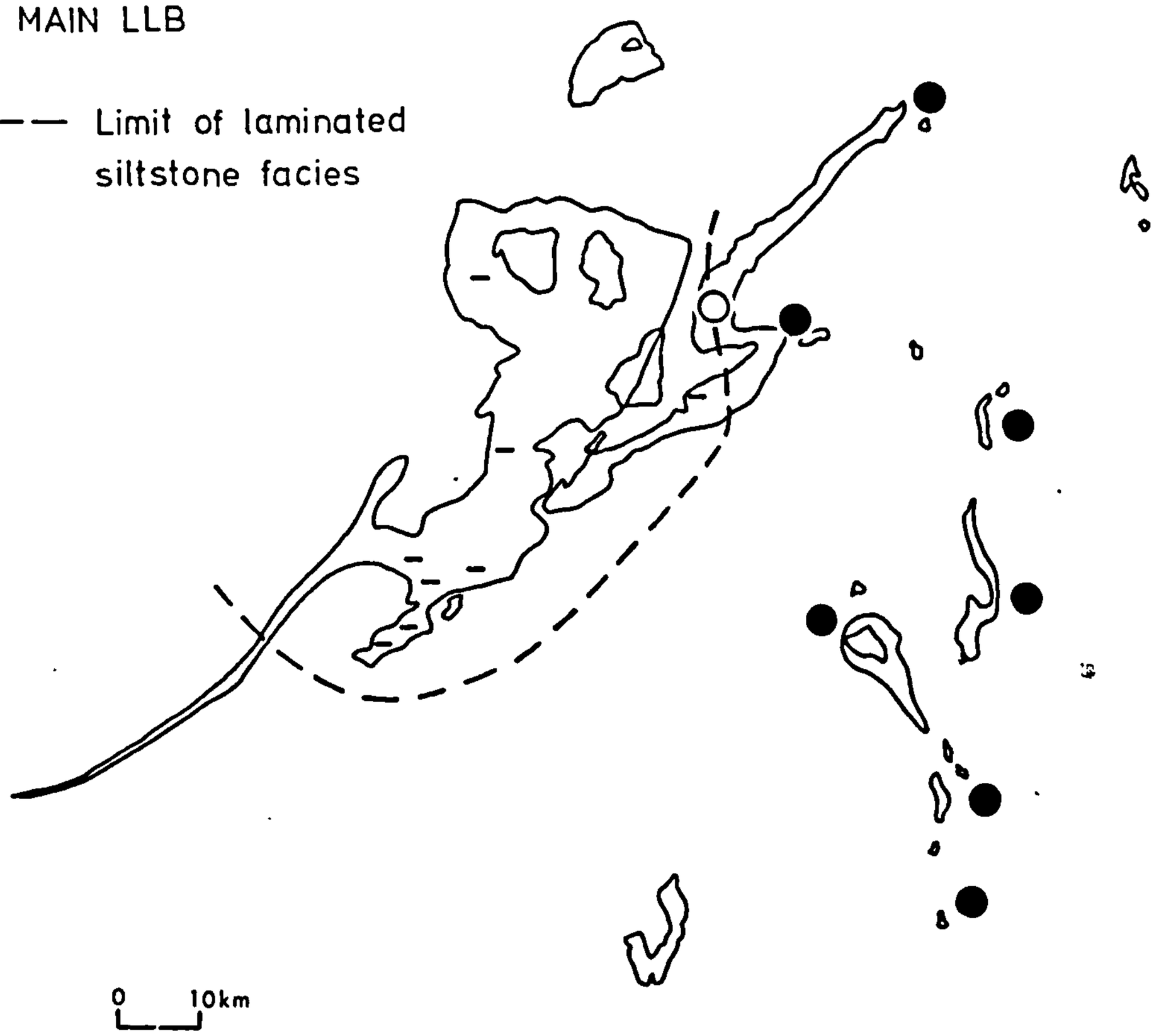
The distribution of bioturbation is shown in Fig 6.28p405. It is closely similar to that for the main benthonic fauna, restricted to the areas of shelf facies until the top of the LLB, when the appearance of burrow traces accompanies the entry of benthonic fossils into some Brecon sequences.

The top beds of the Aymestry Limestone are generally extensively burrowed, mottled with diffuse, narrow traces. A few large K. squamosus tubes perpendicular to the bedding were found at this level at Ludlow, Woodbury, and Chances Pitch, and one such specimen at Aymestrey descended

Bioturbation

MAIN LLB

— — Limit of laminated siltstone facies



TOP LLB

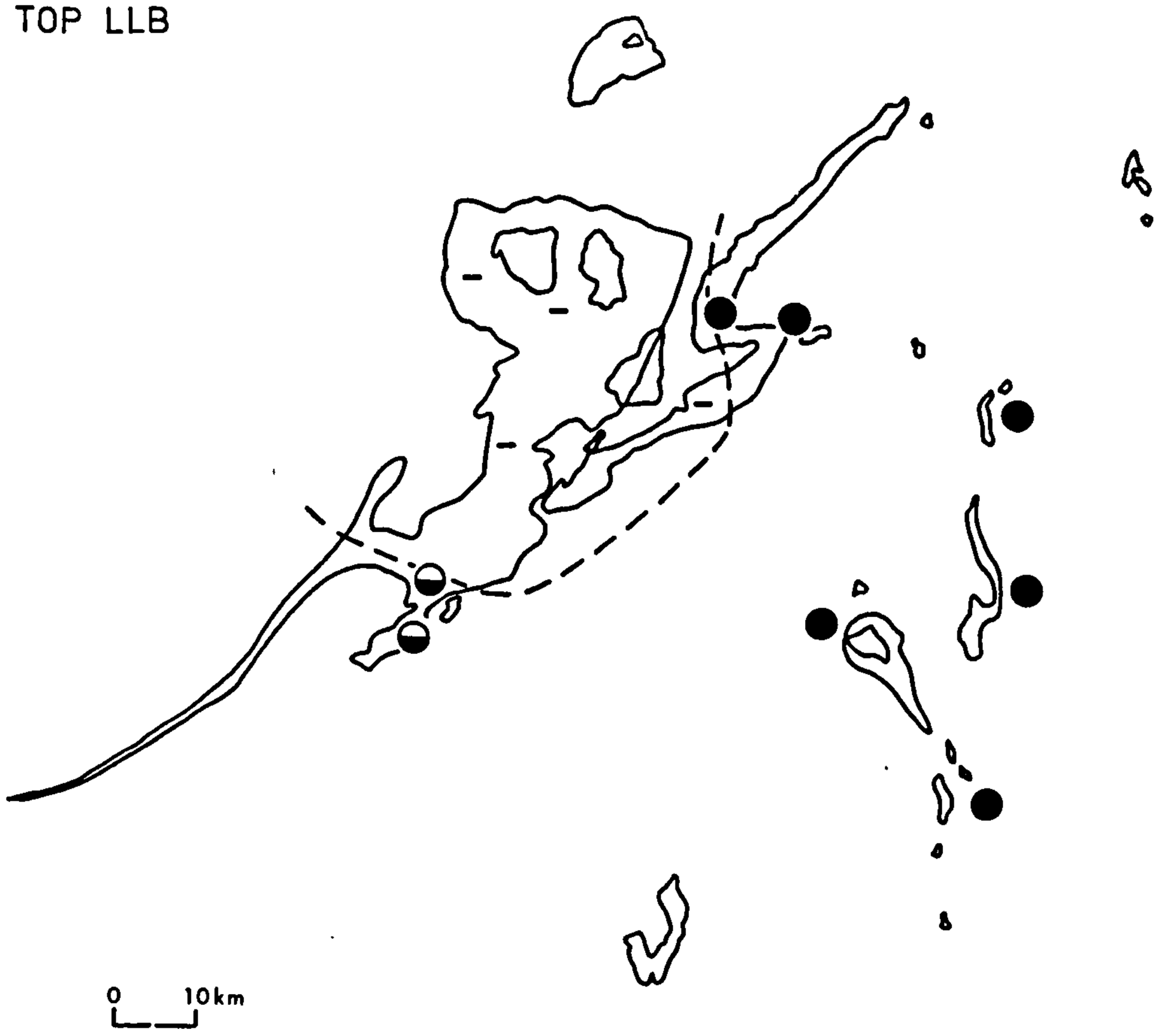


Fig. 6.28 : Distribution of bioturbation.

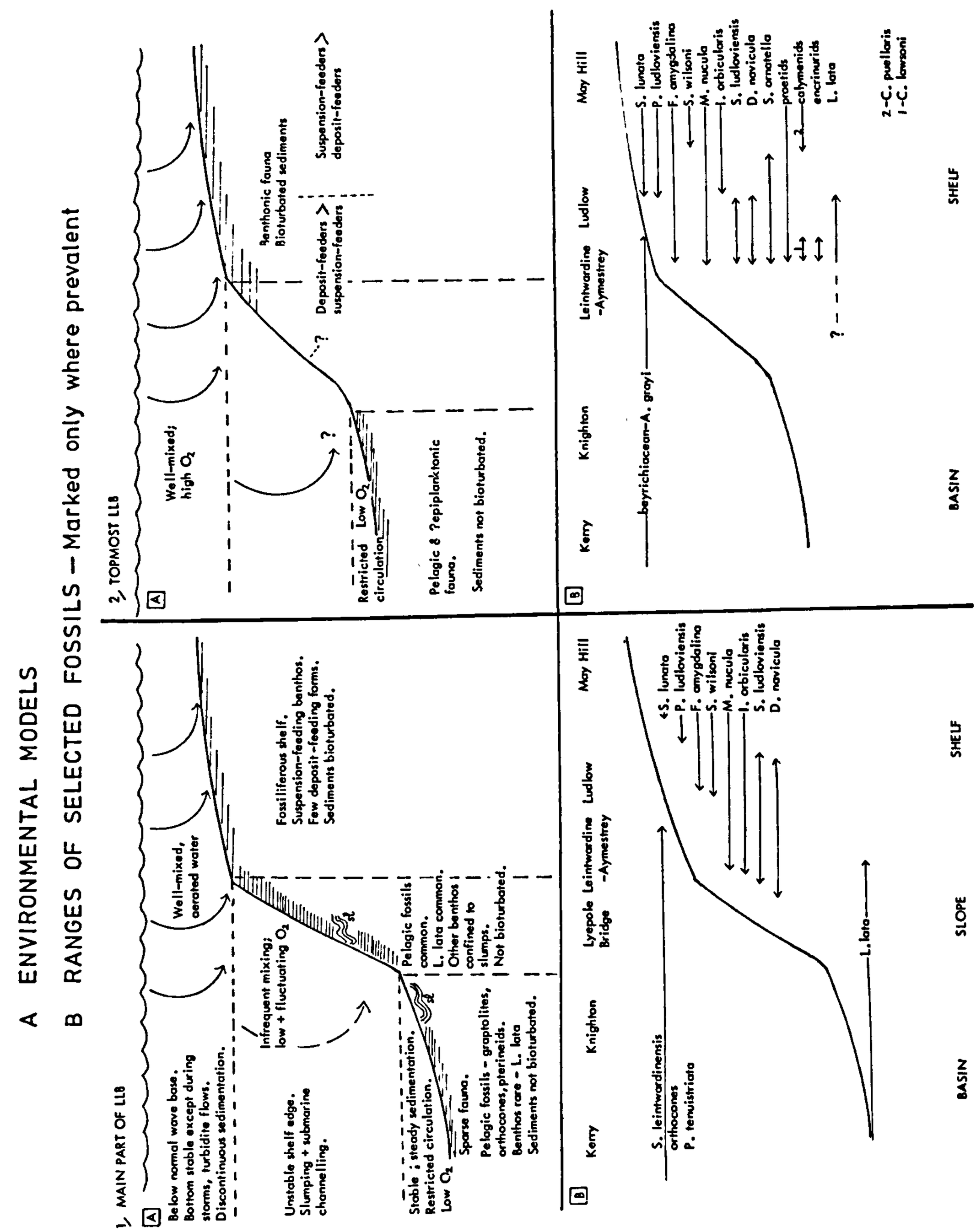


Fig. 6.29 : Environmental models for the LLB - cf. the ranges of selected fossils.

from the eroded surface of the Limestone. The overlying strata in the shelf areas are variably burrowed, but in the shelf edge regions of Aymestrey and Leintwardine, the fine lamination of the thinly-bedded siltstones is not disturbed by biogenic reworking.

The shelf sequences most commonly have beds with narrow traces across bedding-planes or directed shallowly into the sediments. Some flags have a mottled bioturbate texture from more extensive activity. Steeply-inclined or vertical burrows are infrequent, except at Woodbury, where scattered traces with a meniscus-fill (U-in-U) structure were seen in some beds. Both these, and the widespread Chondrites-type deformation which is probably caused by worm-like animals, are thought to be dwelling and feeding traces (Kennedy '75).

The amount of bioturbation is very variable, especially in the sequences with sheet-laminated siltstone facies (eg. Ludlow sections). This suggests that deposition was discontinuous. The parallel-laminated siltstone units were laid down rapidly after slight erosion, and have few burrows except for escape traces. These units alternate with unlaminated or patchily-laminated beds. Biogenic reworking is clear in the latter, but is inferred to have completely destroyed primary sedimentary fabric in the former. These beds have been slowly accumulated, allowing much more time for bioturbation. Typically, the amount of biogenic activity is related to the length of time available rather than to the density of burrowing organisms (Howard '75). In the shelf inliers, the calcareous siltstone facies with its frequent plane assemblages of fossils among bioturbated sediments is interpreted as representing relatively slow accumulation disturbed by periods of bottom reworking by shoaling waves (storm-generated). Variable rates of deposition, and alternation of shell layers and bioturbated sediments, are characteristic of open shelf conditions (Howard '75).

Faunal distributions reflect the physical environment. The majority of LLB shelf fossils are epifaunal, suspension-feeding, benthonic forms, but the fauna is deduced, from evidence of bioturbation in the sediments, also to include soft-bodied deposit-feeders. At the top of the LLB, the marked increase of trilobites, ostracodes, and gastropods (and the occasional appearance of the deposit-feeding bivalve N. antiquus), particularly in the areas from Ludlow westwards, raises the proportion in the fauna of deposit-feeders with hard skeletons. In the basinal

areas of laminated siltstone facies, the suspension-feeding, infaunal brachiopod L. lata appears indigenous but, until the top LLB of some Brecon sequences, other benthonic fossils are rare (except in slumped beds) and bioturbation is not seen.

A spatial separation of suspension-feeding and deposit-feeding benthos along a nearshore to offshore gradient is well-documented for Recent environments (for example, Parker '63). This can be related to the higher proportion of food particles deposited in lower energy conditions, but faunal distributions also depend on many other, generally depth-related, variables. In the LLB of the shelf there is no indication of conditions above normal wave base, so that the effects of salinity and temperature fluctuations can be discounted. Calef and Hancock ('74 p 803) believed "food supply to have been the most important single controlling factor of upper Silurian brachiopod distribution". However, food was considered by Rhoads ('75) not to be a limiting factor for suspension-feeders in epeiric seas, although it may be in abyssal depths, although the amount of deposited food may be restrictive in shallow as well as deep water. The nature of the substrate will be extremely important to benthos, not only factors such as grain size, organic content and hardness, but also bottom stability and sedimentation rate. For instance, high surface turbidity of fine sediments in deeper waters caused by reworking by deposit feeders, may prevent colonisation by suspension-feeders such as filter-feeding bivalves that are sensitive to "clogging" by sediment (Rhoads and Young '70, Steele-Petrovic '75). Rhoads and Morse ('70) noted changes in the benthonic fauna with the decreases in concentration of dissolved oxygen at increasing depths that are found in many Recent marine basins (for example, in the Gulf of California). Shelf assemblages composed mainly of large, shelly invertebrates are replaced by a dominance of small, infaunal deposit-feeders, and then below a limiting oxygen tension, most metazoans disappear. The oxygen-deficient basins have finely-laminated, unbioturbated sediments.

The basinal LLB sediments have similar characteristics to those described for oxygen-deficient basins. The distribution of L. lata in the basin is interesting. Many lingulids appear tolerant of the reduced oxygen levels of very shallow, brackish-water conditions (see Lingula section p182). It is proposed that L. lata could withstand low dissolved oxygen concentrations in the basin which were inimical to

other benthos. Such conditions could result from restricted circulation by bottom currents as well as because of depth.

Intermediate in facies and fauna between shelf and basin is the shelf edge sequence at Aymestrey. Fossils and shell debris are confined to numerous plane assemblages in the fine, laminated siltstones, which do not appear burrowed. "Basinal" fossils - L. lata, pelagic organisms such as graptolites and orthocones, and the possibly epiplanktonic P. tenuistriata - are all common in the fauna, together with epifaunal brachiopods, and bivalves. The benthonic component is dominated by suspension-feeders. The action of westward-flowing bottom currents is evident in the aligned shell assemblages, and erosional scour channels. The alternation of planes of fossils with "barren" layered sediments indicates that the shells are current accumulations. Newall ('66) concluded that some assemblages with a high proportion of S. ludloviensis valves that were unbroken and still retained hinge spines had not travelled far. However, there are many others in which the majority of shells are damaged and may have suffered more extensive transport. If the benthonic fossils are locally-derived, the apparent absence of bioturbation is unusual, because a muddy, distal shelf environment is more typical of deposit-feeding, than of suspension-feeding, benthos. Food is possibly a limiting factor only for the former in this more offshore environment, but a low oxygen level would be expected to affect all benthos. In view of the storm-influenced sedimentation inferred for the shelf sequences, the alternative explanation that the shell layers have been transported by ebb currents in this area, which was generally unfavourable for benthos, is very feasible.

It is the shelf edge region which shows the greatest change in emphasis of the benthonic fauna at the top of the LLB. At Shelderton, deposit-feeders increase rapidly in abundance and diversity among the fossils in the upper 6-7 m of LLB. Thinly-bedded, unbioturbed, laminated siltstones with occasional planes of fossils are replaced by thicker flags, many of which are laminated only in thin bands and patches. The poorly-laminated beds contain evenly-distributed fossils, in contrast to the plane assemblages of well-laminated units, and occasionally have a mottled texture. These beds are inferred to have been extensively biogenically reworked. The faunal and facies changes at this level indicate the development of favourable conditions here for benthos. The diverse, shelly and graptolitic fauna reflects the distal shelf environment.

The appearance of bioturbation in sediments of the SW basinal area towards the top of the LLB (eg. at Ysgwydd Hwch) marks an environmental change here to conditions that are suitable for indigenous deposit-feeding benthos. Assemblages of benthonic fossils enter the fauna of these sequences at this level, and also in more northerly sequences of unbioturbated, laminated siltstones, such as the Whimble (Wmb-). The restriction of such assemblages to discrete bands among beds with graptolite-L. lata faunas at the latter locality though, and absence of burrowing, suggests that these shell layers have been transported into an area that was still unfavourable for most benthos. Further N, at Kerry, the finely-laminated siltstones have a sparse, graptolite-L. lata fauna at this level, and conditions were clearly inimical for bottom-dwellers other than the lingulid species.

The changes in the distribution of benthonic fossils and bioturbation at the top of the LLB, which chiefly affect the shelf edge region and the proximal part of the basin's axial palaeoslope (deduced from thickness variations), can be explained in several ways depending upon the original limiting factors. Thus, shallowing could be responsible, but increased bottom circulation could also raise oxygen and food levels in these regions. The accompanying facies transition to coarser, more thickly-bedded, sediments suggests that the former is very probable.

CHAPTER SEVEN

CONCLUSIONS

Collection method:

It was of fundamental importance for the project that the sampling method adopted should reflect the faunal variation and distribution adequately. Because of the characteristically uneven arrangement of fossils in the strata and the rapidly changing composition of assemblages, bed-by-bed collecting was adopted. Although a slow method of study, the technique enabled the frequent changes of fauna over small vertical thicknesses to be recorded. This pattern of faunal distribution is best illustrated by the detailed range charts for parts of the succession (see p 380). These diagrams also show the fluctuations in relative species abundances that occur particularly in the calcareous siltstone facies of the shelf - for example at Wood Green and MF33 (p 363 ff). The quantitative, as well as qualitative, changes in the fauna so that different species are prevalent in successive assemblages are indicated by the semi-quantitative records taken.

However, the cluster analyses for which the quantitative results from Ludlow were used did not produce clear results (p 38 ff.). Fully quantitative samples would be required in order to discriminate more effectively between collections; this method would distinguish beds dominated monospecifically by one fossil from those in which the fossil was one of several common species (see p 38). Also, for trophic analysis of collections, fully quantitative results would be required.

The qualitative cluster analysis carried out on the Ludlow data selected the overall vertical faunal changes, and indicated the correlation of sections (p 41 ff.). Matching of the fauna in this way enabled section MF/F-, from the middle part of the succession, to be positioned relative to the other sections. The correlation is based largely on the evidence of benthonic fossils, so that ecological as well as stratigraphical controls are likely. However, the relatively small geographical separation of sections, and the large vertical thickness of strata represented by each cluster group mean that the degree of possible diachronism is not significant. This method of treating the data is useful for biostratigraphical work.

The inapplicability of bulk sampling or spaced collecting for the LLB results from the irregular fossil distribution and the frequent wide changes in the fauna. Thus, isolated collections are not adequately

representative of the whole fauna but indicate a minor feature, often very local, of the distribution.

For the sparsely fossiliferous, thick graptolitic basinal sequence at Kerry on the main transect (Fig 1.5 p 9), the collecting technique was modified. Here, the whole succession (about 150 m) was examined fairly briefly, and only the top part (approx. 30 m) up to where the N. lauensis-A. grayi fauna appeared was studied in more detail. The 'normal' and 'slumped' series of Earp ('38) were seen in this area.

Palaeoecological work:

The primary fieldwork survey covered a shelf to basin transect, which allowed the main differences in sediments, fauna and thicknesses to be observed. (These are summarised at the end of the stratigraphical chapters 2-4). In addition, some parts of the succession were studied in other localities which were selected for several reasons. For example, the succession in the intermediate Brecon Anticlinal region was examined to aid in correlation of the shelly fauna of the shelf with the graptolitic strata of the basin; the purpose of visiting Lyepole Bridge Quarry (p 132) to the W of Aymestrey was to compare the faunas of slumped and undisturbed units of the sequence. Palaeoecological surveys were carried out where bedding-plane assemblages were well-exposed (eg. MF33) to supplement the stratigraphical data.

The results obtained were used to compile the facies and faunal distribution maps of Chapter 5. These were extended, for areas not visited (eg. Wenlock Edge - Shergold and Shirley '68) and for the ULB, with information drawn from the literature. However, the detailed information on fossil occurrence within the strata, which is necessary for palaeoecological syntheses, was only available for the sequences studied in this project. For instance, the presence of individuals of Lingula spp. lying perpendicular to the bedding is highly significant because this implies that the shells are in situ (p 176-85). The base maps display the extent of several facies recognised for the Leintwardine Beds. Although the divisions are fairly arbitrary because these facies intergrade, their distinction serves to illustrate the major differences found. Similarly, the levels taken for the 3 LLB maps are general; there are no widespread marker horizons within the LLB which would provide a more definite correlation.

The faunal distribution maps illustrate the vertical and lateral changes in abundance of species, and their relation to the facies and to the overall palaeogeography (reflected by the facies distributions (p167,168)). The species occurrences, together with a review of the ecology, allowed deductions on the parameters influencing distribution to be made. Investigations of several of the facies described for the maps - for example, the basal conglomerates and the sheet-laminated siltstones - provided further evidence of the LLB environment.

The significance of the LLB fossil distributions within strata is discussed in Chapter 6 (p 363 ff). The rapidly-altering composition of the fossil assemblages in the calcareous siltstone facies was concluded to reflect an original mosaic distribution pattern (Petersen '13), with the shell layers resulting from periodic relatively small, current disturbances (p 363-75). Fluctuations in the prevalent species (all of which can be termed 'opportunistic' - Levinton '70) can be explained by local factors, such as differential larval success (Blegvad '25, '28). In contrast, shell transport in the sheet-laminated siltstone units, by analogy with modern examples (Reineck and Singh '73), may be much more extensive, up to several kilometres. But faunal mixing, involving introduction of different assemblages from other areas, has not occurred even in the latter facies (p 380 ff). Therefore, it is reasonable to conclude that faunal belts were wide.

Communities ?:

The concept of "brachiopod communities" in the LLB (Calef and Hancock '74) has been critically evaluated (p 385 ff). The limitations of bulk sampling in assessing the nature of the LLB fauna were mentioned previously (p 385). Calef and Hancock took very few samples, from geographically widely-spaced localities (including the atypical Sawdde Gorge section) to be representative of the fauna - they clearly did not appreciate the heterogeneity of the LLB assemblages. Their collections, which were of minor associations, were allocated to communities defined arbitrarily from "a continuous environmental spectrum". Communities were accorded environmental, depth, significance and were then used to interpret the Ludlow palaeogeography. Recurrent species associations do occur in assemblages of the LLB and these intergrade, but their significance is not the same as that of the major faunal assemblage which characterises the LLB of the shelf and which is fairly distinct from, not completely intergrading with, the Bringewood Beds fauna. The former

have ecological relevance, but the latter combines many smaller associations into an overall stratigraphical grouping.

The interpretation of the assemblages as related chiefly to depth is questioned. Application of the defined "brachiopod communities" to the LLB, because of the fluctuations in species dominance from bed to bed, results in an alternation of different communities on successive planes and even on separate parts of a single plane (p 385). Although rapid large changes in depth (several hundred metres - Hancock, Hurst and Fursich '74) from plane to plane are difficult to envisage, they are inconceivable within one bed. Factors influencing the distribution of brachiopods are discussed in Chapter 5 (p 233 ff). Many variables may be important, for example, turbulence and the nature of the substrate (Fig 5.32). There is often a general, but not consistent relationship with depth - such as the tendency for finer sediment to accumulate in deeper water - but depth itself is not critical.

Reliance upon brachiopods for environmental and stratigraphical interpretations (Calef and Hancock '74) is very limiting. Although brachiopods often form the dominant constituent of many shelf assemblages, it is frequently the associated groups which are of more value both stratigraphically and ecologically. For example, the beyrichiacean ostracode - A. gravi seams, and the appearance of neobeyrichiids indicate levels at the topmost LLB and ULB (p 396). In the graptolite - L. lata association of the basin, the former, and the sediments, show that the lingulid is not in the very shallow (eg. Lingula community) conditions often attributed to the genus (p176-85). Thus, it is much preferable to consider the whole fauna and evidence from the sediments for palaeoecological work.

Biostratigraphy:

The use of various fossils and groups for biostratigraphy is discussed in Chapter 6 (p394 ff.). Graptolites, as pelagic organisms, are potentially most useful. However, their scarcity on the shelf makes it necessary to rely partly on other groups for correlation. The LLB evidence supports the position of the LLB in the leintwardinensis zone and suggests that the incipiens zone occupies a lower position in the succession, as reported in other parts of Britain (eg. Rickards '67 - Lake District).

Ostracodes, which are vagile benthos, could be useful stratigraphical indicators. Non-palaeocope forms are poorly-known, but beyrichiaceans have recently been studied (Siveter '74). The neobeyrichiids have a short time-range and wide distribution, and hence are valuable for correlation. Diachronism in their appearance is unlikely in sequences where they are preceded by beyrichiacean-A. gravi assemblages (eg. Shelderton SR/2-), that is, where the ecological conditions were suitable. N. nutans appears at a slightly lower level than the N. lauensis - N. scissa - N. confluens fauna. N. lauensis was considered by Holland, Lawson and Walmsley ('63 p 126) as the diagnostic fossil for the ULB, although it has not been found at the stratotype. This species has therefore been taken to indicate the ULB in this study. Neobeyrichiids are most common in the "C" gravi Beds of the basinal areas, but are rare east of Ludlow. The fine correlation with the graptolite zone cannot be assessed because the two tend to be mutually exclusive.

Trilobites are also vagile benthos. C. puellaris and Encrinurus sp. were noted by Holland, Lawson and Walmsley ('63 p 117) to be fairly common only in the ULB. The calymenids were found to have distribution patterns which cut markedly across those of the common LLB brachiopods on the shelf, appearing earlier in the SE and extending progressively to the N and W with time. The main spread over the basinal region takes place in the ULB, but C. puellaris is not a consistent index for the ULB in the shelf inliers (p 399). Two encrinurid species (both long-ranging), E. stubblefieldi and E. rosensteinae, are found (frequently together) in the topmost LLB and ULB. Unlike the calymenids, the encrinurids appear slightly earlier (relative to the N. lauensis horizon) at the shelf edge in the topmost LLB (Shelderton SR/2-), and then extend greatly over both basinal and shelf areas in the ULB. This rapid increase in distribution soon after the first appearance means that the encrinurids are fairly good indicators for the ULB (p 398). Proetids show an acme at the top of the LLB in many areas of the shelf, but their long time-range prevents them being useful stratigraphically.

Brachiopods (except lingulids) are sessile epifaunal benthos. This makes them particularly susceptible to facies control. The faunal distribution maps illustrate the individual response of each species to the environment, even where several patterns are generally similar (eg. S. lunata and P. ludloviensis). Some complementary distributions

are seen: for instance, those of S. wilsoni and S. ornatella. Some environmental deductions can be drawn from the shell morphology and mode of life (Fig 5. 32). The significance of associations cannot be assessed without reference to the adjacent assemblages. For example, the M. nucula - S. lunata - P. ludloviensis fauna, typical of the Whitcliffe Beds, first occurs dominantly in assemblages of the LLB in the shelf inliers. But at this level it is found among strata with abundant S. wilsoni, I. orbicularis, and other species which decline by the LWB. Therefore, the conditions indicated by this association in the LLB are not the same as those of the Whitcliffe Beds, to which these three species appear to be very tolerant.

For biostratigraphical correlation, most reliance has therefore been placed upon the graptolites, with N. lauensis and Encrinurus spp. being taken to indicate the ULB. Brachiopod acmes - for example, S. ornatella (ULB), and D. navicula (LLB) - were considered to have some value for shelf correlation by Holland Lawson and Walmsley ('63). The faunal distribution maps show that the position of the acmes is not consistent relative to one another throughout the outcrop (p282 , p290). However, because faunal belts were wide, the degree of diachronism is often not high. Therefore, these acmes have a limited value for correlation, and diachronism of the biostratigraphical units can be concluded not to be serious.

The base of the LLB is marked by the widespread development of conglomeratic facies over the shelf, and by erosion surfaces in parts of the shelf edge region (Aymestrey - p 131 , and SE Wenlock Edge - Shergold and Shirley '68). In several shelf inliers, and at the northern end of Wenlock Edge (Dean borehole), there is evidence of hardground formation (Chapter 6 p 324). These deposits represent intermittent periods of non-deposition of sediment and submarine cementation. Borings in lithoclasts are similar to those attributed by Seilacher ('69) to acrothoracican barnacles, of the ichnogenus Trypanites (Bromley '72). Indications of stromatolites in one of the Tites Point specimens (Fig 6.1) suggest that conditions here were very shallow (Logan et al. '64). The distribution of the hardgrounds closely parallels the inner shelf in the palaeogeography deduced from the isopachyte map (Fig 1.4 p9). Pauses in sedimentation may span several thousands of years (Bromley '75); they serve to accentuate the faunal changes at the

UBB-LLB boundary on the shelf. Sub-aerial uplift and erosion need not be invoked to explain the conglomerates. The absence of the Aymestry Limestone in the SE (eg. May Hill - Lawson '55) may result from non-deposition and/or lateral facies changes. There is little evidence of derived fossils - except fragments of compound corals in WG-Jal (Fig6.5 p318) - to suggest that the Limestone has been eroded away here. Palynological results suggest that the lowest conglomerates at Wood Green may be pre-Leintwardinian (p 402) and there is evidence of instability in the top UBB (Aymestry Limestone) at Aymestrey (Lawson '73(a) - p 262), and Woodbury (p92). The onset of formation of the conglomerates is therefore diachronous, from top UBB to basal LLB times.

The slumps at Lyepole Bridge Quarry, which are low in the leintwardinensis zone (graptolites include S. leintwardinensis s.s. and ? S. incipiens or S. leintwardinensis cf. primus (RBR)) reflect the instability in the shelf edge region at this same level. The axis of down-warping around the Leintwardine to Aymestrey region, which is deduced from the facies and thickness changes (p6), is marked by the cutting and filling of submarine, shelf to basin channels in the Leintwardine area (Whitaker '62). The sequence at Aymestrey is interpreted to show another such channel (p131).

Phosphatised fragment beds and conglomerates are developed in several areas (eg. Shelderton, May Hill) at the level taken to mark the base of the ULB. (Similar horizons and bone-beds become more widespread at the ULB-LWB boundary - Holland, Lawson and Walmsley '63 Table II). The formation of phosphatic deposits suggests further pauses in sedimentation at this level, and probably quiet, shallow conditions (p332). As with the basal LLB conglomerates, there may be some diachronism of these deposits but it is unlikely to be significantly high.

The overall distribution of the fauna and the evidence of bioturbation can be used to interpret the LLB palaeogeography and environment. Benthonic forms, except the infaunal L. lata, and some shells in slumped beds (eg. Cwm Hely Dingle p154, Ring Hole p143), are absent from the sequences of laminated siltstones west of Aymestrey through most of the LLB. Bioturbation is similarly absent from these beds (Fig. 6.28). Conditions appear to have been inimical to most benthos therefore. Several factors could be controlling, such as

inadequate food supply, depth, or low dissolved oxygen level (Rhoads '75). The presence of indigenous L. lata in several areas (Fig 5.8) suggests the latter, because lingulids are commonly tolerant to environments of reduced oxygen content - for example, in beds interpreted to represent brackish-water environments in the Coal Measure cyclothems (Ferguson '63) and in Recent brackish-water environments (Paine '70). Restricted circulation in the basin can explain the faunal distributions. However, the shelf: basin thickness ratio of 1:8 (Holland and Lawson '63) and evidence of shelf edge instability support the concept that the basinal areas were relatively deep.

At the top of the LLB, there is a marked increase in diversity of the fauna on the shelf. Trilobites and ostracodes become important constituents of the fauna, especially in the shelf edge region. The chief change is the increase in the proportion of deposit-feeders with hard skeletons. In the basin, benthonic faunas spread westwards into the SW region (eg. Crickadarn Mill p 151, Ysgwydd Hwch p 149). Articulated benthonic bivalves (eg. F. amygdalina) show that the species inhabited these areas. Lithological changes to coarser, more thickly-bedded siltstones accompany the faunal transition. The westward extension of benthonic fossils into the part of the basin deduced to lie at the upper part of its axial palaeoslope (p 6) could be explained by a shallowing to bring these environments above a critical, limiting level. The facies change is consistent with this explanation. The general, shelf and basin, faunal changes could also relate to increased circulation raising the oxygen levels and the quantities of deposited and suspended food particles.

The major changes in the brachiopod fauna are illustrated by three of the sub-faunas recognised for the LLB (Chapter 6 p 392). A predominance of ribbed, pedically-attached forms in the inner shelf (eg. S. wilsoni, H. elegans - Association 1) passes laterally into an assemblage of unattached, small, smooth-shelled forms in the outer shelf (eg. D. navicula, S. ludloviensis - Association 2). At the LLB-ULB level, unattached or weakly-anchored forms not adapted for conditions of high sedimentation (eg. S. ornatella, L. depressa - Association 3) become prevalent over much of the shelf. The latter assemblage supports the proposal of reduced sedimentation and quiet conditions for the formation of phosphatic material at this level.

LLB environment and palaeogeography:

The LLB environment and palaeogeography may be summarised from the faunal and facies evidence, and their interpretation. The beginning of the period on the inner shelf is characterised by intermittent sedimentation and formation of hardgrounds, with periodic current disturbances and scouring producing the conglomerates. These strata pass up into the calcareous siltstone facies, in which the faunal distributions reflect the effects of current disturbances at intervals. Many of the plane assemblages appear to have been derived locally (eg. Wood Green - p372), but interbedded among these are well-sorted, large scale coquinas (eg. S. wilsoni beds at Perton p 351) and limestones with much shell debris that have undergone more extensive reworking.

The thickness and frequency of the basal conglomeratic beds decreases to the N and NW (ie. towards the outer shelf), and bored clasts are less common (eg. Woodbury). The UBB-LLB transition at Ludlow is conformable - a transitional faunal change in the top of the Aymestry Limestone followed by a facies change to siltier beds. The latter have frequent plane-assemblages of fossils, similar to those of the inner shelf. The middle part of the LLB at Ludlow has units of sheet-laminated siltstones. These (p 378) represent deposits from storm-generated or turbidity flow sediment transport across the shelf.

The dominance of suspension-feeders among the fossils, which are mostly brachiopods and dominated by ribbed, pedically-attached forms, indicates that shelf conditions were fairly turbulent. The progressive, inner to outer shelf changes in the LLB brachiopod fauna involve increased abundance of species which are less well-adapted for high energy environments, such as I. orbicularis, and then D. navicula and S. ludloviensis (Fig. 5.32). This reflects the decreasing strength of currents towards the distal shelf environments.

Instability in the shelf edge region around the UBB-LLB boundary is shown, for example, by the erosion surface at the top of the Aymestry Limestone (UBB) in the Main Quarry at Aymestrey (p125). Shelf-to-basin currents are indicated by the small scour channels at Aymestrey in the overlying LLB siltstones. The influence of periodic current disturbances, and instability in the shelf edge region resulted in NW slumping into the basin (eg. Lyepole Bridge - p132; Woodcock '76), and the cutting of shelf to basin, submarine channels (Whitaker '62; this study - p131).

Comparable SE slumping into the trough affects the sequences of Kerry and SW Clun Forest (Ring Hole p 143, Earp '38, '40, Woodcock '76). In the normal sequences of the basinal successions, the finely-laminated siltstones with their limited, pelagic faunas show that conditions of deposition in the basin were quiet.

At the top of the LLB, the sediments and fauna indicate a reduction in sedimentation and turbulence over much of the shelf, and development of suitable environments for benthos over a large part of the basin. Large-scale slumping has ceased by this level (Earp '38, Woodcock '76).

The allocation of absolute depths to the environment (as in Hancock Hurst and Fursich '74) will not be attempted. However, the concept of continuous regression through the Ludlow (Calef and Hancock '74) can be rejected for the shelf region. Hardground formation suggests shallow conditions, but stromatolites in the Brookend borehole conglomerates are the only evidence of conditions above wave base in the LLB. In contrast, the Aymestry Limestone (UBB), whichhas abundant compound and solitary corals suggesting shallow conditions and Kirkidium banks interpreted by Newall ('66) as forming at or above wave-base, at Aymestrey contained an alga which indicates depths of 30 m or less (Elliott '71, Lawson '73(a)). The overlying fine, thinly flaggy LLB siltstones with D. navicula must show deepening after this. Throughout the shelf, the replacement of the Aymestry Limestone by siltier beds in the LLB supports this conclusion. At the top of the LLB, shallowing of the environment seems likely; the formation of phosphatic material makes a depth estimate of less than 200 m a reasonable conclusion (Bromley '67). The cyclic pattern of transgression and regression of Phipps and Reeve ('67) appears appropriate to the LLB evidence.

It would be interesting to follow the succession to the west of Aymestrey. At Lyepole Bridge, the LLB with their slump units were estimated by Lawson ('73(a) - p 266) to be probably 90 m thick. The Bringewood Beds were not seen, but Lawson noted that their maximum thickness could only be 30 m here. The LLB at Aymestrey, which are cut by a channel, are only 20 m thick. It is possible that the Lyepole Bridge succession represents the continuation of this channel, and that the thick LLB have cut through the Bringewood Beds in a channel-fill (as at Leintwardine: Whitaker '62). Alternatively, the Bringewood Beds might be faulted out (Lawson '73(a)). Mapping in progress at Wigmore

(Whitaker) and Lingen (Holland) should help to elucidate the Lyepole Bridge succession.

Further work remains to be done on the correlation with other areas of Britain - the Lake District, and Dingle Peninsula. The palaeoecological comparison of the British successions with those of other areas of NW Europe - that is, between different facies realms - should elucidate the evolving palaeobiogeography of the upper Silurian.

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1.

D. navicula, Shelderton - χ^2 tests for similar distributions and for similar sample means.

Sample pair	Probability	Rejection (X) at 95% confidence level	μ_o	μ_e	Rejection if $\mu_o > 2\mu_e$
19 and 20	< 0.001	X	0.38	0.22	-
20 and 21	0.01-0.001	X	0.29	0.28	-
21 and 19	< 0.001	X	0.09	0.22	-

2.

Davia, Lamwell Dingle - Rank tests for similar distributions.

Samples	χ^2	n	Probability
16:13	9.21	4	0.1 - 0.05
16:14	18.05	4	0.01 - 0.001
16:15	4.53	4	0.5 - 0.3
16:20(SH/1-)	4.64	4	0.5 - 0.3

3.

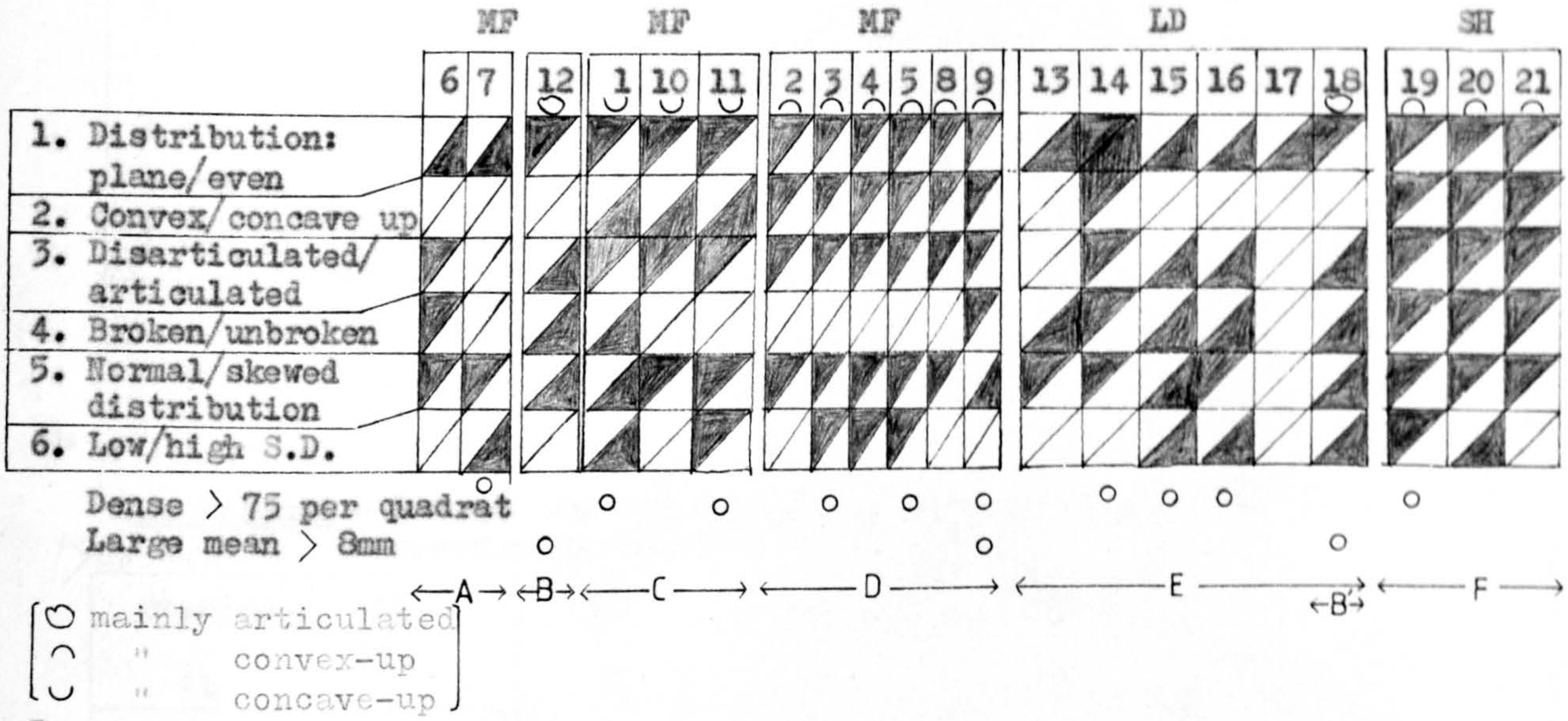
D. navicula, Ludlow - Samples from one population? Hypothesis rejected (X) if $\mu_o > 2\mu_e$

Samples	2	3	4	5
2		X	-	-
3	0.58 / 0.19		X	X
4	0.08 / 0.19	0.66 / 0.17		-
5	0.27 / 0.18	0.85 / 0.15	0.19 / 0.15	

μ_o / μ_e

4.

D. navicula: Criteria of relative current action (High/Low)



5.

S. wilsoni - Tests for similar distributions

Samples	χ^2	Distribution	S.D.	Mean	Significant difference (X)
7 and 10	0.5-0.3	-ve skew	High	Similar	-
8 and 12	0.5-0.3	Normal	"	"	-
7 and 8, 7 and 12	< 0.001-<0.001	Skew, normal	"	"	X,X
10 and 12, 10 and 8	" - "	" "	"	"	X,X

6.

S. wilsoni - Samples from one population?

Samples	μ_o Difference in means	μ_e Mean S.E.	Rejected (X) if $\mu_o > 2\mu_e$
7 and 8	0.43	0.29	-
8 and 10	0.01	0.31	-
10 and 12	0.16	0.31	-
8 and 11	3.22	0.25	X
8 and 9	2.78	0.23	X
9 and 11	6.00	0.20	X

7.

S. wilsoni - Rank tests for similar distribution, LH skewed graphs

Samples	χ^2	Rejected (X) at 95% confidence level
1 and 7	0.98 - 0.95	-
1 and 10	0.7 - 0.5	-
1 and 11	0.05 - 0.02	X

8.

S. wilsoni - Lateral variation: samples from one population?
Hypothesis rejected (X) if $\mu_o > 2\mu_e$

μ_o / μ_e

Samples	A1	A2	A3	Mean A
A1		X	X	-
A2	0.50 / 0.17		X	X
A3	0.50 / 0.17	1.00 / 0.15		X
Mean A	0.00 / 0.13	0.50 / 0.13	0.50 / 0.13	
	B1	B2	B3	Mean B
B1		X	X	X
B2	0.33 / 0.13		X	-
B3	0.66 / 0.17	0.33 / 0.16		X
Mean B	0.33 / 0.12	0.00 / 0.11	0.33 / 0.15	
	C1	C2	C3	Mean C
C1		X	-	-
C2	0.55 / 0.13		X	X
C3	0.24 / 0.13	0.79 / 0.15		X
Mean C	0.10 / 0.10	0.45 / 0.12	0.34 / 0.12	

9.

S. wilsoni - Vertical variation: samples from one population?
Hypothesis rejected (X) if $\mu_o > 2\mu_e$

Samples	μ_o	μ_e	Rejection(X)
A and B	0.88	0.10	X
B and C	1.09	0.09	X
C and A	0.21	0.09	X

10.

S. ornatella - Comparison of distribution profiles ("best fit" matches)

Comparison	Sample pair	Probability	Rejected (X) at 95% confidence level
2 normal distributions	8 and 9	0.3 - 0.2	-
Normal distributions	1 and 8	0.5 - 0.3	-
2 slight - ve skews	2 and 5	0.7 - 0.5	-
High:low S.D.	1 and 4	0.02 - 0.01	X
" "	1 and 3	0.7 - 0.5	-
2 bimodal	6 and 7	<0.001	X
2 low S.D.s	3 and 4	<0.001	X

11.

S. ornatella - Samples from one population?
Hypothesis rejected (X) if $\mu_o > 2\mu_e$

μ_o/μ_e Samples	1	2	3	4	5
1			X		
2	0.87 / 0.66		X	X	
3	2.43 / 0.55	1.56 / 0.62		X	X
4	0.93 / 0.49	1.80 / 0.57	3.36 / 0.45		
5	0.07 / 0.71	0.94 / 0.71	2.50 / 0.69	0.86 / 0.64	

12.

MF33 - χ^2 tests for 1:1 ratio of ∩ : ∪

Samples	∩	∪	χ^2	Samples	∩	∪	χ^2
1	44	57	0.2 - 0.1	8	115	5	<0.001
2	47	14	<0.001	9	19	4	0.01 - 0.001
3	50	19	<0.001	10	238	46	<0.001
4	90	36	<0.001	11	150	7	<0.001
5	110	54	<0.001	12	16	3	0.01 - 0.001
6	20	23	0.7 - 0.5	13	138	17	<0.001
7	46	11	<0.001	14	250	96	<0.001

13.

MF33 - Tests for random orientation (i.e. ∩ : ∪ = 1:1)

	D. navicula			Other disarticulated valves		
Samples	∩	∪	χ^2	∩	∪	χ^2
1	35	56	0.05 - 0.02	9	1	0.02 - 0.01
6	2	16	<0.001	18	7	0.05 - 0.02
4	26	26	1.0	64	10	<0.001

14.

MF33 - Tests for differential sorting of valves of I. orbicularis

	Isorthis PV:BV			∩ : ∪		
Samples	PV	BV	χ^2	Total ∩	Total ∪	χ^2
2	15	21	0.5 - 0.3	24	12	0.05 - 0.02
3	14	10	0.5 - 0.3	9	15	0.3 - 0.2
4	12	24	0.05 - 0.02	26	10	0.1 - 0.001
7	26	29	0.7 - 0.5	44	11	<0.001
8	74	39	<0.001	108	5	"
11	99	48	"	140	7	"

Vertical Faunal Variation: Relative densities of fossils
∩ : ∪ for disarticulated valves

W.G.

	1	2	3	4	5	6	7	8
No. of Fossils/Quadrat = ∝ (20 cm □)	65	54	37	80	60	76	94	24
Relative Density of Fossils (∝/FW10)	3.0	2.5	1.7	3.6	2.7	3.5	4.3	1.1
No. valves / ∩ : ∪								
D. navicula		18 / ∞			3 /			
I. orbicularis		23 / 1.3						
P. ludloviensis				28 / 2.5	16 /		41 / 7.2	21 / 1.6
S. lunata				13 /	17 / 47			
F. amygdalina								
Total disarticulated valves		41 / 3.1		41 / 1.9	36 / 4.1			

F.W.

	1	2	3	4	5	6	7	8	9	10
No. of Fossils/Quadrat = ∝ (20 cm □)	81	112	44	92	36	103	43	44	78	22
Relative Density of Fossils (∝/FW10)	3.7	5.1	2.0	4.2	1.6	4.7	2.0	2.0	3.5	1
No. valves / ∩ : ∪										
D. navicula		31 / 2.9				23 /				
I. orbicularis	42 / 1.6	11		20 /		11 /		13 /		
P. ludloviensis				14 /				15 /		
S. lunata										
F. amygdalina			29 / 28							
Total disarticulated valves		42 / 3.2		34 / 2.1		34 / 5.8		28 / 13		

Faunal Variation, Lateral

Frith Wood
Wood Green

% Fauna: First 50 Fossils Counted.

	Frith Wood						Wood Green					
	C (FW4)			D (FW7)			A (WG6)			B (WG7)		
	1	2	3	1	2	3	1	2	3	1	2	3
M. nucula		6	32		14	24	18	30	10	18	18	52
D. navicula	8											
H. elegans			6	26	18							12
I. orbicularis	40	24	14	18	6		8	20	24			
P. ludloviensis	28	64	46	20	28	4	2	2	14	82	38	34
S. lunata									12		16	
S. wilsoni			2	34	30	70	72	44	40			
F. amygdalina	24	6						4			16	
Other benthos					4	2					12	2

Calef and Hancock LLB Collections

Collection	Community	Species diversity at 60 indivs.	Mean community diversity at 60 indivs.	S.D. of community diversity at 60 indivs.	Species diversity at 100-200 indivs.
USK-1	S	15.3	8.8	3.4	7.2
USK-4	Sp	13.4	11.7	4.0	9.7
MH-3	..	16.8	..	..	..
MH-4	..	9.4	..	..	..
MH-8	..	12.5	..	..	..
LUD-2	1	14.0*	12.0	4.4	10.4
LUD-7	..	11.1	..	..	..
LUD-8	..	10.5	..	..	..
	average	12.9			

* 60 individuals not collected, ∴ rarefied.

Data from Calef and Hancock '74.

DAYIA.

		P	B	⌒	⌣	T
1.	SY/3	70	-	3	67	70
		P	B			T
2.	MF/F-D	67	-	53	14	67
		P	B			T
3.	MF/F-D	75	-	66	9	75
		P	B			T
4.	MF/F	65	-	49	16	65
		P	B			T
5.	MF/F-D	90	-	67	23	90
		P				
6.	MF/F-D	60				
		P				
7.	MF/F-C	105				
		P				
8.	MF/F-L	80				
		P				
9.	MF/F-M	60				
		P				
10.	MF/F-F	66				
		P	B			T
11.	MF/F-P	70	5	6	69	75
						T
12.	MF/F-B					70
						T
19.	SH			72	7	79
						T
20.	SH			51	5	56
						T
21.	SH			35	8	43

	P	B	T		P	B	T
11a.	5	1	6	11b.	65	4	69

ISORTHIS (+ SALOPINA)

			⌒	⌣	T				⌒	⌣	T				⌒	⌣	T
1.	SY/B-C	I60				1a.	BV	I	45	-	45	1b.	PV	I	15	-	15
		S40						S	16	1	17			S	19	4	23
											T						T
2.	MF/A-b	130				2a.	BV	I	14	-	14	2b.	PV	I	16	-	16
		S30						S	9	1	10			S	17	3	20
											T						T
3.	SY/B-D		29	1	30	3a.	BV		25	-	25	3b.	PV		4	1	5
					T						T						T
4.	MF/E		28	2	30	4a.	BV		4	-	4	4b.	PV		24	2	26
					T						T						T
5.	MF/E-W		82	8	90	5a.	BV		42	1	43	5b.	PV		40	7	47
											T						T
7.	MF/E-G					7a.	BV		1	-	1	7b.	PV		58	1	59
					T						T						T
8.	MF/E		38	2	40	8a.	BV		26	-	26	8b.	PV		12	2	14
					T						T						T
9.	WG/1-10		67	3	70	9a.	BV		19	3	22	9b.	PV		48	-	48
					T						T						T
10.	FW		35	5	40	10a.	BV		9	2	11	10b.	PV		26	3	29
					T						T						T
11.	FW		40	-	40	11a.	BV		9	-	9	11b.	PV		31	-	31
					T						T						T
12.	MF33		49	11	60	12a.	BV		23	9	32	12b.	PV		26	2	28
					T												
13.	MF/E		39	1	40												
					T												
14.	MF33		37	3	40												
					T						T						
15.	MF33		39	2	41	15a.	BV		8	-	8						
					T						T						
16.	MF33		67	3	70	16a.	BV		18	-	18						

21. MF33 FAUNAL DATA:

		D. navicula		I. orbicularis		S. wilsoni	F. amygdalina		M. nucula	S. ludlovensis		Other brachiopods		gastropods	Cyrtoceras sp.	Other bivalves	TOTAL	min. ¶	max. ¶
		PV	BV	PV	BV		R	L		PV	BV	PV	BV						
1	C	35		6	2		1										44		
	C	56			1												57		
	T	91		6	3		1		2									100	103
2	C	22		15	9			1									47		
	C	2			12												14		
	T	24		15	21			1										46	61
3	C	32		6	3		6	2					1				50		
	C	3		8	7							1					19		
	T	35		14	10	6	6	2				1	1	4				66	79
4	C	26		12	14		1			16	10	9	2				90		
	C	26			10												36		
	T	52		12	24	2	1			16	10	9	2					104	128
5	C	103		3	2							2					110		
	C	50			4												54		
	T	153		3	6				5			2						166	169
6	C	2		10	2		1	4				1					20		
	C	16		1	5							1					23		
	T	18		11	7		1	4				2						35	43
7	C	1		24	20		1										46		
	C			2	9												11		
	T	1		26	29		1											31	57
8	C	7		70	38												115		
	C			4	1												5		
	T	7		74	39													82	121
9	C	3			1		10	5									19		
	C				4												4		
	T	3			5	2	10	5	2									22	27
10	C	238															238		
	C	46															46		
	T	284																284	284
11	C	10		92	48												150		
	C			7													7		
	T	10		99	48	2												111	159
12	C			11	4							1					16		
	C			1	2												3		
	T			12	6	62			3			1						78	84
13	C	136		1													138		
	C	16										1					17		
	T	152		1					12			1		26	9	1		202	202
14	C	246								3	1						250		
	C	96															96		
	T	342								3	1			3				349	349

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