The Caradoc faunal associations of the area between Bala and Dinas Mawddwy, north Wales

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Contents

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Synopsis

A systematic scheme of sampling in key sections is used to provide a quantitative outline of the distribution of the total fauna in the greater part of the structurally less-disturbed, fossiliferous portion of the Lower Bala Group (and some equivalent deposits) south of Bala Lake. Sampling, data collecting and analysis techniques are discussed and derived quantitative parameters are used to describe six interrelated, brachiopod-dominated associations.

Representatives of five brachiopod, four trilobite and six molluscan genera are recorded in the group for the first time. Four new brachiopod species and a subspecies are described. These are *Paracraniops glaber* sp. nov., *Palaeostrophomena canalis* sp. nov., *Bimuria dyfiensis* sp. nov., *Protozyga musculosa* sp. nov. and *Sericoidea abdita complicata* subsp. nov.; *Parastrophinella brenchleyi* sp. nov. is also described from contemporary deposits in the NE Berwyns.

The composition of faunal associations from the Lower Bala Group is compared with the structure and characteristics of named contemporary associations in adjacent areas.

Introduction

The researches presented here are linked to a reappraisal of the geology of the Llanuwchllyn to Llanymawddwy area presented elsewhere (Lockley 1980). The present paper is principally concerned with the quantitative description of faunal assemblages and associations found in the fossiliferous upper part of the lower to middle Caradoc succession between Bala and Dinas Mawddwy. To this end a series of suitable sections were chosen for detailed examination, at more or less regular intervals along a 20 km portion of the strike belt shown in Fig. 1 (inset). Laterally spaced sample sites provide a framework in which to examine the relationships between faunal distribution patterns and vertical and lateral facies changes.

At each of the twelve localities shown in Fig. 1 a series of from 3 to 84 samples were collected at regular, measured vertical intervals. Horizons from which samples were derived are informally referred to – in conjunction with sample numbers – as 'beds'; e.g. 'bed H1' (Fig. 4) refers to the horizon from which the material of sample H1 was derived.

Where exposure permitted, including key localities such as type sections, beds were extensively sampled; at remoter, less well-exposed sites fewer samples were recovered. In all, 250 collections, totalling 1·5 metric tons of rock, were made from the twelve named sections and subjected to thorough analysis employing the methods described below. All identifiable material was assigned to its respective taxon and counted; in all some 25 000 individual specimens were examined, in addition to numerous fragmentary remains. The resultant tabulated data are presented here as the basis from which further extrapolation and inference is derived. A limited quantity of biometric data is presented in conjunction with the taxonomic descriptions; additional information is given in my unpublished thesis (Lockley 1977). Regional cleavage caused the deformation of a large proportion of the material, prevented some accurate measurement and in some cases even identification.

In the course of mapping the Llanuwchllyn to Llanymawddwy area (Lockley 1980) a few important specimens were recovered from various localities other than those shown in Fig. 1; these, together with new material from the main sections, are described in the taxonomic part of this paper. Sample numbers not prefixed with a consonant (or consonants) correspond to map locality numbers on the author's field maps (1 : 10 000) and generally refer to isolated outcrops or poorly exposed parts of minor sections; these numbers fall between 1 and 1162, and in certain cases have a suffix (e.g. A or B).

Full taxonomic descriptions are confined to the new Brachiopoda from this region and to a single new form from the Berwyns. Other figured material, including representatives of the Trilobita and Mollusca, is distinguished either by being previously unknown or undescribed in the Caradoc succession of this area or in having a particular stratigraphical significance (e.g. a considerably extended stratigraphical range). Numbers BB92200–BB92264 are used for the Brachiopoda, It.14294–It.14309 for the Trilobita, PL 4440–PL 4451 for the Bivalvia and PG 5022, C 81324, E 53698 and E 67750 for four other miscellaneous specimens; all other material is housed in the National Museum of Wales under accession number NMW 79.5G.

Conclusions are confined to correlative comparisons between the faunal assemblages and associations described here and the known contemporary faunas and named communities elsewhere. Brief comments on the definition of contemporary faunal associations (and communities) are also included where appropriate.

Stratigraphy

The stratigraphy of the Lower Bala Group was outlined by Bassett *et al.* (1966), who recognized four formations within the group in the Bala area (Fig. 1). Recognition, and indeed definition, of these formations is considerably facilitated by the occurrence of distinctive ash members within the succession. In contrast, however, the monotony of the entirely argillaceous Hengae Group described by Pugh (1923, 1928) in the Corris and Dinas Mawddwy areas is broken only by the black graptolitic shales of the Nod Glas Formation which represent the uppermost 20 m of the group.

Although Pugh (1929) attempted detailed correlations between the Bala and Dinas successions in the intervening Llanuwchllyn to Llanymawddwy area, his efforts have recently been shown to be at best imprecise and at worst quite inaccurate (Lockley 1977, 1980). Stratigraphical revisions of the succession in the Llanuwchllyn to Llanymawddwy area have not only been

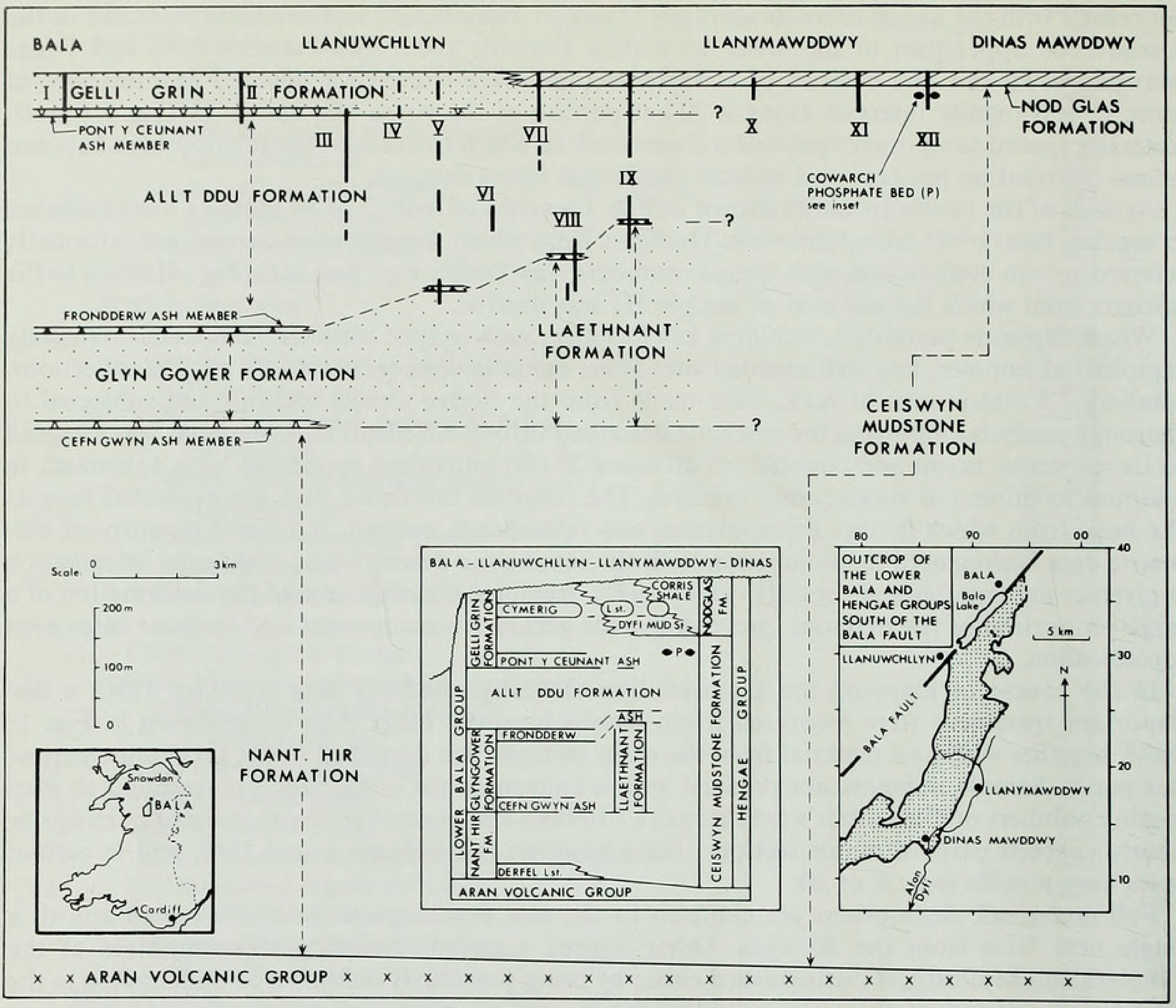


Fig. 1 Scale representation of sampled sections (solid vertical bars I–XII) in the fossiliferous upper part of the Lower Bala and Hengae Groups between Bala and Dinas Mawddwy. I, Gelli-grîn type section. II, Maes-Meillion section. III, Craig y Gath. IV, Lledwyn Bach. V, Ty nant. VI, Beudy Isaf. VII, Nant Tan y Bwlch. VIII, Afon Twrch. IX, Craig Ty nant section at Rhiw March. X, Pistyll Gwyn. XI, Y Ceunant. XII, Aber Cowarch. Insets (left, centre and right) respectively show regional setting, local stratigraphy and local geographical and geological setting.

effected by the discovery of outcrops representing distal extensions of the Frondderw Ash but have also been considerably facilitated by detailed examination of the faunal succession in sections throughout the area. The stratigraphical revisions (Lockley 1980) are summarized in Fig. 1 (inset).

The Llaethnant Formation is proposed as a name for a thick group of alternating mudstones and siltstones which, in addition to representing a different facies from the stratigraphically thinner Glyn Gower Formation, is not necessarily the chronostratigraphical equivalent of that unit.

The base of the Allt Ddu Formation, defined, following Bassett *et al.* (1966) as the base of the Frondderw Ash member, is accurately located as far south as Rhiw March in the Dyfi Valley. Similarly the base of the Gelli-grîn Formation is accurately located as far south as this locality. The greater part of the Nod Glas Formation (between Aber Cowarch and Rhiw March) is shown to be equivalent to the upper part of the Gelli-grîn Formation and to include the distal portions of the Cymerig Limestone member which becomes discontinuous towards the south.

Distinctive lateral changes in the Nod Glas facies in the area in question have resulted in the subdivision of the formation into two members which both represent facies of a diachronous nature. The Dyfi Mudstone is dominated by a distinctive *Sericoidea*-dominated fauna and the Corris Shale is characterized by being generally unfossiliferous except for local graptolitic assemblages.

Aims, sampling procedures and data analysis

The primary aim of this study has been to name and describe quantitatively the Caradoc faunal associations and assemblages found between Bala and Dinas Mawddwy, and to compare these with contemporary associations outlined by Williams (1973) and described by Pickerill & Brenchley (1979). Thorough sampling provides a census of the fossil faunas, whether representative of various biocoenoses or thanatocoenoses, which furnishes data from which recurrent combinations of taxa may be noted. Where similar combinations of taxa show chronological (stratigraphical) and geographical persistence in like facies (which lack current-produced sedimentary structures) they are referred to as 'associations' and considered to resemble disturbed neighbourhood assemblages (*sensu* Scott 1974) or *in situ* communities. Such 'associations' predominate in the area considered here. Where clearly transported shelly deposits are noted they are categorized as 'assemblages'.

Collecting techniques

Bulk samples of rock (mean weight 6 kg) were collected at vertical intervals varying from 0·5 m to > 3 m, depending on the extent of the section and the faunal content. It was found to become increasingly impracticable to collect large, closely-spaced samples as the succession got progressively less fossiliferous, as in some parts at lower horizons of the Caradoc of this area, so discretion in the choice of sample interval was exercised. However, in general it was necessary to collect a larger sample in poorly fossiliferous rocks to recover a representative number of specimens. In the six most thoroughly sampled sections (i.e. numbers I, II, III, VII, VIII and IX of Fig. 1) a mean sample interval of 2·75 m was employed for a total of over 500 m of section. Locally, as in the perfectly exposed fossiliferous upper 135 m of the Rhiw March section (IX), a smaller mean interval was employed, in this case 1·75 m.

To eliminate preferential collecting biases all samples were 'broken up' on a rock crushing machine in such a way as to ensure that all the fossils or fossil fragments were retained for identification purposes. All rock fragments were reduced to a size of 1–2 cm^3 before being discarded if unfossiliferous. With the crushing machine (a converted fly press) it was easy to reduce fossiliferous rocks to a series of chips only fractionally larger than the individual fossils themselves which, in this case, generally approximated to the above chip size. All extracted identifiable specimens were then examined under a binocular microscope and counted, totals for each taxon being considered to represent random samples of residual fossil species populations.

Faunal densities

Essentially only two types of faunal density may be calculated, density per unit volume of rock or density per unit area of bedding plane. Neither method is entirely adequate for the analysis of more than a limited variety of fossiliferous lithologies. Volumetric densities are more suited for the expression of faunal densities in homogeneous (or isotropic), poorly-bedded strata, whereas areal densities better describe the density of fossils on bedding planes in strata where the rock fabric is essentially anisotropic. Both methods are size dependent; i.e. the mean size of the fossils controls the mean number of specimens per unit area. The calculation of areal and volumetric densities produces more accurate results when applied to relatively low density assemblages and associations; it becomes more difficult to derive accurate measurements from high-density deposits such as shell beds. The practical problems of accurate counting increase with the density of specimens in the rock.

Not only are contemporary sections of varying lithology likely to require different methods of density measurement, but within the same section it may be necessary to apply alternative methods of density evaluation at successive horizons. In the present study it was primarily volumetric densities which were calculated, although a few areal density measurements were obtained from well-defined bedding planes (Fig. 2). The volumetric densities calculated for the two sections shown in Fig. 2 are a useful guide to the faunal content (i.e. density of fossils) in the sequence at successive horizons. For example, the 'faunal depletion' zone described by Bassett *et al.* (1966 : 236) is graphically illustrated and shows a marked contrast to the fossiliferous horizons of the overlying Gelli-grîn Formation, which include the dense accumulation of small *Sericoidea* valves indicated.

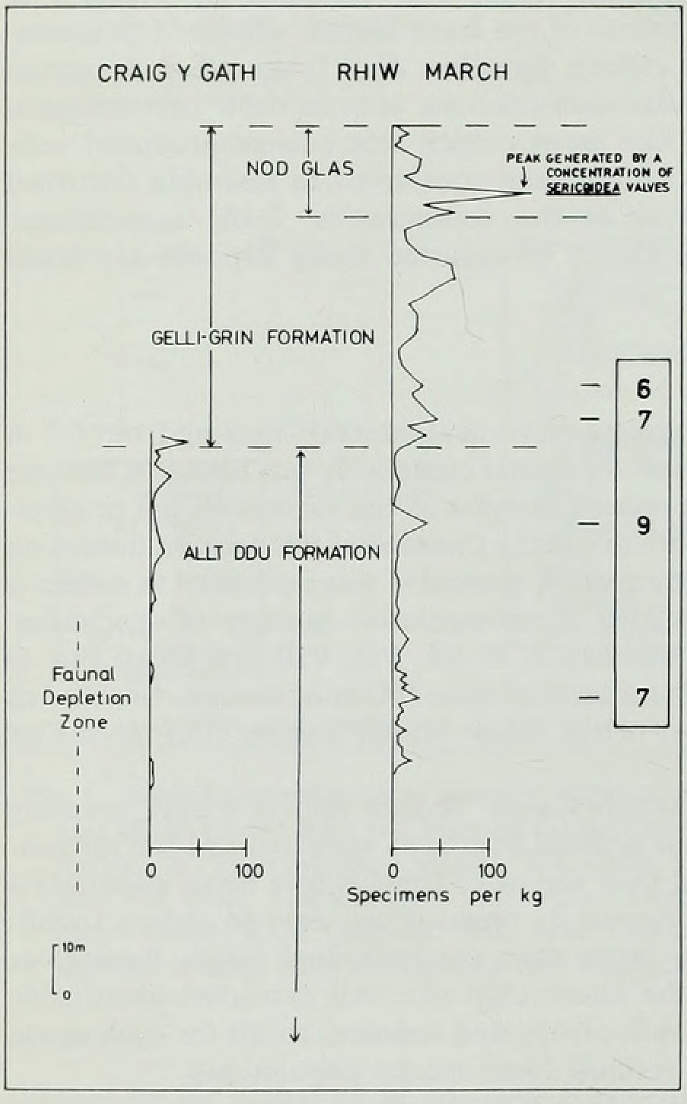


Fig. 2 Density of fossils per kg in the Craig y Gath and Rhiw March sections. Box (right) contains counts of specimens per 10 cm² on bedding planes in the latter section.

The use of volumetric density measurements in this study was preferred not only because of the disposition of fossils in the rock (i.e. generally scattered throughout rather than concentrated on easily sampled bedding planes) but also because of the strong regional cleavage inclined at a high angle to bedding, which almost invariably has the effect of breaking up bedding planes to the extent that a complete sample of more than 100 cm² is hard to obtain; the mean area of the four bedding surface samples shown in Fig. 2 is only 25 cm². The single most significant effect of cleavage on sampling procedure in the area under study is that rock splits so as to produce a sample representing a vertical range of strata extending at least 15 cm above and below any given horizon. In effect the vertical range of a sample approximates to 0·3 m.

Volumetric and areal density measurements may be compared and shown to have consistent relationships. Theoretical considerations and empirical observations support the validity of relating the two methods of evaluation. It is easily shown that 1 kg of rock (400 cm³ at a density of 2·5 g/cm^3), if broken into cubic chips between 2 cm^3 and 1 cm^3, will expose a surface area of between 600 cm^2 and 1200 cm^2 of which one third of the area (200–400 cm^2) will represent surface area in the horizontal (bedding) plane. Empirical observations by the author and Dr J. M. Hurst (personal communication 1977) have consistently shown that, when measuring the surface area of exposed bedding plane during the 'breaking up' of weighed samples, about 400 cm^2 of fresh surface is exposed for each kilogram of processed rock. When processing homogeneous, poorly-bedded lithologies it is generally found that the rock can be reduced to a smaller chip size thereby exposing up to double the surface area. For example, Hurst & Hewitt (1977 : 154) equated 2500 cm^2 with a 3·5 kg sample (i.e. > 700 cm^2 per kg).

Although faunal density is a useful parameter which aids in the description of fossiliferous successions, values should be used with caution; for comparative purposes, only like or similar facies should be compared. It should also be noted that fossil remains at any given horizon not only represent the remains of the 'standing crop' or the living (biological) populations which inhabited that surface but also represent dead assemblages representing contemporary and earlier generations. However, since palaeoecologists can rarely distinguish between these categories effectively, density estimates refer simply to fossils in the rock and are not in any way precisely indicative of original population structures.

Identification and counting

All the fossils extracted from the rock by the 'crushing' process were identified and counted. The counting procedures outlined below are aimed at assessing the number of individual organisms in any sample. Different counting methods are required for the various fossil groups under consideration and produce varying degrees of accuracy. However, consistent methods are used for counting all representatives of any given group.

The Brachiopoda represent the most diverse and abundantly represented phylum encountered in this study. The number of individuals (N) per sample was estimated using the formula $N = A + \frac{1}{2}I + P$ (if $P > B$) or $A + \frac{1}{2}I + B$ (if $B > P$), where A, P, B and I represent the number of articulated pairs of valves, pedicle valves, brachial valves and indeterminate valves, respectively. The same method (with right and left being substituted for pedicle and brachial) was used to count the Bivalvia. This method has been used by other workers including Hurst (1975) and Watkins (1979). The numbers of individual gastropods, cephalopods, macheridians, tentaculitids and graptolites were counted singly.

Estimates of individual numbers in the five above-mentioned groups are far more accurate than for the other groups considered here. In assessing numbers of bryozoa it was assumed that a single complete colony could be regarded as an individual 'unit'. Since fragmentary remains do not generally outnumber complete or relatively complete specimens they too were regarded as each representative of a complete individual colony. Bryozoans were therefore also counted on a one to one basis; a significant overestimate of the abundance of colonies is considered no more probable than the likelihood of biased quantification in assessment of the numbers of other groups also to some extent represented by fragmentary remains.

The number of individuals represented by a collection of arthropod fossils is problematical since individuals may shed their exoskeleton many times during ontogeny (ecdysis). Ostracods almost invariably moult seven times before their ontogeny culminates in the eighth, maturation moult. Similar ontogenetic patterns are recorded in modern and fossil ostracods (Anderson 1964). In contrast, however, existing evidence on the ontogeny of various trilobite groups suggests considerable variation in the number of moults produced, for example between representatives of the Agnostina (Hunt 1967) and the Olenellinae (Raw 1927) or the Olenidae (Palmer 1957, Cisne 1973). Estimates of the number of instars produced during ontogeny range from 9 in the case of the agnostids to about 29 for the olenellids and olenids, with the majority considered representative of the adult (holaspid) stage. Variations in trilobite and ostracod moult patterns are reviewed in greater detail elsewhere (Lockley 1977).

A consideration of arthropod ecdysis favours the conclusion that a given number of trilobite or ostracod exoskeletons in any fossil assemblage is likely to represent fewer individual organisms.

For example, an ostracod could theoretically produce up to eight pairs of valves (albeit of differing sizes) whilst a trilobite could produce many exoskeletal moults, with up to 50% representing adult instars showing little or no significant size differences. With our present incomplete understanding of trilobile ecdysis, in addition to known variation amongst groups and complicating factors such as sexual dimorphism and fragmentation associated with ecdysis, any correction factor used to avoid overestimation of numbers is highly arbitrary. Nevertheless, various authors have estimated numbers of trilobites either without using any correction factor (e.g. Bayer 1967, Hurst 1975) or by dividing a total number of exoskeleton remains by a correction factor such as 10 (e.g. Pickerill 1974). This later example echoes the suggestion of Harrington *et al.* (1959 : 111) that less than 10% of trilobite remains are likely to belong to dead individuals. Either method tends to produce estimates approaching theoretical extreme values.

In this study correction factors of 8 and 4 were used for the Ostracoda and Trilobita respectively. Since all ostracod valves were counted without making a distinction between left and right, it was assumed that, ignoring the first instar (the egg), an individual could be represented by between 0 and 16 valves. A correction factor of 8 was therefore chosen as a mean estimate between theoretical minima and maxima. Similarly, it was assumed that if none of the trilobites encountered in this study were represented by more than eight holaspid instars then a mean correction factor would approximate to four. Corrected counts were therefore derived by estimating one individual for every four pygidia or cephala depending on which fragment was most numerous. Throughout the study fragments of pygidia or cephala for all species were generally found to be complete and representative of the holaspid stage. It could therefore be argued that the absence of a complete series of instars would call for a relatively low correction factor (i.e. less than 10) to avoid excessive underestimation. However, since the correction factors are acknowledged as arbitrary it is emphasized that the use of a correction constant does not obscure the original data.

In this study most of the crinoid remains recovered were fragmentary; it was therefore impossible to assess a representative number of individuals. Counts made of all ossicles and stem fragments are presented in the data tables where the presence of crinoid material is otherwise indicated simply by the addition of one to the total of individuals per sample.

Data synthesis and presentation

Having assessed the number of individuals in each taxon, totals for each sample were calculated; these totals accompany counts for each taxon and are presented in a series of tables which each represent one of the sampled sections.

The taxonomic level of classification employed in these tables, although variable, is essentially specific. In all but a few cases the generic names of Brachiopoda and Trilobita refer unequivocally to members of single-species populations as defined by Williams (1963) and Whittington (1962–68). Categories which do not necessarily represent only a single species population are as follows: Inarticulata, dalmanellid indet., Stroph. indet. and Trilobita indet. The remaining fauna is classified into the following series of generic or suprageneric groups: Mollusca or Bivalvia, Gastropoda (or *Sinuites* and *Cyclonema*), Cephalopoda, Macheridia, Monoplacophora, Tentaculites, Ostracoda (or *Tallinnella* and *Primitia*), Bryozoa indet. (or ramose bryozoa, '*Prasopora*' and cateniform bryozoa) and Crinoidea. These classifications generally represent one morphotype or morphospecies, although in certain cases categories such as Mollusca are used either to group minimal numbers of representatives of different molluscan taxa or to indicate uncertainty about the taxonomic affinities of particular specimens.

Where known species or genera are grouped within a broader classification (e.g. the Bivalvia, in Fig. 8, p. 179, are represented by *Modiolopsis*, *Cuneamya*, *Cyrtodonta* and others), full details are given at the appropriate point in the text.

All tabulated figures refer to original counts of specimens except in the case of the trilobites where numbers represent 25% of the maximum number of either pygidia or cephala following the rationalizations given above. Although ostracod numbers are assessed by a similar arbitrary method the original counts of valves are given (in brackets). Similarly, for Crinoidea counts of ossicles (in brackets) and stems [in square brackets] are also presented.

The totals of individuals per sample are tabulated and used as a basis for estimating the relative abundance (%) of the taxa at each horizon. Graphic representations of these distributions are presented in Figs 5 (p. 177), 11 (p. 182) and 16 (p. 189) where the percentage of taxa from all samples with over 20 individuals is plotted; those with less than 50 individuals are indicated by a dot to the left of the columns. A sample with at least 50 individuals is considered to reflect the composition (%) of the fauna at a given horizon adequately (Watkins 1975), whilst samples with 20-50 individuals, which characterize many less fossiliferous horizons, are invariably found to give consistent percentage values when compared with larger (>50) samples. Although arbitrarily chosen, these minimum sample size figures ensure at least a consistent and minimum level of statistical constraint on data used for further extrapolation.

The size (weight) of each sample is indicated on most tables and can be used to assess faunal densities.

The total number of taxa in any sample is used as an estimate of the faunal diversity (or species richness) at any horizon. The diversity values presented here cannot necessarily be calculated from the tables since, in certain cases, the suprageneric taxonomic categories represent two or more taxa. In addition to the gross species richness (taxa per sample) presented here corrected, size-standardized diversity graphs are also given using the Margalef (1958) method and the Sanders (1968) rarefaction technique.

Trace fossils

Trace fossils in the Bala to Dinas Caradoc succession are neither common nor varied; for this reason they are not described in detail. However, a few examples are noted (Lockley 1977, 1980); Pickerill (1977) has outlined contemporary Caradoc trace faunas from the Berwyn region.

The faunal succession

The sections (numbered I–XII according to geographical location in Fig. 1, p. 168) are described here in a different sequence based on relative stratigraphical position. The description of these twelve sections is prefaced by the presentation of some additional information on the faunal composition of the Derfel Limestone, the basal member of the Lower Bala Group.

The Derfel Limestone

A large (10 kg) sample from the fossiliferous shelly shales representative of the Derfel Limestone at the type locality (SH 850395) was subjected to routine processing and analysis, to compare the composition of the fauna with that found in the younger Gelli-grîn Formation. Since Williams (1973) referred faunas from both stratigraphical levels to the *Nicolella* association, after having described the older fauna as a *Nicolella–Kullervo–Palaeostrophomena* association (Williams *in* Whittington & Williams 1955), both faunas were similarly analysed to establish points of comparison. The sample yielded specimens representative of at least 28 taxa, which are listed below in ranked order of abundance, with corrected numbers of individuals in brackets. Ramose bryozoans (35), *Dolerorthis* (28), *Platystrophia* (15), *Anisopleurella** (13), *Oxoplecia* (10), *Nicolella* (9), *Salopia* (9), Plectambonitacea indet. including *Sericoidea* and three other* listed genera (9), dendroid graptolite (9), *Onniella* (6), *Leptestiina** (4), prasoporid (4). *Howellites*, *Kullervo*, *Eoplectodonta**, *Leptaena*, *Deacybele* ? sp., *Broeggerolithus* (all 2). ? *Lingulella*, *Palaeostrophomena*, *Cyrtonotella*, Brachiopoda indet., *Platylichas*, Ostracoda, Macheridia, Crinoidea, Cystoidea, spicules (all 1). A total of 173 individuals is estimated from the above list.

Cyphoproetus is recorded in the Ordovician of Wales for the first time; similarly the occurrence of *Lingulella* is the first record of a representative of the Inarticulata in this member (Lockley 1980). The relative abundance of the brachiopods *Dolerorthis* and *Nicolella* compare with abundances noted in parts of the Gelli-grîn Formation, whilst the occurrence of *Platystrophia*, *Anisopleurella*, *Oxoplecia*, *Salopia*, *Onniella*, *Leptestiina*, *Sericoidea*, *Eoplectodonta* and *Palaeostrophomena* at both horizons is also noteworthy.

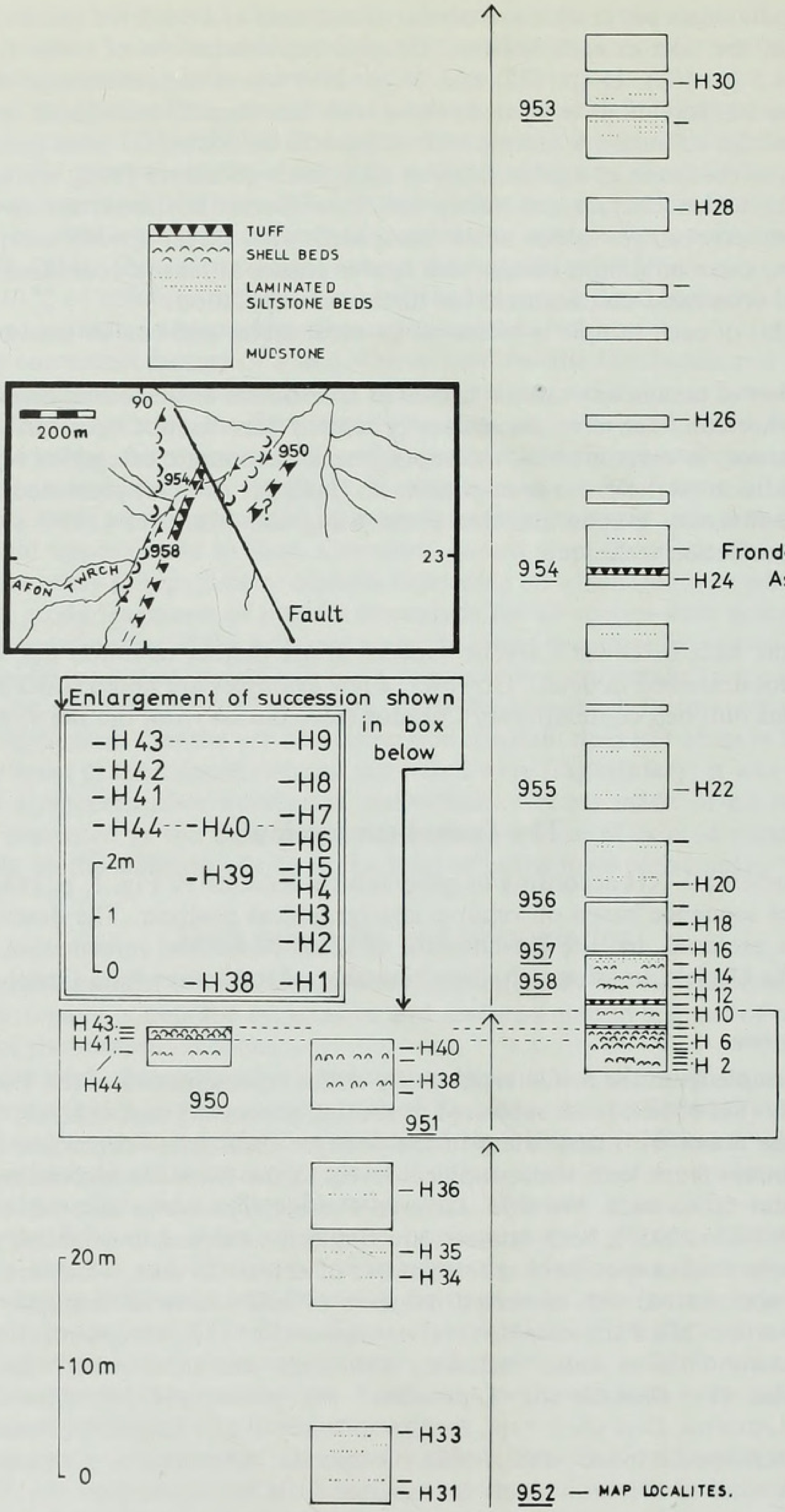


Fig. 3 Sample points in the Afon Twrch section with inset map showing outcrop of sampled beds associated with shell beds and the Frondderw Ash in the upper reaches of Afon Twrch.

The Nant Hir Mudstones, Glyn Gower Siltstones and equivalent deposits

Although Bassett *et al.* (1966 : 229–230) listed faunas from various horizons in the Nant Hir Formation, no shelly fauna is known from the Nant Hir or the equivalent part of the Ceiswyn Mudstone at any locality south of northing 315. Similarly a large part of the overlying Glyn Gower Formation and equivalent beds to the south are only sparsely fossiliferous, with a low diversity fauna typified by the forms listed by Bassett *et al.* (1966 : 231). For this reason ambitious sampling schemes were not applied to sections through this part of the succession. However, near the headwaters of Afon Twrch an important series of fossiliferous beds is exposed in a section which contains a newly-discovered outcrop of the Frondderw Ash Member. The fauna, although dominated by *Heterorthis* and *Sowerbyella*, also contains elements previously considered as representative of the *Nicolella* association.

The Afon Twrch section and equivalent beds

The horizons sampled in this section are representative of the upper part of the Llaethnant Siltstone Formation (equivalent to the upper part of the Glyn Gower Formation) and the lower part of the Allt-Ddu Formation. Figs 3, 4 and 5 show respectively the field location and sample grid, faunal distribution and relative abundance patterns relating to this part of the succession. A series of 44 samples (total weight 232 kg) was collected from riverside exposures between map locs 950 (grid ref. 9133 2330) and 958 (9101 2305). However, in this section faulting (Lockley 1977, 1980) has caused duplication of part of the faunal succession (Figs 3, 5). Outcrops of *Heterorthis*-dominated shell beds are found in the repeated parts of the sequence and, since both outcrops are sampled at close vertical intervals, samples representative of beds thought to be precisely equivalent are bracketed together in Fig. 4.

There is a dual significance in the distribution of taxa recorded in the Twrch section. Firstly, the occurrence of *Heterorthis* (in abundance) at an horizon some 40 m below the Frondderw Member contrasts with the occurrence, elsewhere to the north, of *Heterorthis* assemblages in the Lower part of the Allt-Ddu Formation (see Bassett *et al.* 1966 : 234 and Fig. 6, p. 178).

A second noteworthy aspect of the distributions shown here is the occurrence of certain genera hitherto thought to be confined to the Gelli-grîn Formation and the Derfel Limestone Member. These include *Orthisocrania*, *Nicolella*, *Onniella*, *Salopia* and *Chasmops*. *Dolerorthis* is also recorded; although known from the Upper Allt Ddu Formation it is otherwise confined to the Derfel Limestone and the Gelli-grîn Formation. All these forms are characteristic of the *Nicolella* association and although, with the exception of *Onniella*, they are rare at this horizon, their occurrence can be considered indicative of the sustained establishment of this type of association, in this general area, through the Lower Caradoc. With the exception of *Dolerorthis* and *Chasmops*, representatives of the above-mentioned genera are figured in the taxonomic section.

When traced southwards to a gully on the north side of the Dyfi Valley (map and sample loc. 202, grid ref. 896217) beds equivalent to the Frondderw Member and the underlying shell beds are known (Lockley 1977, 1980). Fig. 5, which outlines the faunal distributions recorded at horizons in this part of the succession, indicates a significant lateral change in the composition of the shell bed beneath the Frondderw Ash. There is no evidence for the presence of *Heterorthis* and only the occurrence of *Onniella*, *Bicuspina* and the association of a minor ash are comparable with characteristics of the Twrch section. Since these shell beds are associated with thin parallel laminated, storm-generated siltstone sheets they are considered to represent transported material.

It is of particular interest to note that *Sowerbyella* and *Heterorthis* are almost entirely mutually exclusive though the two forms occur in abundance in beds separated by only a fraction of a metre (Fig. 5). J. M. Hurst (personal communication, 1978) has noted some degree of segregation between these two genera in the Alternata Limestone of Shropshire. It is possible that such patterns represent a differential response to the effects of transportation. Both forms have atrophied pedicles and would have therefore been relatively susceptible to disturbance by currents.

The Beudy Isaf and Ty-nant sections

Unlike the relatively remote Twrch and Dyfi sections, the Beudy Isaf and Ty-nant sections are

	wt	N	Inarticulata	Nicolella	Dolerorthis	Dinorthis	dalmanellid, indet	Howellites	Onniella	Reuschella	Heterorthis	Salopia	Bicuspina	Sowerbyella	Sericoidea	Leptaena	Macrocoelia	Brongniartella	isotelinid	Broeggerolithus	Gastropoda	Bivalvia	Cephalopoda	prasoporid	ramose bryozoa	Tallinnella		Crinoidea		
H 30	6	511	—	—	—	—	—	149	9	2	—	—	7	336	—	1	1	—	—	1	—	—	1	1	2	—	—	1	(35)	—
H 29	10	70	2	—	—	—	—	—	—	35	3	—	—	—	—	—	—	2	—	2	—	—	1	—	23	1	(7)	1	(234)	[5]
H 28	6	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H 27	4	43	2	—	—	—	—	10	—	3	—	—	—	21	—	—	—	1	—	1	—	—	—	—	3	1	(6)	1	(20)	[3]
H 26	8	8	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	2	1	(2)	1	(27)	—
H 25	5	13	—	—	—	—	—	2	—	3	—	—	—	—	—	—	—	—	—	1	—	—	—	1	5	—	—	1	(50)	[4]
H 24	6	15	—	—	—	—	—	2	—	2	—	—	—	—	—	—	—	1	—	—	—	—	—	—	9	—	—	1	(13)	[1]
H 23	2·5	5	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	(5)	—
H 22	4	11	—	—	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	1	(1)	1	(18)	[1]
H 21	6	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H 20	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	(3)	—
H 19	1·5	141	—	—	—	—	3	—	—	—	—	—	—	137	—	—	—	—	—	—	—	—	—	—	—	—	—	1	(8)	—
H 18	2	106	—	—	—	—	—	—	3	3	—	—	—	98	—	—	—	—	—	1	—	—	—	—	—	—	—	1	(20)	—
H 17	3	251	—	—	—	—	7	—	—	2	—	—	—	238	—	—	—	—	—	1	—	—	—	—	2	—	—	1	(28)	[2]
H 16	3	126	—	—	—	—	26	—	1	4	—	—	—	92	—	1	—	—	—	1	—	—	—	—	—	—	—	1	(27)	—
H 15	6	259	—	—	—	—	7	—	—	3	236	—	3	—	1	—	—	1	—	2	2	—	—	—	2	1	(11)	1	(20)	—
H 14	7·5	285	—	—	—	—	14	—	—	—	241	—	1	5	—	—	—	1	—	7	2	1	1	8	—	3	(25)	1	(1)	[1]
H 13	6	169	2	—	—	—	5	—	—	5	122	—	7	5	—	—	—	—	—	3	4	1	1	4	7	2	(17)	1	(238)	[5]
H 12	5·5	211	4	—	2	2	13	—	—	8	141	—	22	1	—	1	—	—	—	1	1	1	3	5	4	1	(5)	1	(79)	—
H 11	6·5	199	1	—	—	2	14	—	—	13	125	1	12	—	—	—	—	1	—	2	—	—	1	12	13	1	(7)	1	(47)	—
H 10	5·5	362	4	—	—	—	12	—	—	10	282	—	18	—	—	1	—	—	—	2	—	1	4	16	10	1	(6)	1	(27)	—
H 9	3·5	99	1	—	—	—	6	—	1	12	52	—	5	—	—	1	—	—	—	4	—	—	—	5	10	1	(10)	1	(31)	—
H43	6	176	1	—	—	—	12	—	—	13	127	—	8	1	—	—	—	1	—	1	2	—	2	4	2	1	(4)	1	(40)	—
H42	4	203	2	—	—	—	3	—	—	4	167	—	10	—	—	—	—	—	—	2	—	—	2	5	6	1	(1)	1	(11)	—
H 8	2·5	85	2	—	—	4	2	2	4	10	48	—	3	1	—	—	—	—	—	2	—	—	2	—	3	1	(2)	1	(16)	—
H41	4·5	141	1	—	—	2	—	—	9	8	115	—	—	1	—	—	—	—	—	1	—	—	—	1	1	1	(4)	1	(8)	—
H 7	4·5	210	2	—	—	1	27	7	25	86	5	—	19	2	—	1	—	—	—	2	—	—	1	11	16	4	(30)	1	(25)	—
H40	10	213	—	3	—	10	—	—	31	35	—	—	6	103	—	—	—	2	1	2	3	—	5	11	—	—	—	1	(53)	—
H44	1·5	67	—	—	—	1	10	—	—	38	3	—	7	—	—	—	—	—	1	1	—	—	—	2	2	1	(3)	1	(23)	—
H 6	5·5	365	1	2	—	4	13	2	35	52	—	1	15	214	—	—	—	1	1	1	—	—	1	8	12	1	(1)	1	(47)	—
H 5	6	400	2	—	—	—	2	66	62	4	—	—	10	247	—	—	—	1	—	1	—	—	—	2	1	1	(3)	1	(14)	[1]
H39	6	109	—	—	—	—	3	—	—	1	—	—	4	89	1	—	—	1	—	1	—	—	—	6	2	—	—	1	(67)	[3]
H 4	8	385	1	—	—	—	4	43	81	8	—	—	9	226	—	1	—	1	—	2	—	—	—	7	—	1	(5)	1	(129)	—
H 3	4	19	1	—	—	—	3	—	—	3	—	—	1	7	—	—	—	1	—	1	—	—	—	—	1	—	—	1	(15)	—
H 2	6	50	1	—	—	—	4	—	—	13	—	—	—	29	—	—	1	—	—	1	—	—	—	—	—	—	—	1	(7)	—
H 1	6·5	29	—	—	—	1	3	—	1	12	—	—	—	—	—	—	—	1	—	1	1	—	—	1	6	1	(6)	1	(31)	[1]
H38	6·5	306	1	—	1	1	48	12	79	85	5	1	12	45	—	—	—	1	1	3	1	—	—	8	—	1	(10)	1	(73)	[2]
H37	6	53	2	—	—	—	7	—	—	12	3	—	—	—	—	—	—	2	—	1	—	—	—	—	24	1	(4)	1	(200)	[1]
H36	6	24	2	—	—	—	11	—	—	—	—	—	—	2	—	—	—	2	—	1	1	—	—	—	4	1	(7)	1	(17)	[6]
H35	4·5	47	4	—	—	—	—	33	—	1	1	—	—	—	—	—	—	1	—	1	—	—	—	—	3	2	(12)	1	(18)	[1]
H34	5	22	—	—	—	—	—	14	—	—	—	—	—	2	—	—	—	1	—	1	—	—	—	—	2	1	(1)	1	(1)	—
H33	5·5	11	—	—	—	—	—	2	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	1	(5)	[4]
H 32	6	13	—	—	—	1	—	1	—	4	—	—	—	—	—	—	—	1	—	—	—	—	—	2	2	1	(1)	1	(32)	[3]
H 31	6	7	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	2	1	(1)	1	(41)	—

Fig. 4 Fauna from the Afon Twrch section.

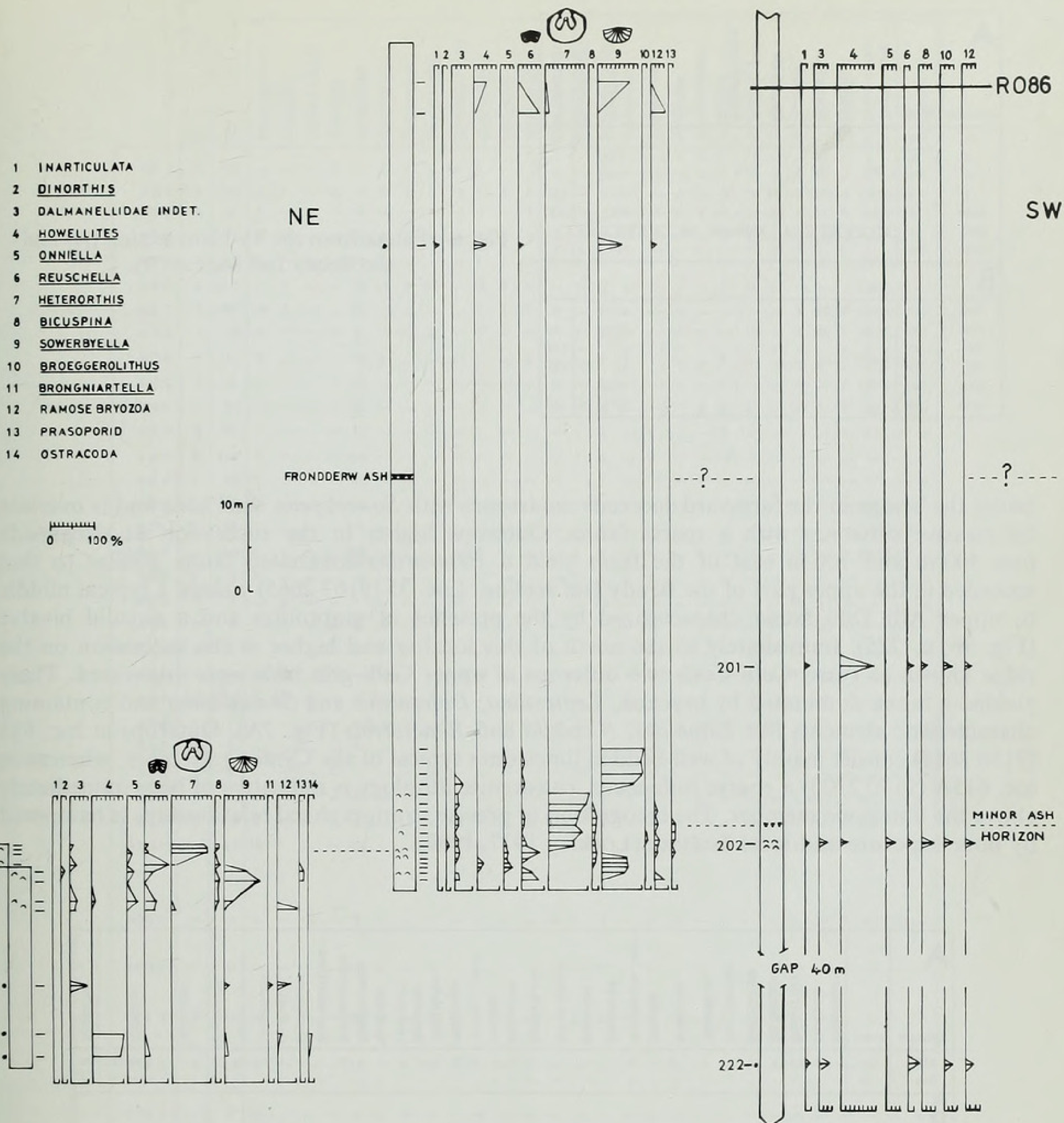


Fig. 5 Sample points in Afon Twrch section (NE) and the lower part of the Dyfi Valley section (SW) below lowest upper Allt Ddu sample (R086). Dotted lines indicated inferred correlations.

accessible by road. Fig. 6B shows the composition of faunas collected from six stratigraphically sequential horizons in the small stream gully east of Beudy Isaf (9105 2495). The section covers some 20 m of beds, passing upward from the gully to fossiliferous roadside exposures (9115 2505) containing numerous *Heterorthis* specimens. This section represents a part of the lower to middle Allt Ddu Mudstone (Fig. 1, p. 168) and is not therefore contemporary with the deposit found in the upper reaches of Afon Twrch. *Sowerbyella* and *Heterorthis* are again found to be mutually exclusive.

The Ty-nant section (Fig. 6A) is represented by a series of widely-spaced samples recovered from the Nant Bwlch-y-pawl valley east of Ty-nant (9050 2625). The Frondderw Ash exposed

LOCALITY	TOTAL	Paracraniops	Dalmanellidae	Reuschella	Heterorthis	Bicuspina	Sowerbyella	stroph. indet.	Broeggerolithus	nuculid	Gastropoda	Bryozoa	Ostracoda	Crinoidea	Graptoloidea	DIVERSITY
A																
35	18	1	9	-	-	-	-	-	1	1	-	-	1(3)	-	5	6
9	36	-	4	5	22	-	-	2	1	-	-	1	-	1(10)	-	7
6	66	-	9	-	47	1	-	2	1	-	-	4	1(2)	1(69)	-	8
2	4	-	-	1	-	-	-	-	-	-	-	2	-	1(1)	-	(3)
1022B	2	-	-	1	-	-	-	-	-	-	-	-	-	1(6)	-	(2)
1022	-	x x x x x x x x x FRONDDERW ASH x x x x x x x x x x														
1022A	103	-	1	1	-	-	99	1	-	-	-	-	-	1(14)	-	5
B																
790B	61	1	4	12	37	4	-	-	1	-	-	1	-	1(13)	-	8
790A	66	1	3	1	56	1	-	-	1	-	-	2	-	1(65)	-	8
790	27	-	2	-	-	-	24	-	-	-	-	-	1	-	-	(3)
789	13	-	9	-	-	-	-	-	1	-	3	-	-	-	-	(3)
997B	38	-	2	-	-	-	33	-	1	-	-	1	1	1(10)	-	5
997A	13	-	-	12	-	-	-	-	-	-	-	-	-	1(1)	-	(2)

Fig. 6 Fauna from the Ty Nant section (A) and the Beudy Isaf section (B).

under the bridge in the farmyard succeeds mudstones with *Sowerbyella* shell beds and is overlain by massive siltstones with a sparse fauna. Outcrops higher in the succession at streamside locs 400 m and 700 m east of the farm yield a *Heterorthis*-dominated fauna similar to that recorded in the upper part of the Beudy Isaf section. Loc. 35 (9167 2665) yielded a typical middle to upper Allt Ddu fauna characterized by the presence of graptolites and a nuculid bivalve (Fig. 96, p. 225). Immediately to the north of this locality and higher in the succession on the ridge known as Pen-y-Cefn-Coch two outcrops of upper Gelli-grîn beds were discovered. These yielded a fauna dominated by bryozoa, *Leptestiina*, *Dolerorthis* and *Skenidioides* and containing characteristic elements like *Estoniops*, *Nicolella* and *Rhactorthis* (Fig. 7A). Outcrops at loc. 615 (9150 2685) consist mainly of well-bedded limestones typical of the Cymerig Member, whereas at loc. 615A (9170 2700) a coarse tuffaceous, calcarenite lithology is indicative of beds immediately above the limestone member. The recognition of precise stratigraphical relationships is hampered by poor exposure and local faulting (Lockley 1977, 1980).

LOCALITY	TOTAL	Paracraniops	Nicolella	Dolerorthis	Rhactorthis	Skenidioides	Platystrophia	Dalmanella	Howellites	Onniella	dalmanellid, indet.	Reuschella	Bicuspina	Eoplectodonta	Leptestiina	Sericoidea	Leptaena	stroph. indet.	Cyclospira	Platylichas	Estoniops	isotelinid	Kloucekia	Flexicalymene	Brongniartella	Broeggerolithus	Cephalopoda	Conularida	tentaculite	ramose bryozoa	prasoporid	Ostracoda	Crinoidea	DIVERSITY
A																																		
615A	109	-	4	10	4	11	1	-	-	-	9	1	-	-	9	3	2	6	3	1	1	-	-	-	-	-	-	1	6	13	13	-	1(10)(2)	28
615	28	-	1	-	-	-	-	-	-	-	4	-	-	-	6	1	-	-	-	-	-	1	-	-	-	-	-	-	-	12	2	-	1(110)(3)	8
B																																		
555B	366	-	3	6	1	4	-	-	245	-	7	1	-	7	-	-	2	3	-	-	-	-	2	2	-	18	-	-	-	46	17	1(9)	1(5)	17
555A	188	-	-	-	1	3	-	-	63	-	29	-	3	12	1	-	1	1	-	-	-	-	3	3	2	9	1	-	1	38	14	2(19)	1(8)(2)	19
		(Stratigraphical gap of 35 m)																																
557	419	1	4	-	-	1	-	39	18	-	35	1	10	230	15	-	1	7	-	-	-	-	1	2	1	7	-	-	-	35	7	3(23)	1(30)	19

Fig. 7 Fauna from Pen y Cefn Coch (A) and Lledwyn Bach (B). (For Conularida read Macheridia.)

The Allt Ddu Formation at Craig y Gath and Rhiw March

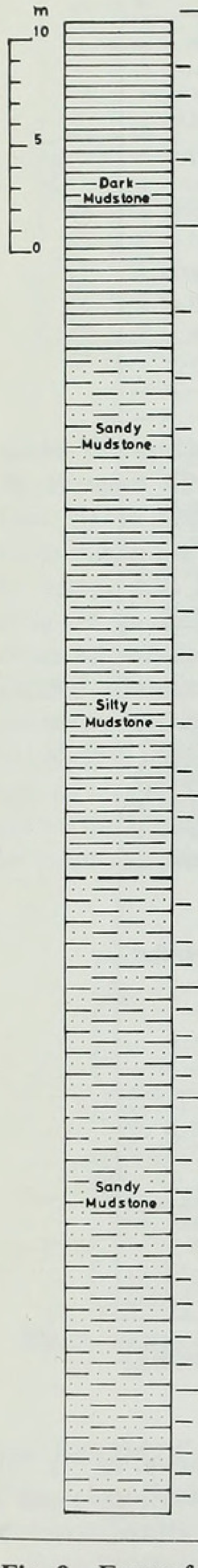
Figs 8 and 9 show the distribution of faunas in the upper part of the Allt Ddu Formation at Craig y Gath and Rhiw March respectively and Fig. 11 shows percentage abundances.

Bassett *et al.* (1966 : 235) stated that the Allt Ddu succession 'is best seen at Craig y Gath (915306)' and pointed out that, in addition to considerable repetition caused by faulting at the type locality, the junctions with neither the underlying nor with the overlying member are seen in this area. For this reason Craig y Gath is regarded here as the alternative type section.

	wt	N	Paracraniops	Cinorthis	Skenidioides	Onniella	Howellites	Reuschella	Bicuspina	Sowerbyella	Eoplectodonta	Macrocoelia	Leptaena	Rostricellula	Flexicalymene	Brongniartella	Broeggerolithus	isotelinid	Gastropoda	Bivalvia	Cephalopoda	ramose bryozoa	prasoporid	Conularida	Ostracoda	Crinoidea	Graptoloidea
AD Z	4	50	—	—	—	9	—	1	1	—	18	1	1	—	—	—	1	—	—	—	—	3	10	3	1 (9)	1 (76) —	—
AD Y	5	193	3	1	5	46	—	8	2	—	76	1	6	—	2	1	1	—	—	—	—	8	17	13	2 (13)	1 (243)—	—
AD X	6	51	5	—	—	—	13	14	—	—	—	3	—	1	—	2	2	—	—	1	1	1	1	3	2 (18)	1 (18)[1]	1
ADW	7	83	10	6	—	—	37	9	—	—	—	3	—	1	—	1	3	—	—	—	—	3	8	—	2 (15)	— — —	—
AD V	7	26	5	—	—	—	10	—	—	—	—	1	1	—	1	1	1	—	—	2	—	—	1	1	1 (5)	1 (1) —	—
ADU	6	217	3	7	—	—	59	13	7	86	—	13	4	1	—	1	2	—	1	—	—	3	14	2	— —	1 (34) —	—
ADT	6	51	18	2	—	—	22	—	—	—	—	1	2	1	1	—	1	—	—	—	—	—	1	—	1 (5)	1 (22) —	—
ADS	7	35	11	—	—	—	8	—	—	2	—	7	—	—	1	1	2	—	—	—	—	—	1	—	1 (8)	1 (5) —	—
ADR	7	32	2	—	—	—	18	3	—	—	—	1	—	2	—	—	1	1	1	—	—	2	—	—	— —	1 (24)[1]	—
ADQ	7	15	—	—	—	—	12	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	— —	1 (8) —	—
AD 3 L	—	57	10	—	—	—	30	—	—	—	—	2	—	—	—	—	6	—	—	1	2	1	4	—	— —	1 (8) —	—
AD P	8	91	1	—	—	—	73	—	—	—	—	1	—	—	—	1	5	—	1	—	—	6	2	—	— —	1 (1) —	—
ADO	9	179	7	—	—	—	144	—	—	—	—	—	—	—	—	1	3	—	9	1	—	14	—	—	— —	— — —	—
ADN	4	26	1	—	—	—	23	—	—	—	—	—	—	—	—		1	—	—	—	—	1	—	—	— —	— — —	—
ADM	4	6	1	—	—	—	4	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	— —	— — —	—
ADL	4	18	2	—	—	—	13	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	— —	— — —	1
AD3 J	—	246	4	—	—	—	201	—	2	—	—	7	—	—	—	1	9	1	1	4	1	—	14	—	— —	1 (15) [1]	—
ADK	4	9	2	—	—	—	3	—	—	—	—	—	—	—	—	1	1	1	1	—	—	—	—	—	— —	— — —	—
AD J	5	3	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1 (1)	— — —	—
ADI	6	5	—	—	—	—	—	—	—	—	—	—	—	2	—	1	1	—	—	—	—	—	—	—	1 (2)	— — —	—
ADH	5	2	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	— —	— — —	—
ADG	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1 (2)	— — —	—
ADF	5	10	1	—	—	—	5	—	—	—	—	—	—	—	—	—	1	—	—	1	—	1	—	—	1 (1)	— — —	—
ADE	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1 (1)	— — —	—
ADD	4	3	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	— —	— — —	—
ADC	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	— —	— — —	—
ADB	5	22	5	—	—	—	4	—	—	1	—	—	—	—	—	—	2	—	—	4	1	—	—	—	1 (5)	1 (1) —	3
ADA	7	17	3	—	—	—	3	—	—	—	—	1	—	—	—	1	2	—	—	4	—	—	—	—	1 (1)	1 (1) —	1
AD3H	—	97	16	1	—	—	53	—	—	—	—	6	—	—	—	—	5	1	2	4	2	2	3	—	1 (7)	1 (12) —	—
AD3 G	—	16	6	—	—	—	5	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	1 (1)	1 (4) [12]	—
AD3 F	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	— —	— — —	—
CYG 6	3	80	11	—	—	—	58	—	—	7	—	—	—	—	—	1	2	—	—	—	—	1	—	—	— —	— — —	—
CYG 5	3	46	5	—	—	—	25	—	—	10	—	—	—	—	—	—	1	—	—	5	—	—	—	—	— —	— — —	—
CYG 4	—	5	—	—	—	—	4	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	— —	— — —	—
AD3C	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	— —	— — —	—

Fig. 8 Fauna from the Craig y Gath section. (For Conularida read Macheridia.)

The sample grid (covering 150 m of the succession) and a locality map are shown in Fig. 10. The two uppermost samples, recovered from the base of the Gelli-grîn Formation, yield a characteristic fauna dominated by *Onniella* and *Eoplectodonta*. However, the distribution of upper Allt Ddu faunas, both here and at Rhiw March, is characterized by an association of mainly long-ranging forms, all of which maintain a relatively consistent pattern of relative abundance throughout the succession. The fauna is dominated by *Howellites*, *Paracraniops*, *Macrocoelia* and *Broeggerolithus*.



			Paracraniops	dalm. indet.	Dalmanella	Howellites ult.	Onniella	Reuschella	Bicuspina	Sowerbyella	Sericoidea	Macrocoelia	Leptaena	Kiaeromena	Rostricellula	Flexicalymene	Brongniartella	isotelinid	Broeggerolithus	Trilobita, ind.	Bellerophon	Cyclonema	Bivalvia	Cephalopoda	Conularida	ramose bryozoa	Prasopora	bryozoa, indet.	cateniform br.	Tallinnella		Crinoidea		
	4·5	18	1	7	—	—	—	—	—	—	2	—	—	—	—	—	1	—	1	1	—	—	—	—	—	—	—	1	—	3	(25)	1	(2)	—
	4·5	6	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	2	(16)	—	—	—
	5	15	—	7	—	—	—	—	—	—	1	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	5	(37)	—	—	—
R20	6	32	3	3	—	—	—	—	—	—	4	—	—	—	—	—	1	—	2	—	—	—	—	—	—	—	—	—	—	19	(150)	—	—	—
	4	7	2	—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	2	(16)	—	—	—
	7	263	—	—	1	134	5	—	7	53	10	—	4	—	—	—	2	—	2	1	—	—	—	—	15	—	24	—	—	4	(31)	1	(16)	[1]
	5	47	2	—	—	20	2	—	8	—	—	—	—	—	—	1	1	1	2	—	3	—	—	—	3	1	2	—	—	1	(2)	1	(53)	[4]
	7·5	43	9	—	—	4	—	—	5	—	—	1	4	—	—	1	1	—	2	—	2	—	—	1	2	4	2	—	—	4	(29)	1	(12)	[13]
15	6	24	2	—	—	9	—	—	—	—	—	1	—	—	1	1	1	—	3	—	—	—	1	—	—	3	—	—	—	1	(6)	1	(12)	—
	8	19	5	—	—	4	—	—	—	—	—	—	—	—	—	—	1	—	3	1	1	—	—	—	—	1	1	—	—	1	(9)	1ˣ	—	—
	5·5	33	2	—	—	8	—	—	2	—	—	—	—	—	—	—	—	—	2	—	—	10	—	—	—	7	—	—	—	1	(1)	1	(12)	[2]
	6	22	4	—	—	10	—	—	—	—	—	—	—	—	—	—	—	—	2	1	1	—	—	—	—	2	—	—	—	1	(3)	1	(14)	[3]
	4·5	27	—	—	—	18	—	—	—	—	—	—	—	—	—	—	1	—	2	—	—	—	—	—	1	4	—	—	—	—	—	1	(15)	[1]
10	5	20	—	—	—	16	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	1	(2)	—	—	—
	3	5	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	1	(1)	1	(1)	—
	3·5	58	7	—	—	33	—	—	—	—	—	—	—	1	1	—	1	—	2	—	—	1	2	—	—	8	—	—	—	1	(1)	1	(25)	—
	4	29	—	—	—	10	—	4	5	—	—	—	—	—	—	1	1	—	2	—	—	1	—	—	—	3	1	—	—	—	—	1	(27)	—
	5·5	37	2	—	—	25	—	—	1	—	—	—	—	—	—	—	1	—	4	—	1	—	—	—	—	1	—	—	—	1	(6)	1	(85)	[16]
5	7	35	3	—	—	18	—	—	—	—	—	—	—	—	—	—	1	—	6	—	—	—	1	1	1	2	—	—	—	1	(5)	1	(8)	[2]
	3	9	1	—	—	2	—	—	—	—	—	1	—	—	—	—	—	—	3	—	—	—	—	—	—	1	—	—	—	—	—	1	(7)	[4]
	4	11	—	—	—	2	—	—	—	—	—	—	—	2	—	—	—	—	1	—	—	—	—	—	—	3	2	—	—	—	—	1	(16)	[1]
	6	71	2	—	—	37	—	—	3	—	7	—	2	—	—	—	1	—	4	—	—	2	—	—	4	5	2	—	—	1	(5)	1	(195)	[5]
	7	39	—	—	1	9	—	3	5	—	5	—	—	—	—	—	1	—	4	—	2	1	—	1	—	3	2	—	—	—	—	1	(28)	[2]
0	8	111	3	—	2	9	—	6	20	—	7	11	—	3	—	2	1	—	3	—	—	3	—	1	3	10	25	—	—	1	(3)	1	(125)	[10]
	7·5	44	—	—	—	5	—	3	6	—	1	3	5	—	—	—	1	—	1	—	1	1	1	—	—	10	5	—	—	—	—	1	(45)	[4]
	5·5	148	—	—	3	38	2	1	9	—	3	3	10	3	—	1	1	—	9	—	1	3	1	2	7	38	11	—	—	1	(1)	1	(105)	[10]
	6·5	25	3	—	—	—	—	—	—	—	1	—	—	—	1	—	2	—	10	—	—	—	—	1	—	4	1	—	—	1	(6)	1	(10)	—
	7·5	62	13	—	—	6	—	—	2	—	8	1	1	—	2	—	1	—	7	—	1	—	1	2	—	14	1	—	—	1	(2)	1	(18)	[2]
095	5·5	13	2	—	—	—	—	—	1	1	—	1	1	—	—	—	—	—	3	—	—	—	—	—	—	1	1	—	—	1	(2)	1	(11)	—
	2·5	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	7·5	103	32	—	4	35	—	—	—	—	3	3	1	—	1	1	2	—	11	—	1	—	1	—	—	2	—	4	—	1	(7)	1	(27)	[1]
	5	13	2	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	5	—	—	—	1	1	—	—	—	1	—	1	(6)	1	(3)	[1]
	4·5	15	3	—	—	1	—	—	—	—	1	—	—	—	1	—	1	—	5	—	—	—	—	—	—	—	1	1	—	1	(1)	—	—	—
090	6·5	45	1	—	—	30	—	—	1	—	—	3	—	—	—	—	1	—	2	—	1	—	1	—	—	1	1	—	1	1	(1)	1	(16)	—
	5	34	1	—	—	21	—	—	—	—	3	—	—	—	—	—	1	—	2	—	—	—	—	—	—	3	—	—	—	—	—	1	(3)	—
	6	128	4	—	2	77	3	—	3	—	7	—	1	—	—	1	1	—	6	—	—	2	—	—	—	6	10	—	1	1	(3)	1	(50)	[3]
	4·5	16	2	—	—	4	—	—	—	—	2	—	—	—	—	—	1	—	2	—	—	—	—	1	—	—	—	2	—	1	(2)	1	(6)	—
	5	11	—	—	—	6	—	—	—	—	1	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	1	(1)	—	—	—

Fig. 9 Fauna from the Rhiw March section (Allt Ddu beds). (For *Bellerophon* read *Sinuites*, and for Conularida read Macheridia.)

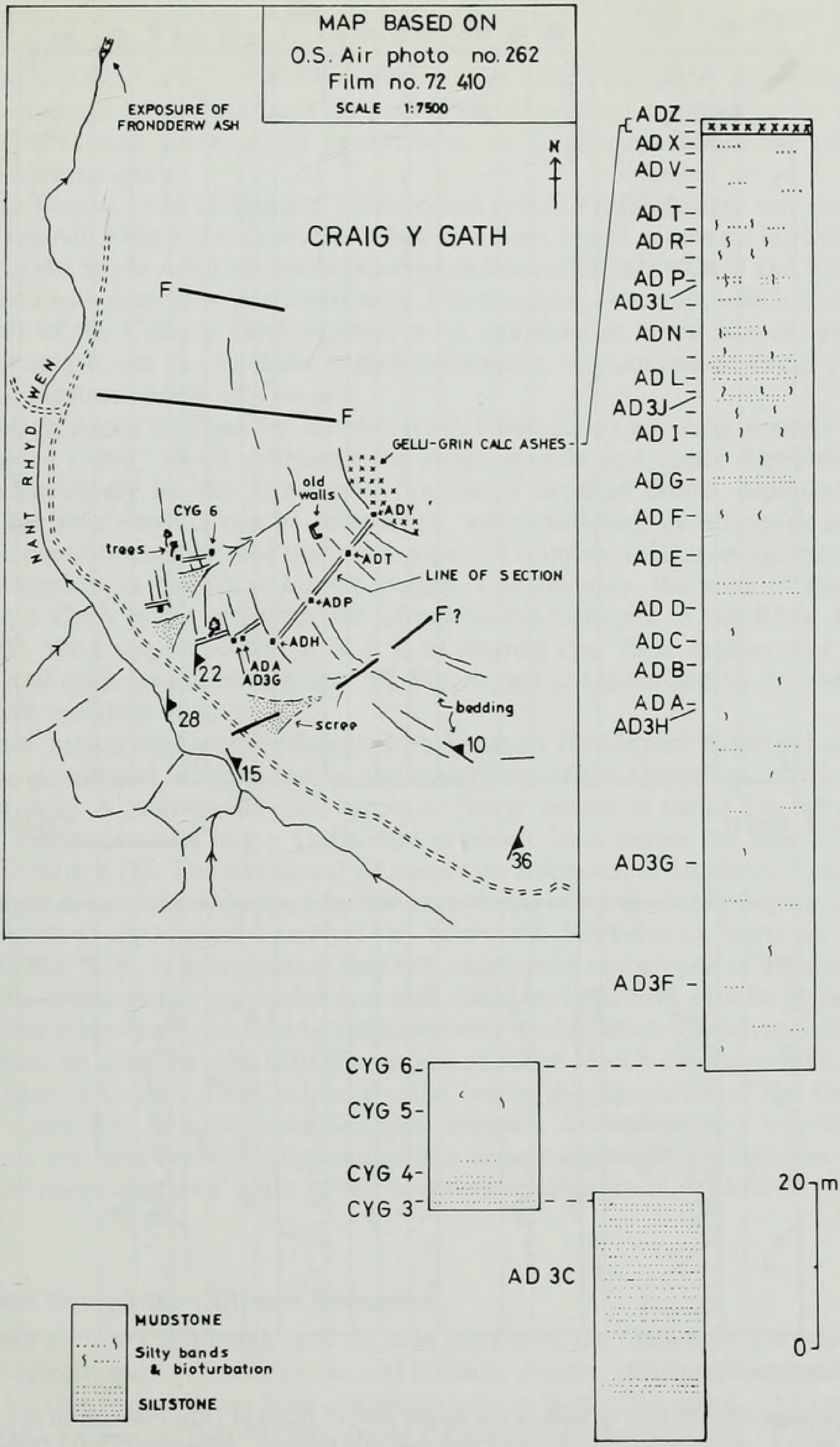


Fig. 10 Map of Craig y Gath exposures showing sample points and their stratigraphical relationships.

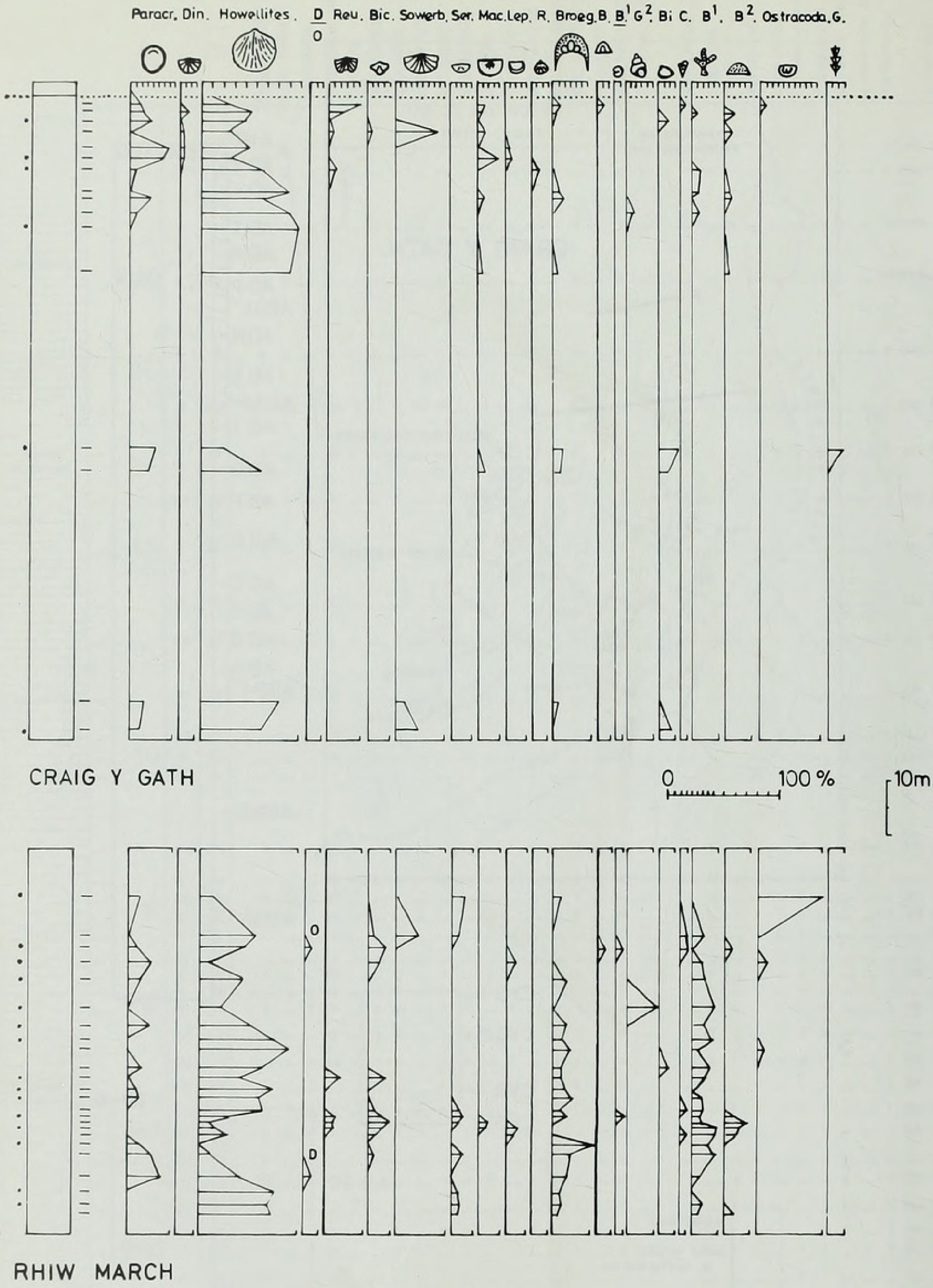


Fig. 11 Percentage distribution of taxa in the upper part of the Allt Ddu Formation at Craig y Gath and Rhiw March. Abbreviations refer to *Paracraniops* (Paracr), *Dinorthis* (Din), *Dalmanella* (D), *Onniella* (O), *Reuschella* (Reu), *Bicuspina* (Bic), *Sowerbyella* (Sowerb), *Sericoidea* (Ser), *Macrocoelia* (Mac), *Leptaena* (Lep), *Rostricellula* (R), *Broeggerolithus* (Broeg), *Brongniartella* (B), *Sinuites* (B[1]), Gastropoda (G[2]), Bivalvia (Bi), Macheridia (C), ramose Bryozoa (B[1]), prasoporid Bryozoa (B[2]), Graptoloidea (G). Lithostratigraphical boundary shown by dotted line.

Paracraniops (*P. glaber* sp. nov., Figs 33–36, p. 207) is an important element throughout the Allt Ddu and is even known from upper Glyn Gower and Llaethnant horizons. This form was previously unrecorded by workers in this area (e.g. Bassett *et al.* 1966), who ignored it because of uncertainty about its taxonomic affinity (A. Williams, personal communication, 1976). However, in the Caradoc successions of the Berwyn Hills to the east, Pickerill & Brenchley (1979) have described *Paracraniops* as an important element in the *Howellites* community. As demonstrated below their observations allow useful comparisons to be made between the composition of related faunal associations.

According to Bassett *et al.* (1966) and Whittington (1968) *Flexicalymene* was unknown in the upper part of the Allt Ddu Formation, but it has now been found at several horizons (Figs 8, 9).

Differences in the upper Allt Ddu faunal succession between Craig y Gath and Rhiw March are only pronounced with respect to particular taxa. For example, *Dinorthis*, which is confined to the uppermost part of the Craig y Gath succession, is unknown at Rhiw March, and *Sericoidea*, which is commonly found in the Rhiw March succession, is unknown at Craig y Gath and at other Allt Ddu localities north of Ty-nant.

The assemblage zones outlined by Bassett *et al.* (1966 : 236) are only entirely valid for the area they mapped (1966 : pl. 2). Although the lower, middle and upper Allt-Ddu assemblages (represented respectively by the *Heterorthis* faunule, a zone of faunal depletion and a zone characterized by 'new' stocks) can be recognized, where exposed, as far south as the Ty-nant area – with the possible exception of the upper zone – it is impossible to recognize these divisions within the formation in the Rhiw March section. For example, the zone of faunal depletion noted at Craig y Gath is not characteristic of equivalent horizons in the Rhiw March section (Fig. 2, p. 170). With respect to this zone it is of interest that these argillaceous beds, both at Craig y Gath and other localities (e.g. loc. 35, Fig. 6), are characterized by the presence of graptolites and small nuculoid bivalves.

Characteristic 'bursts' of *Sowerbyella* noted by Bancroft (1945) and Bassett *et al.* (1966 : 236) are apparently widespread in space but, in the upper part of the formation, restricted in time to only a few horizons. A *Sowerbyella* shell carpet or 'burst' occurs at about 8 m below the base of the Gelli-grîn Formation at Craig y Gath, and at about 16 m below the base at Rhiw March (samples ADU and R18). The likelihood of these two horizons, at localities 7 km apart, being contemporaneous is strongly supported by the occurrence of an unusually high concentration of archaeogastropods at an horizon exactly 14 m below the *Sowerbyella* 'burst' in both sections (samples ADO and R13). It is suggested that the widespread occurrence of abundant gastropod and *Sowerbyella* specimens at particular horizons could be indicative of a large successful spatfall or conditions otherwise conducive to the temporary proliferation of such specific groups.

The uppermost 30 m of the Allt Ddu Formation at Rhiw March are apparently equivalent to only 22 m of beds at Craig y Gath, where erosion before the deposition of the Gelli-grîn could have removed some 8 m of uppermost Allt Ddu deposits. Since respective lithologies for these uppermost beds are well-bedded silty mudstones and fine-grained argillaceous mudstones it is probable that reworking took place in the north while continuous deposition prevailed in the south.

Sampled sections through the Gelli-grîn Formation

Dominant faunal elements. Although only 60 m in thickness, the Gelli-grîn Formation represents the most lithologically varied, fossiliferous, and faunally diverse, stratigraphical unit in the Lower Bala Group; for this reason it has been examined here in particular detail. The formation crops out between Pont y Ceunant (SH 944346, about 1 km north of the type locality west of Gelli-grîn farm) and the Rhiw March section in the Dyfi Valley. To the south of this latter locality the formation passes laterally into argillaceous beds representative of the upper part of the Ceiswyn Mudstone and the overlying Nod Glas Formation. The distribution of faunas in five sections through the formation is shown in Figs 7B, p. 178, and 12–15. The chosen sections are at the following localities: west of Gelli-grîn farm, 944340 (Fig. 12), Maes-Meillion, 925305 (Fig. 13, p. 185), Lledwyn Bach, 912279 (Fig. 7B), Nant Tan y Bwlch, 914240 (Fig. 14, p. 186) and the

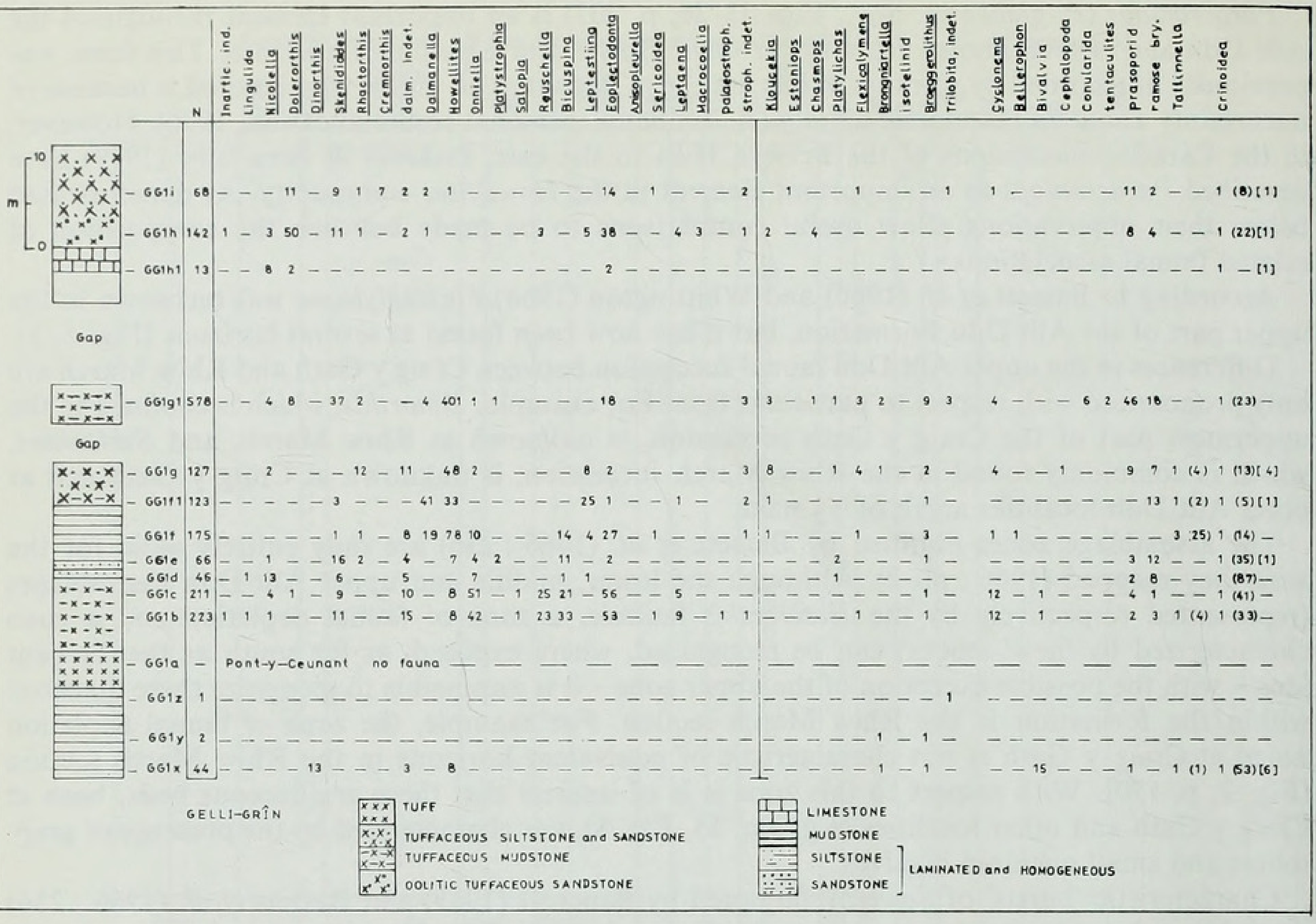


Fig. 12 Fauna from the Gelli-grîn (type) section. (For *Bellerophon* read *Sinuites*, and for Conularida read Macheridia.)

cliffs north of Rhiw March, 899219 (Fig. 15, p. 187). All sections, with the exception of the poorly-exposed outcrops at Lledwyn Bach, have been sampled thoroughly throughout.

In the Tan y Bwlch and Rhiw March sections the uppermost 20 m of beds not only belong to the Gelli-grîn Formation, but also represent the northern part of the outcrop of the Nod Glas Formation now known to be equivalent to this upper part of the Gelli-grîn Formation (Lockley 1977, 1980). The relative abundance of faunas in the four main Gelli-grîn sections is shown in Fig. 16, p. 189.

At the type locality a series of 15 samples was collected. Here the underlying uppermost Allt Ddu beds, where fossiliferous, contain a fauna dominated by *Dinorthis*, *Howellites* and bivalves. The succeeding coarse Pont y Ceunant Ash is unfossiliferous at this locality but is in turn overlain by highly fossiliferous, tuffaceous mudstones containing a diverse brachiopod-dominated fauna. Various elements of these lowermost Gelli-grîn faunas, in particular *Eoplectodonta*, are found so closely packed that in a few instances they show primary growth distortions; such a phenomenon indicates an *in situ* association. These fossiliferous beds are characterized by the following rapidly changing succession of local associations; an association dominated by *Onniella*, *Eoplectodonta*, *Bicuspina* and *Reuschella* is succeeded firstly by a *Nicolella*-dominated fauna, then by a *Skenidioides*-dominated fauna. These horizons are in turn overlain by beds containing *Dalmanella*, *Leptestiina* and *Howellites*. A species of the latter, *H. antiquior* (M'Coy), occurs in particular abundance in the middle part of the Gelli-grîn Formation and is associated with *Rhactorthis* and an abundance of the trilobites *Kloucekia*, *Broeggerolithus* and, to a lesser extent, *Flexicalymene*.

Although the middle part of the formation is not entirely exposed, examination of other contemporary sections has revealed that the *Howellites*-dominated fauna persists into sub-Cymerig beds. The change in facies associated with the onset of Cymerig Limestone deposition

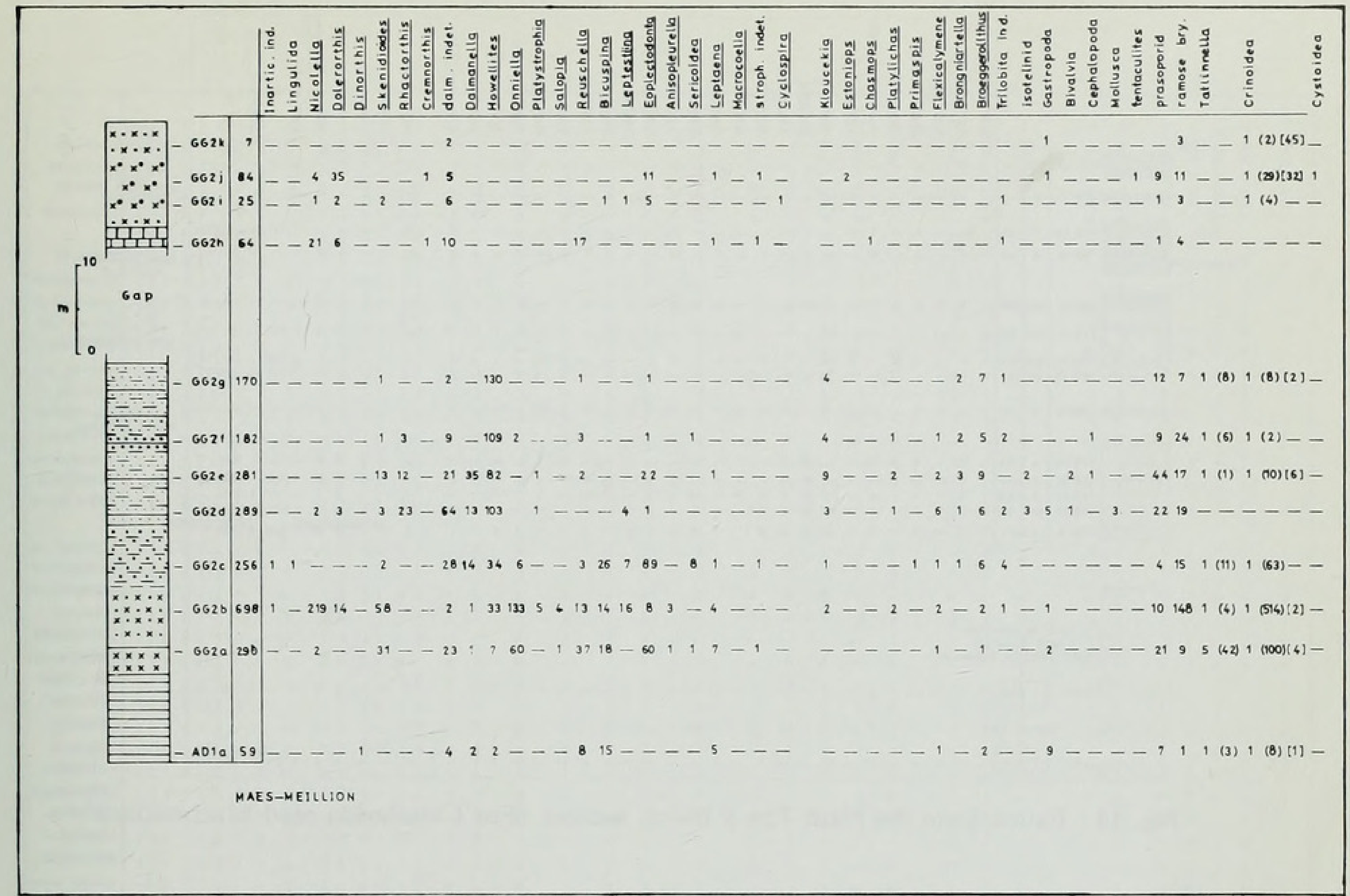


Fig. 13 Fauna from the Maes-Meillion section.

is accompanied by a corresponding change in the fauna. Cymerig and supra-Cymerig beds contain a fauna dominated by *Dolerorthis*, *Nicolella*, *Eoplectodonta* and *Skenidioides*. Other characteristic elements include *Cremnorthis*, *Chasmops* and *Estoniops*; the latter form is only known from horizons above the limestone member.

At Maes Meillion the faunal succession is remarkably similar to that recorded at Gelli-grîn (Figs 12, 13). Notable differences include the composition of the uppermost Allt Ddu fauna (dominated by *Bicuspina*, *Reuschella* and gastropods) and the occurrence of a fauna in the upper part of the Pont-y-Ceunant Ash Member which is thinner and finer here than to the north. The faunal succession throughout the formation mirrors the pattern observed in the Gelli-grîn section; all the dominant genera named above are found at equivalent horizons in this section 4 km to the south.

Three samples from newly-discovered Gelli-grîn exposures on Lledwyn Bach have yielded a fauna characteristic of the lower to upper middle part of the formation (i.e. from 5–10 m to 40–45 m above the base). The lowest, poorly-exposed beds contain an association characterized by *Eoplectodonta*, *Dalmanella*, *Howellites* and *Leptestiina* and are succeeded, after a 35 m gap, by larger outcrops yielding (from two sampled horizons 1 m apart) a fauna dominated by *Howellites* and trilobites (Fig. 7B, p. 178).

Analysis of the Gelli-grîn sequences in the Tan y Bwlch and Rhiw March sections reveals patterns of faunal succession in the lower and middle part of the formation which compare closely with those noted in the sections to the north (Figs 14–16). However, the faunal succession in the upper part of the formation differs from that recorded to the north and corresponds to a distinctive lateral facies change occurring south of Pen y Cefn Coch. At Tan y Bwlch the Gelli-grîn Formation is only about 45 m in thickness and is mainly argillaceous throughout.

The lower part of the formation at Tan y Bwlch is dominated by *Onniella* and *Eoplectodonta*,

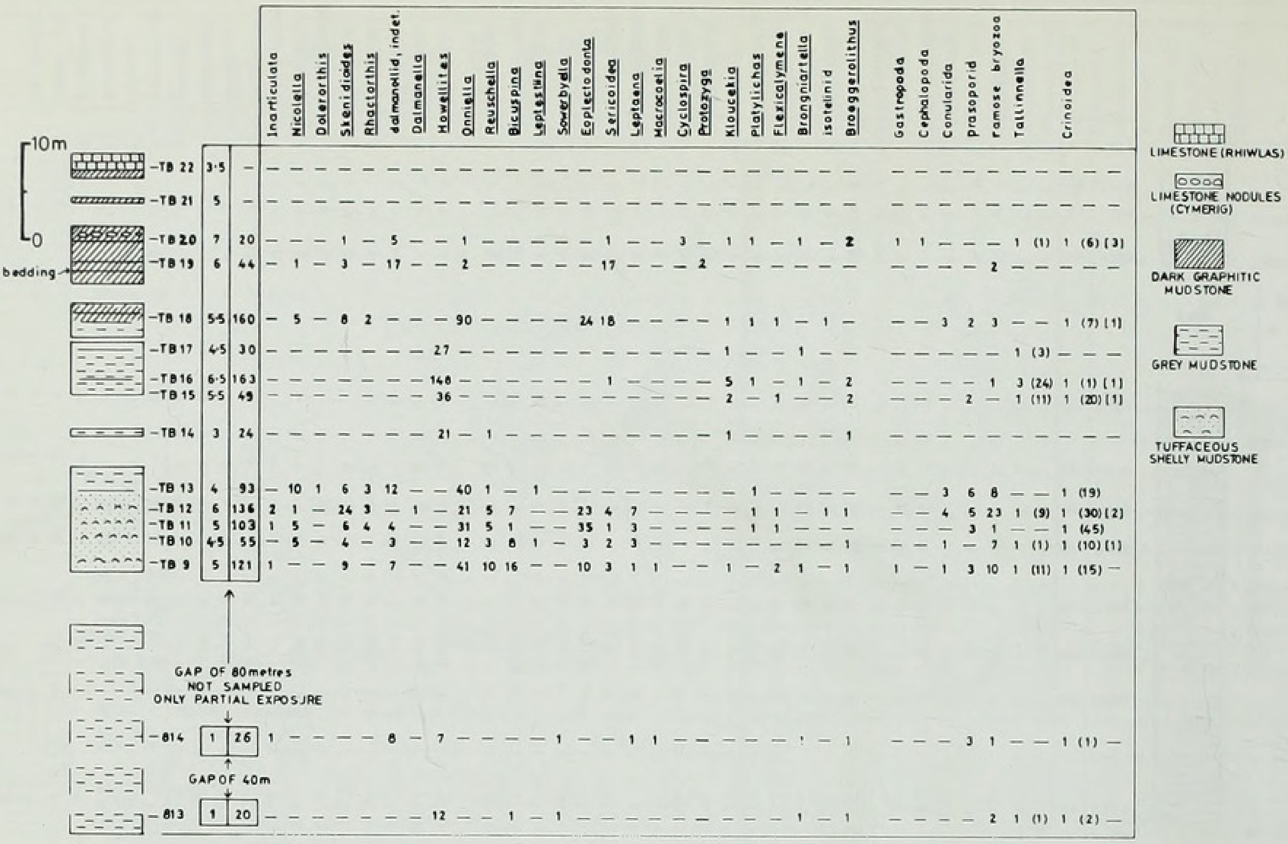


Fig. 14 Fauna from the Nant Tan y Bwlch section. (For Conularida read Macheridia.)

with *Skenidioides* and *Nicolella* also representing important elements. The middle part of the formation is dominated by *Howellites* and, to a lesser extent, *Kloucekia*, *Broeggerolithus* and the Ostracoda. However, in the uppermost part of the formation (i.e. the Dyfi Mudstone Member) the fauna is characterized mainly by *Sericoidea* and rarer forms like *Cyclospira.*

In the Rhiw March section the Gelli-grîn Formation has been sampled more thoroughly than at any other locality. The pattern of faunal distribution is similar to that noted in the Tan y Bwlch section. The lower beds are dominated by *Onniella* and *Bicuspina*, with *Eoplectodonta* being less abundant than at contemporary horizons to the north. The *Onniella*-dominated beds pass up into strata in which *Nicolella* and *Skenidioides* are important elements and are in turn succeeded by mudstones of the middle part of the formation which are dominated by *Howellites*, *Kloucekia*, *Broeggerolithus* and the Ostracoda. The upper (Dyfi Mudstone) part of the formation is dominated by *Sericoidea* and *Onniella* in association with less abundant forms including *Skenidioides*, *Cyclospira*, *Eoplectodonta*, *Nicolella*, various inarticulates and macheridians. The uppermost metre of the Rhiw March succession consist of soft, coal-black graptolitic shale containing a monospecific assemblage of *Climacograptus minimus* (Carruthers); specimens were not counted for inclusion in Fig. 15.

Non-dominant elements in the Gelli-grîn Formation. Throughout its area of outcrop the lowermost beds of the formation contain a number of brachiopod genera which are either unique to this part of the Lower Bala Group or only otherwise known from the Derfel Limestone. These genera include ? *Pseudolingula*, *Platystrophia*, *Anisopleurella*, *Oxoplecia*, *Palaeostrophomena* and *Bimuria.* Of these *Bimuria* was previously unknown in Wales and *Palaeostrophomena* and *Anisopleurella* were hitherto unknown in the Gelli-grîn Formation. *Salopia* is also characteristic of the lower part of the formation but, in addition to being known from the Derfel Limestone, is now also recorded from horizons beneath the Frondderw Ash in Afon Twrch. A few specimens assigned to *Kjaerina* (*Hedstroemina*) have been recovered from sample R28; this genus was previously only known from the Glyn Gower 'unit' of the Lower Bala Group (Williams 1963 : 460). The distribution of seven of the eight above-mentioned genera is shown in Figs 12–15; the eighth genus,

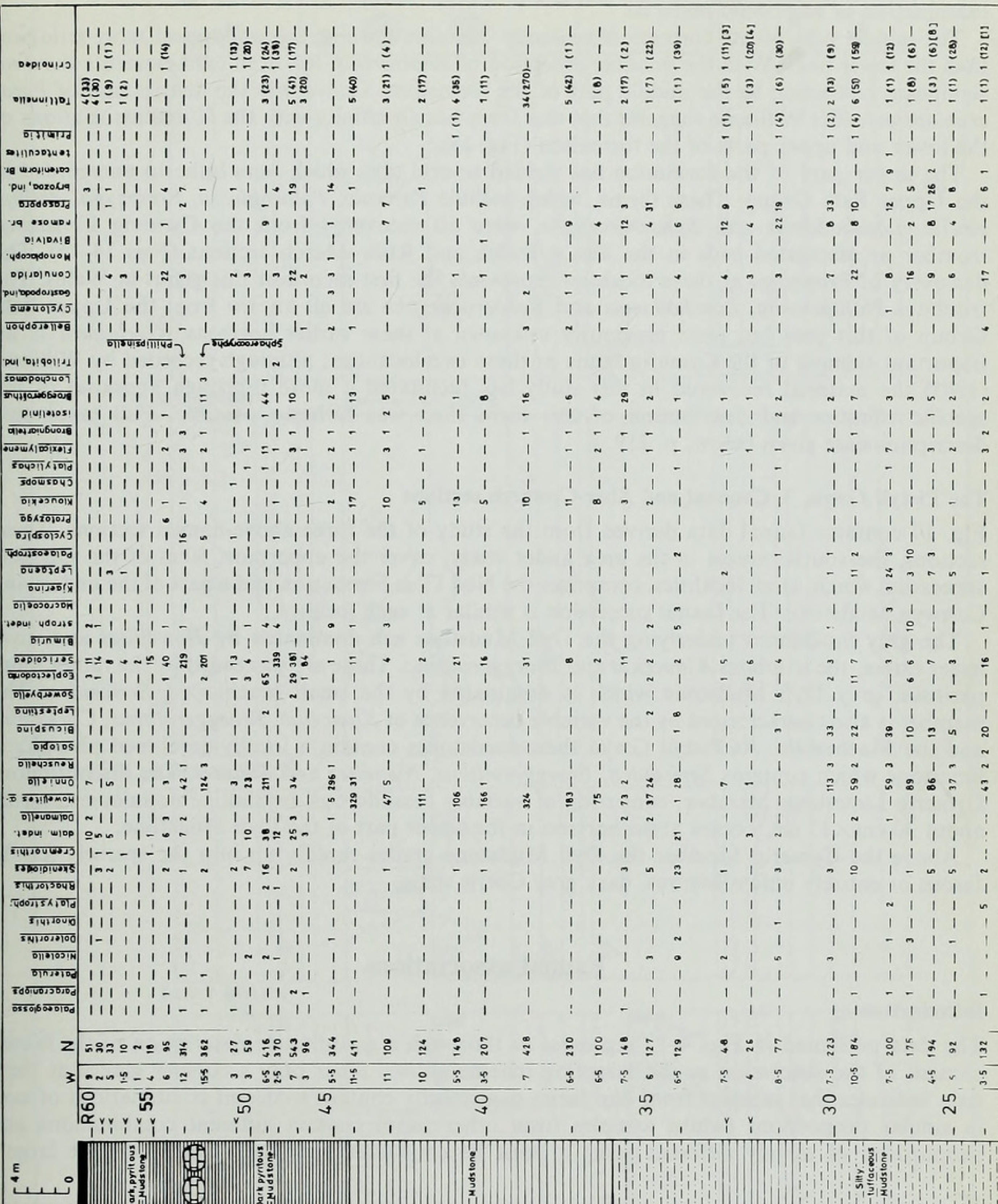


Fig. 15 Fauna from the Rhiw March section (Gelli-grîn/Nod Glas beds). (For *Bellerophon* read *Sinuites*, and for Conularida read Macheridia.)

Oxoplecia (not recorded in the samples from which the data tables were compiled) is now known to occur at horizons GG1c and GG1e (Fig. 12) and TB9 and TB12 (Fig. 13), following the examination of additional material.

The middle part of the formation generally contains fewer brachiopods and more trilobites than the lower beds. With the possible exception of *Rhactorthis*, less dominant elements show no significant restriction to the middle part of the formation. Conversely the distribution of *Paracraniops macellus* Williams suggests that this form has an affinity with the faunal associations of the lower and upper parts of the formation (Fig. 15).

The upper part of the formation has yielded several taxa which were hitherto unrecorded in the Upper Bala Group. These forms, which include *Paterula*, *Palaeoglossa*, *Protozyga*, *Phillipsinella*, *Lonchodomas* and *Sphaerocoryphe*, were all recovered from the Cymerig Limestone member or associated beds in the Tan y Bwlch and Rhiw March sections (Figs 14–15). The discovery of *Protozyga* at these localities represents the first record of this genus in Wales. The trilobites *Phillipsinella*, *Lonchodomas* and *Sphaerocoryphe* are all known from the Upper Bala Group of this area but were previously unknown at these earlier horizons. *Cyclospira* is an important element of the Cymerig fauna at these two localities; although recorded by Williams (1963) the material recovered in this study has facilitated a more thorough appraisal of the specific affinities and distribution of this form than was hitherto possible. Full taxonomic descriptions are given below, p. 219.

The Pistyll Gwyn, Y Ceunant and Aber-Cowarch sections

Fig. 17 contains faunal data derived from the study of the three above-named sections. These sections, the southernmost in the area under study, cover the uppermost 30 m of the Caradoc succession which, at all localities, comprises the Nod Glas Formation and a part of the underlying Ceiswyn Mudstone. The faunal succession is similar at each locality.

The grey mudstones underlying the Dyfi Mudstone are dominated by *Howellites* and, to a lesser extent, the trilobites *Kloucekia* and *Broeggerolithus*. These are succeeded by the rather more pyritous, grey Dyfi Mudstone which is dominated by the small brachiopod *Sericoidea*. The member is also characterized by the variable occurrence of *Kloucekia*, *Broeggerolithus*, *Cyclospira* and the Macheridia. At Pistyll Gwyn these mudstones contain a locally-developed phosphatic limestone which contains *Sericoidea*, *Broeggerolithus*, *Nuculites* and *Sinuites*. The discontinuous Cymerig Limestone Member, consisting of variably fossiliferous, crystalline nodules measuring about 30 cm × 15 cm, occurs at an horizon in the upper part of the Dyfi Mudstone.

Above the Cymerig Member the Dyfi Mudstone grades rapidly up into the sparsely fossiliferous or entirely unfossiliferous, dark grey Corris shale.

Faunal associations

Introduction

The data presented in Figs 4–17 represent as thorough a quantitative description of the faunal content of the succession as the sampling scheme allows. Since only a cursory glance at these data indicates that samples from like facies consistently contain recurrent combinations of taxa in similar proportions (whilst samples from other facies contain different combinations and proportions of mainly different taxa) it must be concluded that the associations are largely

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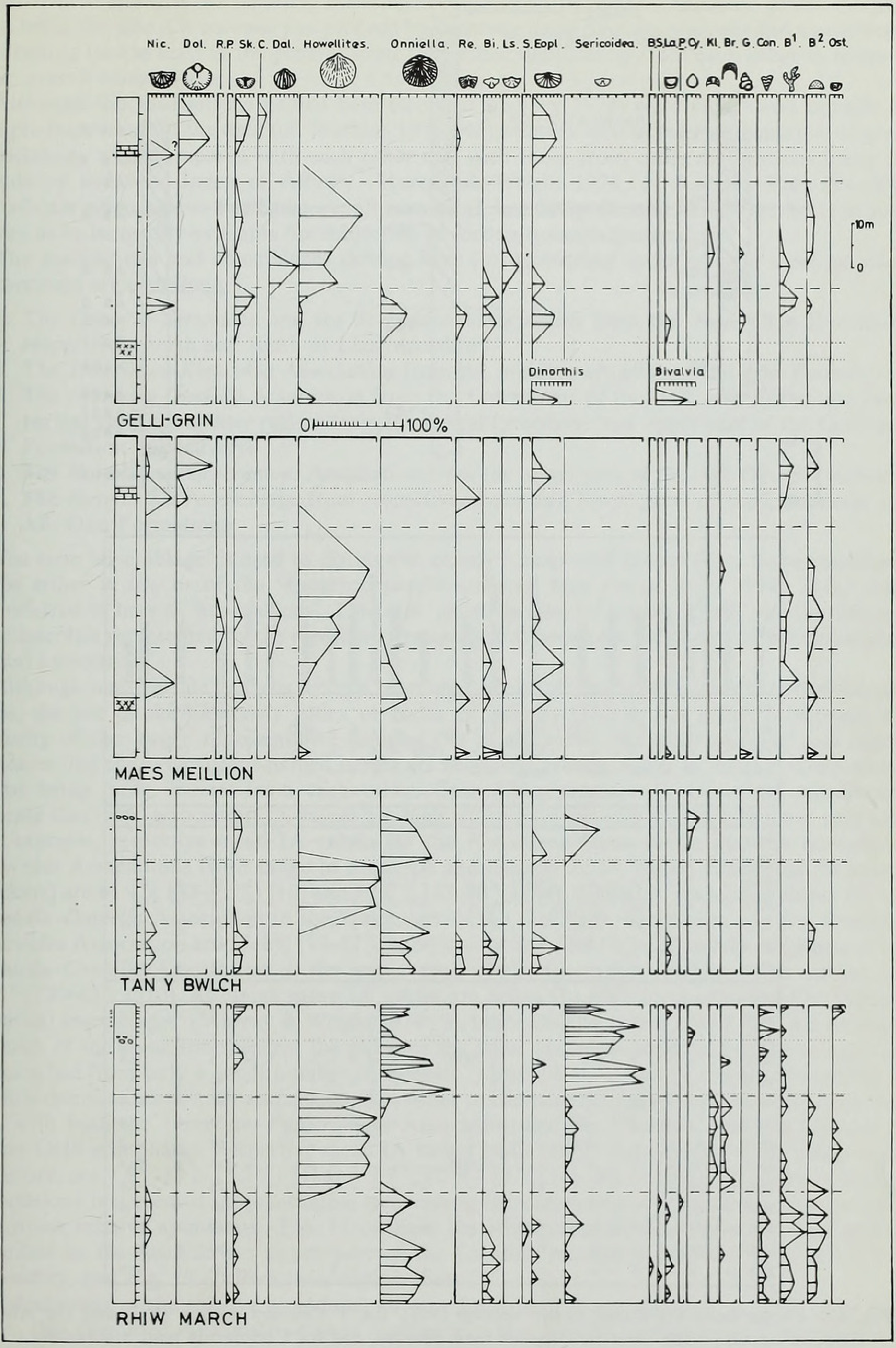
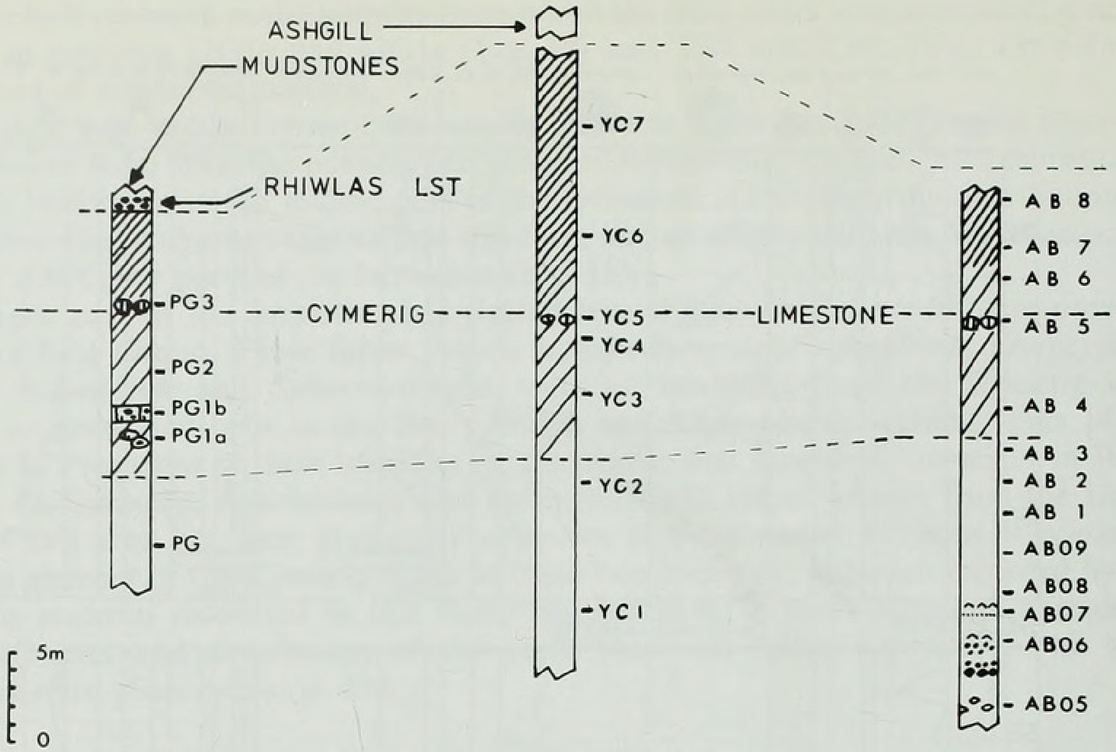
Fig. 16 Percentage distribution of taxa in named sections through the Gelli-grîn Formation. Abbreviations refer to *Nicolella* (Nic), *Dolerorthis* (Dol), *Rhactorthis* (R), *Platystrophia* (P), *Skenidioides* (Sk), *Cremnorthis* (C), *Dalmanella* (Dal), *Reuschella* (Re), *Bicuspina* (Bi), *Leptestiina* (Ls), *Sowerbyella* (S), *Eoplectodonta* (Eopl), *Bimuria* (B), Strophomenacea/*Macrocoelia* (S), *Leptaena* (La), *Palaeostrophomena* (P), *Cyclospira* (Cy), *Kloucekia* (Kl), *Broeggerolithus* (Br), Gastropoda (G), Macheridia (Con), ramose Bryozoa (B^1), prasoporid Bryozoa (B^2), Ostracoda (Ost). Dashed lines represent boundaries between faunal associations.


Nic. Dol. R.P. Sk. C. Dal. Howellites. Onniella. Re. Bi. Ls. S. Eopl. Sericoidea. B.S. La. P. Cy. Kl. Br. G. Con. B1. B2. Ost.
10m
0
Dinorthis
Bivalvia
GELLI-GRIN
0 100%
MAES MEILLION
TAN Y BWLCH
RHIW MARCH



SAMPLE NO.	Inarticulata	Dalmanellidae, indet. (Howellites)	Reuschella	Sericoidea	Cyclospira	Kloucekia	Broeggerolithus	Trilobita, indet.	Ostracoda	Bivalvia	Bellerophon	Other Gastropoda	Conularida	Bryozoa	Crinoidea	Graptoloidea	Miscellanea?	TOTAL	DIVERSITY	SPECIMENS PER Kg
PG 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	(1)	(1)	-
PG 2	-	7	1	21	-	1(2)	1(1)	1	-	-	-	-	6	1	1(3)	-	-	40	8	-
PG1b	-	-	-	-	-	-	1(14)	1	-	(1)	-	1	-	-	-	-	1	7	(5)	-
PG1a	-	-	-	260	-	-	2(7)	-	-	-	1	-	1	-	-	-	-	264	4	-
PG	-	79	-	3	-	5(20)	5(20)	1	1(3)	-	-	-	-	1	-	-	-	95	7	-
YC 7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0
YC 6	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0.7
YC 5	-	1	-	12	-	-	1(3)	-	-	-	-	1	-	-	-	-	-	15	4	20
YC 4	-	-	-	53	-	-	-	-	-	-	-	-	1	-	-	-	-	54	2	36
YC 3	-	-	-	50	-	-	-	1	-	-	-	-	2	-	-	-	-	53	3	70.6
YC 2	-	47	-	31	-	1(3)	1(3)	-	-	-	-	-	-	-	-	2	-	82	5	82
YC 1	-	48	-	3	-	-	-	1	-	-	-	-	-	-	-	-	-	53	3	104
AB 8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	0
AB 7	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1
AB 6	1	-	-	1	-	-	-	-	1(2)	-	-	-	-	-	-	6	-	3	3	0.6
AB 5	1	-	-	28	4	-	-	-	-	-	-	-	-	-	-	-	-	40	5	5
AB 4	-	1	-	55	1	-	-	-	-	-	-	-	-	-	-	-	-	57	3	32.6
AB 3	-	1	1	4	1	-(5)	1(4)	-	-	-	-	-	-	-	-	-	-	9	6	2.25
AB 2	-	63	-	-	-	1(1)	-	-	-	-	-	-	-	-	-	-	-	64	2	18.3
AB 1	-	112	-	3	-	-	-	-	1(1)	-	-	-	-	-	-	-	-	116	3	33.1
AB09	-	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24	1	10.7
AB08	-	42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	42	1	7.0
AB07	-	112	-	7	-	-	1(1)	-	-	-	-	-	-	-	-	-	-	120	2	20
AB06	-	86	-	3	-	-	1(1)	-	-	-	-	-	-	-	-	-	-	90	3	90
AB05	-	4	-	9	-	-	-	-	-	-	-	-	1	5	-	-	-	20	5	6.2

Fig. 17 Fauna from the Pistyll Gwyn section (PG), the Y Ceunant section (YC) and the Aber Cowarch section (AB). (For *Bellerophon* read *Sinuites*, and for Conularida read Macheridia.)

facies-related and that the sampling procedures consistently provide an adequate census method. This being the case it is necessary to proceed by outlining distinctive associations and assemblages and testing that at least in the general sense they differ significantly from each other in terms of their overall composition.

Although the associations named here (see also Lockley 1978) were picked out initially by 'simple inspection' of the data (cf. Watkins 1975 : 48) samples considered representative of given associations were compared with each other and with those from other associations using the Similarity Index or Index of Affinity (Murray & Wright 1974 : 3; Rogers 1976 : 504–506). Details are given below. Furthermore, all numerical data are presented here (Figs 4–17) in such a way as to be readily available for subjection to further quantitative analysis.

The associations and assemblages defined here (in descending order of their stratigraphical occurrence) are as follows.

5. The *Onniella–Sericoidea* and the *Sericoidea* Associations from the Nod Glas Formation respectively north and south of Llanymawddwy
4. The *Howellites–Kloucekia* Association from the middle part of the Gelli-grîn Formation
3. The *Nicolella–Onniella* Association from the Lower part of the Gelli-grîn Formation (with variant earlier and later phases from the Derfel Limestone and upper part of the Gelli-grîn Formation respectively)
2. The *Howellites–Paracraniops* Association from the upper part of the Allt Ddu Formation
1. The *Heterorthis* Assemblage from respective upper and lower parts of the Llaethnant and Allt Ddu Formations.

The term 'assemblage' is used to distinguish clearly transported faunas from those considered to be either *in situ* or of the 'disturbed neighbourhood' type (*sensu* Scott 1974: 321), which are referred to here as 'associations'. The term 'phase' is used informally to indicate the different time intervals represented by the repetitive stratigraphical occurrence of the same (albeit varying) faunal association.

Although multivariate analysis has not been used to cluster like samples and to define associations, the use of the Similarity Index or Index of Affinity (IA) to test affinities between the majority of the larger representative samples (90 in all) serves the same purpose and clearly indicates that the associations named herein are relatively homogeneous in internal composition whilst being quite distinct from each other. Over 220 representative IA values consistently indicate that intra-association IA values are high whilst inter-association IA values are very low. For example, respective mean IA values for the *Howellites–Paracraniops* and the *Howellites–Kloucekia* Associations (with range in brackets) and number of IA values considered [in square brackets] are 61·4% (40–91%) [16] and 72·8% (37–98%) [54]. Similarly, respective values for the *Nicolella–Onniella* Association in the lower part of the Gelli-grîn Formation and the *Onniella–Sericoidea* Association are 57·4% (17–87%) [59] and 48·8% (7–83%) [36], whilst the phase of the *Nicolella–Onniella* Association in the upper part of the formation exhibits lower values, i.e. 40·8% (20–63%) [10]. Although mean IA values are below the 80% level considered to indicate 'identical assemblages' (Murray & Wright 1974 : 3), individual IA values above 80% are recorded for each of the associations except the phase of the latter one mentioned here which in any case is described from only a small number of samples. Mean IA values show a marked contrast to the low inter-association values calculated in order to compare the *Howellites–Kloucekia* Association with both the *Howellites-Paracraniops* Association and the *Nicolella–Onniella* Association (lower Gelli-grîn phase). Respective mean IA values (with range) and number of IA values used, as before, are 7·8% (3·2–13·2%) [4] and 9·9% (2·5–13·1%) [4]. An outline of these recognizable associations is presented in quantitative terms using the parameters of persistence of occurrence and mean relative abundance. Fig. 18 outlines the stratigraphical distribution of associations identified in the fossiliferous upper part of the Caradoc succession between Bala and Dinas Mawddwy, and Fig. 19 outlines their composition.

Calculations of the relative abundance of taxa from each sample (Figs 5, p. 177, 11, p. 182, 16, p. 189) permitted the construction of a series of tables (one for each sample) in which faunal elements were ranked in order of abundance (Lockley 1977). The numerically dominant taxa which make up 80% of the fauna may be regarded as the Trophic Nucleus; Neyman (1967) proposed this quantitative definition of the nucleus originally defined by Turpaeva (1948). The dominant faunas listed in Fig. 19 therefore represent the Trophic Nucleus of their respective named associations either at named localities or for the association as a whole.

Although some palaeontologists (e.g. Titus & Cameron 1976) have named associations or communities after their rarer component species, such methods do not conform with the more popular tendency of naming associations after their dominant component taxa. The classic work of Petersen (1924), summarizing his studies of marine animal communities in Danish waters, included an outline of four categories of component taxa – 1st, 2nd and 3rd order characterizing species and associated animals. Thorson (1957 : 477) subsequently proposed that these respective characterizing species be quantitatively defined as representing at least 5, 5, 10 and 2% of the total living weight (biomass) in at least 50, 50, 70 and 25% of samples from any given community.

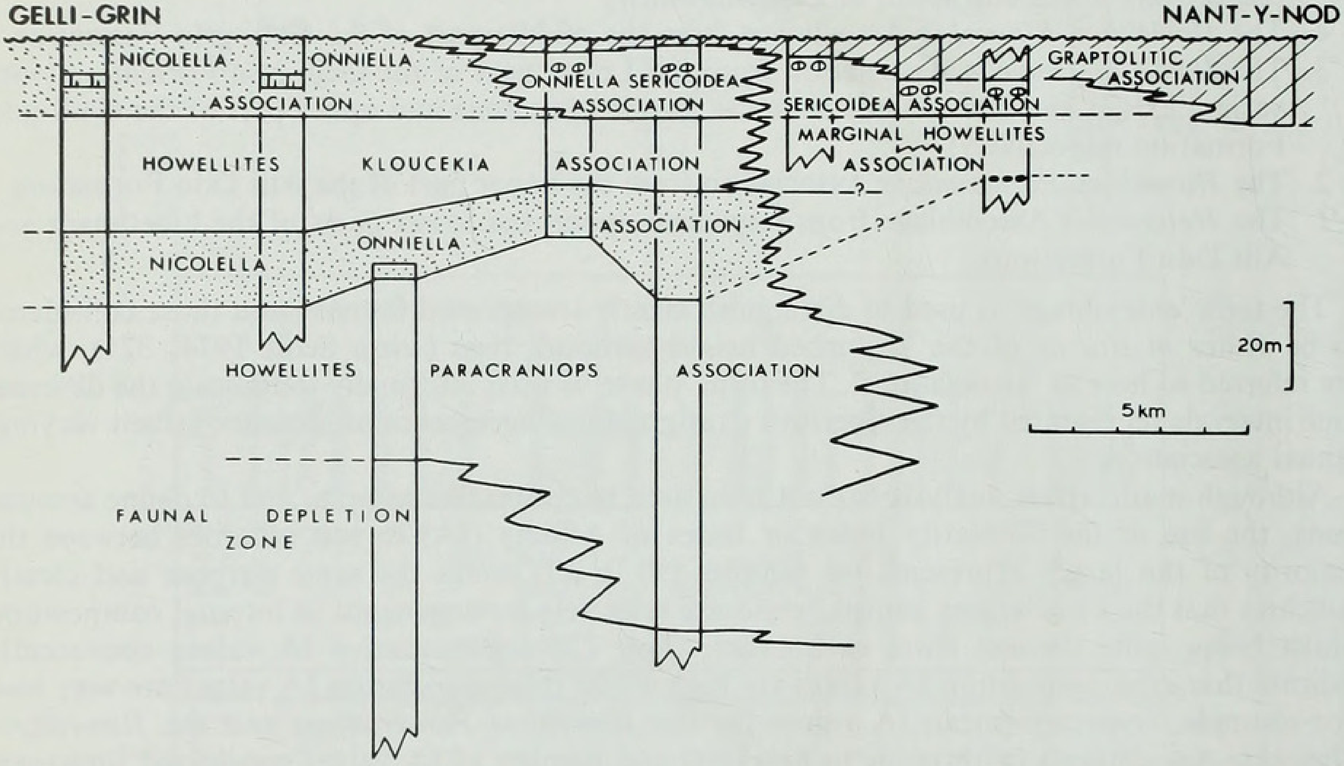


Fig. 18 Stratigraphical distribution of named faunal associations in the upper part of the Lower Bala Group (drawn to scale).

The only differentiation made between 1st and 2nd order characterizing species was that 1st order species occur 'practically everywhere' in a specific community whereas 2nd order species occur 'only in certain parts' of such specific communities. Biomass estimates cannot be derived from fossil associations without at least making numerous assumptions and repetitive measurements for the calculation of the mean size of each population. Nevertheless, in the absence of other evidence, relative abundance can be used as it is in this study as an alternative estimate of an association's composition. If this is done with the aim of identifying characterizing species it becomes clear that only the dominant species fall within this category.

Named Associations from the Caradoc Series of the Bala to Dinas Mawddwy area

Associations in the Allt Ddu Formation

(i) The *Howellites–Paracraniops* Association, characteristic of the upper part of the Allt Ddu Formation, contains no genera, other than these two and *Broeggerolithus*, which are representative of biospecies which could be considered strictly analogous to 1st or 2nd order characterizing species (Fig. 19). Although several other genera listed here occur in at least 50% of samples, in

TAXA/GENERA	A OCCURRENCE	(%)	MEAN ABUNDANCE	B OCCURRENCE	(%)	MEAN ABUNDANCE
Howellites	12/12	100 %	53.45%	23/24	95.8%	37.42%
Paracraniops	12/12	100 %	11.95%	17/24	70.8%	7.13%
Bryozoa	12/12	100 %	5.98%	22/24	91.7%	13.35%
Broeggerolithus	12/12	100 %	4.02%	24/24	100 %	8.67%
Macrocoelia	10/12	83.3%	4.32%	8/24	33.3%	1.51%
Brongniartella	8/12	66.7%	1.19%	20/24	83.3%	2.03%
Ostracoda	5/12	41.7%	1.25%	19/24	79.2%	4.42%
Bivalvia	5/12	41.7%	1.13%	8/24	33.3%	0.75%
Gastropoda	5/12	41.7%	0.84%	16/24	66.7%	3.39%
Reuschella	4/12	33.3%	4.47%	5/24	20.8%	1.42%
Dinorthis	3/12	25.0%	1.20%	0/24	-	-
Leptaena	3/12	25.0%	0.80%	10/24	41.7%	1.73%
Sowerbyella	2/12	16.7%	3.78%	1/24	4.7%	0.84%
Bicuspina	2/12	16.7%	0.34%	14/24	58.3%	4.49%
Sericoidea	0/12	-	-	12/24	50.0%	3.48%
		TOTAL	94.72%		TOTAL	90.63%

TAXA/GENERA	C OCCURRENCE	(%)	MEAN ABUNDANCE	D OCCURRENCE	(%)	MEAN ABUNDANCE
Onniella	26/26	100 %	27.52%	0/7	-	-
Bryozoa	26/26	100 %	17.11%	6/7	85.7%	14.18%
Skenidioides	23/26	88.5%	6.08%	4/7	57.1%	5.58%
Bicuspina	22/26	84.6%	7.11%	1/7	14.3%	0.57%
Eoplectodonta	18/26	69.2%	10.59%	5/7	71.4%	13.69%
Reuschella	17/26	65.4%	2.93%	3/7	42.8%	4.24%
Nicolella	15/26	57.7%	4.26%	5/7	71.4%	15.25%
Dolerorthis	7/26	26.9%	0.32%	7/7	100 %	19.28%
		TOTAL	75.92%		TOTAL	72.79%

TAXA/GENERA	E OCCURRENCE	(%)	MEAN ABUNDANCE	F OCCURRENCE	(%)	MEAN ABUNDANCE
Howellites	21/21	100 %	65.98%	10/10	100 %	83.66%
Kloucekia	21/21	100 %	3.69%	3/10	30 %	0.80%
Broeggerolithus	20/21	95.2%	3.83%	4/10	40 %	0.84%
Sericoidea	12/21	57.1%	2.46%	7/10	70 %	10.34%
Skenidioides	11/21	52.4%	0.97%	0/10	-	
		TOTAL	76.93%		TOTAL	95.64%

TAXA/GENERA	G OCCURRENCE	(%)	MEAN ABUNDANCE	H OCCURRENCE	(%)	MEAN ABUNDANCE
Onniella	16/16	100 %	36.77%	-	-	-
Dalmanellidae	-	-	-	3/7	42.8%	3.70%
Sericoidea	14/16	87.5%	38.39%	7/7	100 %	84.2 %
Bryozoa	13/16	81.2%	2.68%	-	-	-
Skenidioides	11/16	68.7%	4.51%	-	-	-
Conularida	11/16	68.7%	5.52%	4/7	57.1%	3.01%
Cyclospira	7/16	43.7%	2.27%	2/7	28.6%	1.68%
Ostracoda	7/16	43.7%	2.18%	-	-	-
Kloucekia	7/16	43.7%	1.13%	2/7	28.6%	0.71%
Eoplectodonta	6/16	37.5%	2.99%	-	-	-
Broeggerolithus	5/16	31.2%	2.25%	3/7	42.8%	1.42%
Nicolella	5/16	31.2%	0.59%	-	-	-
Graptoloidea	0/16	-	-	1/7	14.3%	2.14%
		TOTAL	99.28%		TOTAL	96.88%

Fig. 19 A & B. Dominant and persistent taxa/genera in the *Howellites–Paracraniops* association in the upper part of Allt Ddu Formation at Craig y Gath (A) and Rhiw March (B); in the *Nicolella–Onniella* association from the (C) lower and (D) upper parts of the Gelli-grîn Formation; in the *Howellites–Kloucekia* association from the middle part of the Gelli-grîn Formation (E) and the marginal *Howellites* association from the uppermost Ceiswyn Mudstone Formation (F); in the *Onniella–Sericoidea* association (for Conularida read Macheridia) (G) and the *Sericoidea* association (H) of the Dyfi Mudstone.

most cases their mean relative abundance is less than 5%. With the probable loss of soft-bodied representatives of the fauna in the process of fossilization, all relative abundance figures would tend to be proportional overestimates. It is therefore probable that even fewer species can be confidently considered analogous to characterizing species (*sensu* Thorson 1957).

Although it is only possible confidently to use samples with at least 20 individuals for the purposes of calculating relative mean percentages of taxa comprising associations, the calculation of mean diversity is derived from the consideration of all samples in order to avoid an overestimate of diversity. The *Howellites–Paracraniops* Association has a mean diversity of 9·68 but can locally be found to yield samples with a diversity of up to 17. The association is named after *Howellites ultimus* Bancroft and *Paracraniops glaber* sp. nov. (p. 204) which both occur persistently and relatively abundantly; respective values for the two sections studied are 95·8–100% occurrence (with mean relative abundance of between 37·4 and 53·5%) for *H. ultima* and 70·8–100% occurrence (with a mean relative abundance of between 7·1 and 12%) for *P. glaber*. *Broeggerolithus* (cf. *B. soudleyensis* Bancroft) is of equal importance, occurring in all samples with a mean relative abundance of between 4 and 8·7%. Bryozoa are also an important element of the fauna with two morphospecies (a prasoporid and a ramose bryozoan) representing 6–13·4% of the fauna in almost all samples (92–100%); see Fig. 19, p. 193. Amongst the other more important 'associated species' are *Macrocoelia prolata* Williams and *Reuschella horderleyensis undulata* Williams from the Craig y Gath section and *Bicuspina spiriferoides* (M'Coy), *Sericoidea* sp. and *Brongniartella* cf. *minor* (Salter) from the Rhiw March section, all of which occur in at least 25% of samples with a mean relative abundance of between 2 and 4·7%. The Gastropoda (including *Sinuites* sp. and *Cyclonema* sp.) are an important element of the association at the latter locality.

Although there is variation in the composition of the association between the two localities of Craig y Gath and Rhiw March its extent is insufficient to suggest the existence of more than one association at these horizons.

Associations in the Gelli-grîn Formation

The Gelli-grîn Formation is characterized by three stratigraphically successive associations (Figs 16, 18), which are here described in sequence. These are the *Nicolella–Onniella* Association (phase 2) and the *Howellites–Kloucekia* Association respectively from the lower and middle parts of the formation between Gelli-grîn and Rhiw March, and also the *Nicollela–Onniella* Association (phase 3) of the upper part of the formation between Gelli-grîn and Pen y Cefn Coch. This latter association is related to the association from the lower part of the formation and to the *Onniella–Sericoidea* Association of the Dyfi Mudstone.

(ii) The *Nicolella–Onniella* Association (phase 2). From the lower part of the Gelli-grîn Formation this is a high diversity association (mean 17·5) named after *Nicolella actoniae obesa* Williams and *Onniella ostentata* Williams. The latter form is particularly abundant (Fig. 19) and is associated with large numbers of *Eoplectodonta rhombica* (M'Coy). This association is to some extent similar in composition to the Derfel Limestone association (phase 1 of the *Nicolella–Onniella* Association), which includes *Dolerorthis tenuicostata* Williams, *Nicolella humilis* Williams, *Onniella* aff. *avelinei* Bancroft and *Eoplectodonta lenis* Williams amongst the most common Brachiopoda. The Derfel Limestone association is also of a high diversity, yielding up to 28 species from a single large sample; such values compare with maximum values of 25 for samples from the lower part of the Gelli-grîn Formation. The association from the upper part of the Gelli-grîn Formation (phase 3; mean diversity 13·7 and maximum 19) is also referred to here as the *Nicolella-Onniella* Association although it is again different in composition from the association in the lower part of the formation (Fig. 19). *N. actoniae obesa* Williams and *E. rhombica* (M'Coy) are common at horizons in both the lower and upper parts of the formation; however, *Dolerorthis duftonensis prolixa* Williams, which is uncommon from the lower part of the formation, occurs abundantly in the uppermost parts. *O. ostentata* Williams is not recognized from the upper part of the formation; the Dalmanellidae are poorly represented and assigned to *Onniella* sp., *Dalmanella* sp. or in a few cases *Bancroftina* sp.; Figs 7A, 12 and 13 do not distinguish between these three genera.

The composition of the *Nicolella–Onniella* Association (phase 2) from the lower part of the Gelli-grîn Formation is calculated from the analysis of samples GG1b–GG1e, GG2a–GG2c, ADZ, ADY, TB9–TB13 and R24–R35. The summary of these data, shown in Fig. 19, indicates that, at this level, *Onniella* and *Eoplectodonta* are analogous to 'characterizing species' with *Reuschella* and *Nicolella* representing 'associated' forms. Although *Skenidioides*, *Bicuspina* and *Reuschella* are important constituents of this association, conspecific forms also constitute a significant element in other associations; they cannot therefore be considered strictly analogous to 1st or 2nd order characterizing species in the *Nicolella–Onniella* Association.

There is some lateral variation in the composition of the lower Gelli-grîn faunal association; this corresponds to a decrease in sediment coarseness towards the SSW. The most notable changes are a relative increase in the abundance of *Bicuspina* and *Leptaena* in this direction and a corresponding decline in the abundance of *Eoplectodonta* and *Nicolella* (Figs 12, 13). Rare occurrence of *Sowerbyella* in the Rhiw March section are unique to the formation and indicative of the modification of this association towards the SSW.

(iii) The *Howellites–Kloucekia* Association. The middle part of the Gelli-grîn Formation is mainly argillaceous; representative samples from beds GG1f–GG1gl, GG2d–GG2g, TB14–TB17 and R36–R44 reveal a faunal association dominated by *Howellites antiquior* (M'Coy), *Kloucekia apiculata* (M'Coy) and *Broeggerolithus nicholsoni* (Reed). The association has a mean diversity of 12·7. Maximum diversity values in excess of 20 have been recorded from samples GG1gl, GG2d and GG2e; however, these are atypical in being recovered from horizons closely associated with overlying and underlying strata containing higher diversity associations. The other 18 samples, particularly those from Tan y Bwlch and Rhiw March, exhibit lower diversities; minimum values do not exceed 4.

Although *Kloucekia* and *Broeggerolithus* are considered to each represent less than 4% of the total fauna (Fig. 19) in this association (when using the arbitrary correction factor of 4 as a compensation for ecdysis), it is clear that a correction factor of say 2 or 3 would indicate a mean relative abundance analogous with that of 'characterizing' species. *Sericoidea*, whilst being analogous to an 'associated' species, is known to be mainly restricted to the two southern sections (Figs 12, 13). The occurrence of *Skenidioides* in most samples from the Gelli-grîn associations is noted.

(iv) The *Nicolella–Onniella* Association (phase 3). The composition of this in the upper part of the Gelli-grîn Formation differs from that noted for the related phases of the association elsewhere in the succession; for example, it is only at this level that *Dolerorthis duftonensis prolixa* Williams can be considered analogous to a characterizing species (Fig. 19). Differences in composition are thought to be directly related to the distinctive calcareous facies associated with the Cymerig Limestone Member north of Pen y Cefn Coch. Caradoc strata above the Cymerig member in this region consist predominantly of coarse, shelly calcarenites containing tuffaceous material and ? ferruginous oolites. At certain horizons (GG2k and sample 615) vertical crinoid stems and bryozoan fronds are noted; these are considered indicative of the rapid deposition of coarse material in a shallow-water environment. Bulk samples are only readily obtained from a few horizons in the Cymerig and higher beds; in general the limestones and associated rocks are unyielding enough to present practical sampling problems. Of the 9 samples collected in this study only 7 yielded sufficient specimens to permit the estimation of relative abundances (Fig. 19). Owing to the small number of relatively variably composed samples, it is considered that the only clearly-defined characteristics which distinguish this facies fauna from related associations elsewhere in the area is the relative dominance of *Dolerorthis* and *Nicolella* and the small numbers of dalmanellids.

(v) The *Onniella–Sericoidea* Association. This facies fauna is found in association with the argillaceous Dyfi Mudstone Member between Tan-y-Bwlch and Rhiw March (Fig. 18). It is laterally equivalent to the coarse, calcareous beds containing the continuous Cymerig Member north of Pen y Cefn Coch and, although containing the discontinuous 'distal' parts of the Cymerig Member south of this locality, otherwise represents the most marked lateral facies and faunal change observed in this study.

The association is dominated by *Sericoidea abdita complicata* subsp. nov. (p. 212) and *Onniella* sp., which between them represent over 75% of the total fauna and are the only forms analogous to 'characterizing 'species. Poor preservation (associated with relatively intense cleavage in this argillaceous facies) militates against sound statistical assessment of the *Onniella* specimens for a specific determination. Less distorted specimens from the Cymerig Member display only external features.

Cyclospira, *Skenidioides* and *Eoplectodonta*, together with the ostracod *Tallinnella*, can all be considered analogous to 'associated animals'. The association has a mean diversity of 10·9 with maximum values (up to 17) representative of the Limestone Member and associated more calcareous shales. *Broeggerolithus* and *Flexicalymene* are particularly abundant at certain horizons (e.g. R49) in the Rhiw March section.

Similarities between the fauna from this association and the *Nicolella–Onniella* Association to the north help substantiate correlations between quite different facies, respectively of argillaceous and coarse calcareous sediment (Fig. 18). It is of interest to note that *Nicolella*, *Dolerorthis*, *Eoplectodonta*, *Leptestiina*, *Reuschella*, *Rhactorthis*, *Leptaena*, *Flexicalymene*, *Cyclospira*, *Onniella* and *Sericoidea* are amongst the genera common to both associations; the latter three dominate in the *Onniella–Sericoidea* Association whilst the other forms, common to the north, are rarer here to the south. *Protozyga*, *Paterula*, *Phillipsinella*, *Lonchodomas* and *Sphaerocoryphe* are all unique to this association being currently unknown elsewhere in the area.

(vi) The *Sericoidea* Association, although related to the *Onniella–Sericoidea* Association, is considerably less diverse (mean diversity 4·25, maximum 8). The association characterizes the Dyfi Mudstone Member between Pistyll Gwyn and Aber Cowarch (Fig. 18). Representative samples (PG1a, PG1b, PG2, YC3, YC4, YC5, AB4 and AB5) indicate an association entirely dominated by *Sericoidea* with a few poorly-preserved macheridians and dalmanellids showing distribution patterns analogous to those of 'associated animals'. *Broeggerolithus*, *Kloucekia* and unidentifiable graptolites also occur. *Cyclospira* and a spired gastropod are known from the Cymerig member whilst additional molluscan material is known from the locally-developed underlying limestone beds at Pistyll Gwyn.

(vii) The Marginal *Howellites* Association. Samples PG, YC1–2, AB05–09 and AB1–2 (Fig. 17, p. 190) have yielded a low diversity (mean 3·25) *Howellites*-dominated fauna. Although preservation of most of the material is poor it has been possible to identify *H. antiquior* (M'Coy) as the dominant species (83·7%). *Sericoidea* is also 'characteristic' of this association; however, its abundance is almost one order of magnitude less than in the succeeding *Sericoidea* Association. *Kloucekia* and *Broeggerolithus* both occur relatively abundantly in beds underlying those associated with the first major influx of *Sericoidea* (i.e. samples PG, YC2 and AB3; Fig. 17). Elsewhere throughout these successions their distribution is variable.

The Marginal *Howellites* Association is clearly related to the *Howellites–Kloucekia* Association typical of the middle part of the Gelli-grîn Formation both in terms of faunal composition and stratigraphical relationships. However, since the Cowarch Phosphate Bed and associated shell beds may be contemporaneous with the Pont y Ceunant Ash (Lockley 1980), the Marginal *Howellites* Association could also have been established in the Abercowarch area in Lower Gelli-grîn times and subsequently migrated diachronously northwards in middle Gelli-grîn times.

(viii) The Graptolitic Association. The uppermost part of the succession in the Tan y Bwlch to Aber Cowarch sections (Figs 13–17) consists of dark grey or black graptolitic or virtually unfossiliferous shales referred to as the Corris Shale Member (Lockley 1977, 1980). These beds are lithostratigraphically equivalent to the graptolitic Nod Glas seen at the type locality Nant y Nod. Since these dark pyritous shales have yielded only one or two small shelly fossils (samples

YC6, AB6 and AB7), from lower beds, it is convenient to refer to the fauna of this member as a graptolitic association.

(ix) The *Heterorthis* Assemblage. The shell beds dominated by *Heterorthis* and *Sowerbyella* beneath the Frondderw Ash in the Llaethnant Siltstone in Afon Twrch are considered separately from the younger named associations described above. The distinctive shell beds are concentrated in only about 15 m of strata (samples H1–H19 and equivalents, see Figs 3–5, pp. 174–177), and are considered to represent transported assemblages. These richly fossiliferous beds are underlain and overlain by mudstones and siltstones which are generally sparsely fossiliferous (Fig. 3); mean percentage values from these small samples would be of little value. Even within the shell bed sequence there are sudden changes in the composition of the faunas at successive horizons; samples H2, H4–H6 and H16–H19 are dominated by *Sowerbyella*, sample H7 is dominated by *Reuschella* and the Dalmanellidae whilst samples H8–H15 are dominated by *Heterorthis*. Mean Index of Affinity (IA) values for samples H8–H15 and H16–H19 respectively are 84·3 and 88·2; these contrast markedly with the IA value of 5·0 derived from a comparison of samples H15 and H16 and serve to demonstrate just how pronounced the sudden changes in faunal composition are. Similarly, the mean diversity of taxa (species) in the shell bed sample H1–H19 is 11·25 (maximum value 17) whereas the mean diversity for overlying samples H20–H29 is 4·5 (maximum 9).

The composition of faunas above and below the shell beds is essentially similar to that observed in less fossiliferous parts of the Allt Ddu, Glyn Gower and Llaethnant Formations and so could be considered a poorly-developed expression of the *Howellites–Paracraniops* Association described from the upper part of the Allt Ddu Formation.

In contrast, however, the shell beds containing *Heterorthis* cf. *retrorsistria* (M'Coy) and *Sowerbyella sericea permixta* Williams, whilst being reminiscent of the *Heterorthis* 'faunule' (*sensu* Bassett *et al.* 1966 : 237), contain *Onniella ostentata* Williams, *Nicolella* sp., *Orthisocrania* sp., *Salopia* sp., *Dolerorthis* sp. and *Chasmops* sp., all of which are considered characteristic of the *Nicolella–Onniella* Association. They are also characterized by significant numbers of *Dinorthis* and *Reuschella* and various cephalopod and gastropod species.

Although the relationship between this *Heterorthis–Sowerbyella* Assemblage and its rare elements is unknown, it is reasonable to assume that a *Nicolella–Onniella* type of association was established locally in pre-Frondderw times.

Diversity patterns

There are various methods by which relative diversity values D may be calculated. The two methods chosen here are the Margalef method which uses the formula $D=(S-1)/\log N$ (Margalef 1958) and the Sanders (1968) rarefaction technique which is similarly designed to calculate diversity values for a standard sample size (in this case 50 individuals). Both methods have been applied to palaeoecological studies; for example, Ziegler *et al.* (1968) used the Margalef index in the modified form $D=S/(\log N)$, and various authors including Calef & Hancock (1974), Antia (1977), Fürsich (1977) and Watkins (1979) have used the Sanders rarefaction techniques.

MacArthur (1965 : 511) stated that the simplest measure of species diversity was a count of number of species. Similar simple definitions of species diversity or species richness given in numerous standard texts, e.g. Krebs (1978 : 374) and Valentine (1973 : 288), usually refer to community diversity but may equally well be applied to the diversity of individual samples.

Since a simple count of species diversity is a prerequisite for the calculation of relative diversity values in a series of samples, the original, size-dependent diversity values are plotted alongside standardized values for comparative purposes (Figs 20, 21).

The two standardizing methods applied here have the effect of smoothing out patterns of excessive fluctuation which are related to sample size; they also serve to emphasize real patterns of variation like the pronounced fluctuations observed in the Rhiw March succession (Fig. 20). Here a moderately diverse association in the lower part of the sampled Allt Ddu succession is succeeded by less fossiliferous strata, with a less diverse fauna, in the uppermost part of the

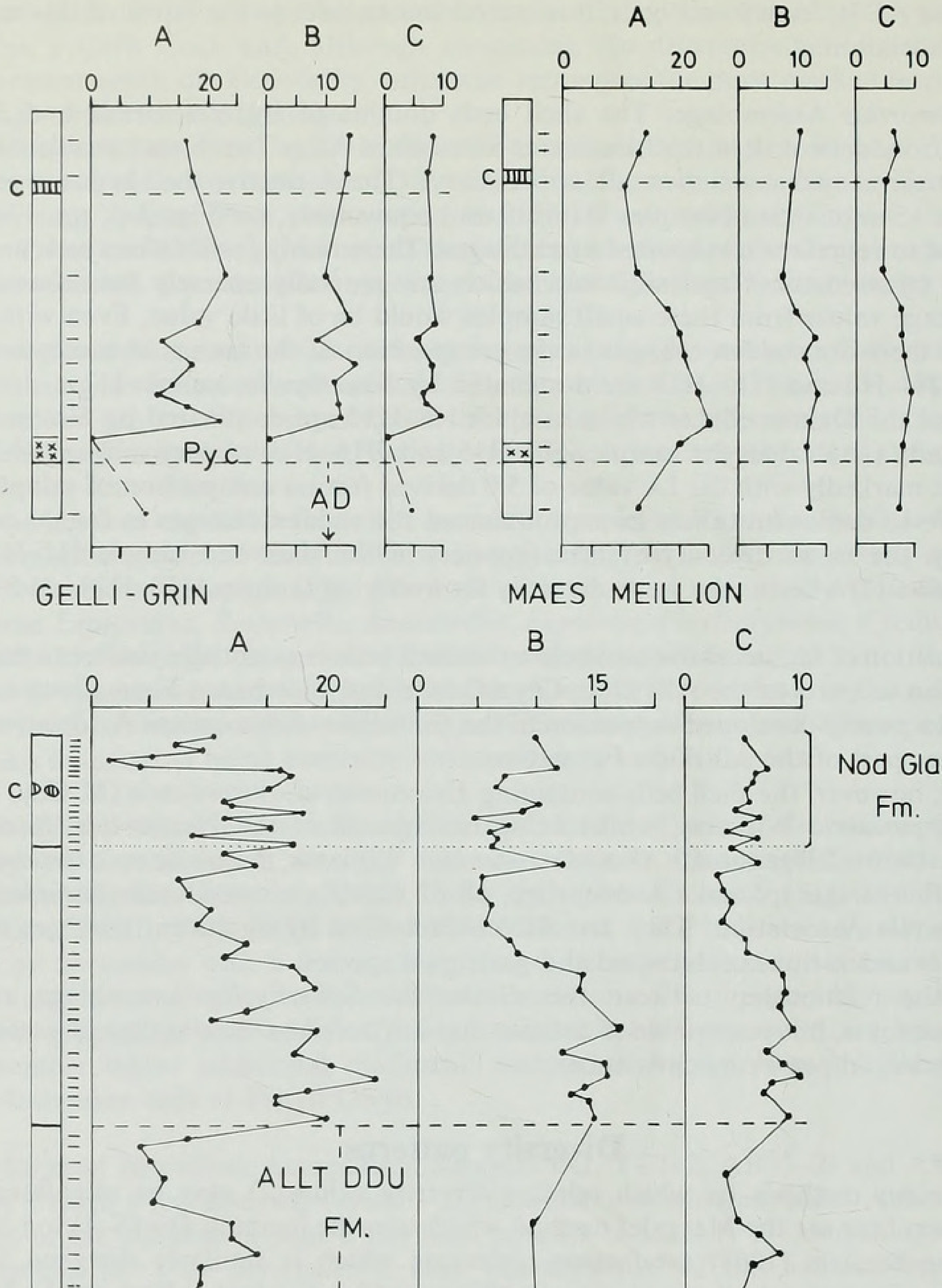


Fig. 20 Faunal diversity patterns in parts of the Allt Ddu (AD) and Gelli-grîn Formations (including the Cymerig (C) and Pont y ceunant (Pyc) Members) at three named localities. A represents species per sample; B represents diversity values standardized to a sample size of 50 individuals using the Sanders (1968, 1969) rarefaction technique; C represents diversity values derived from the Margalef (1958) index.

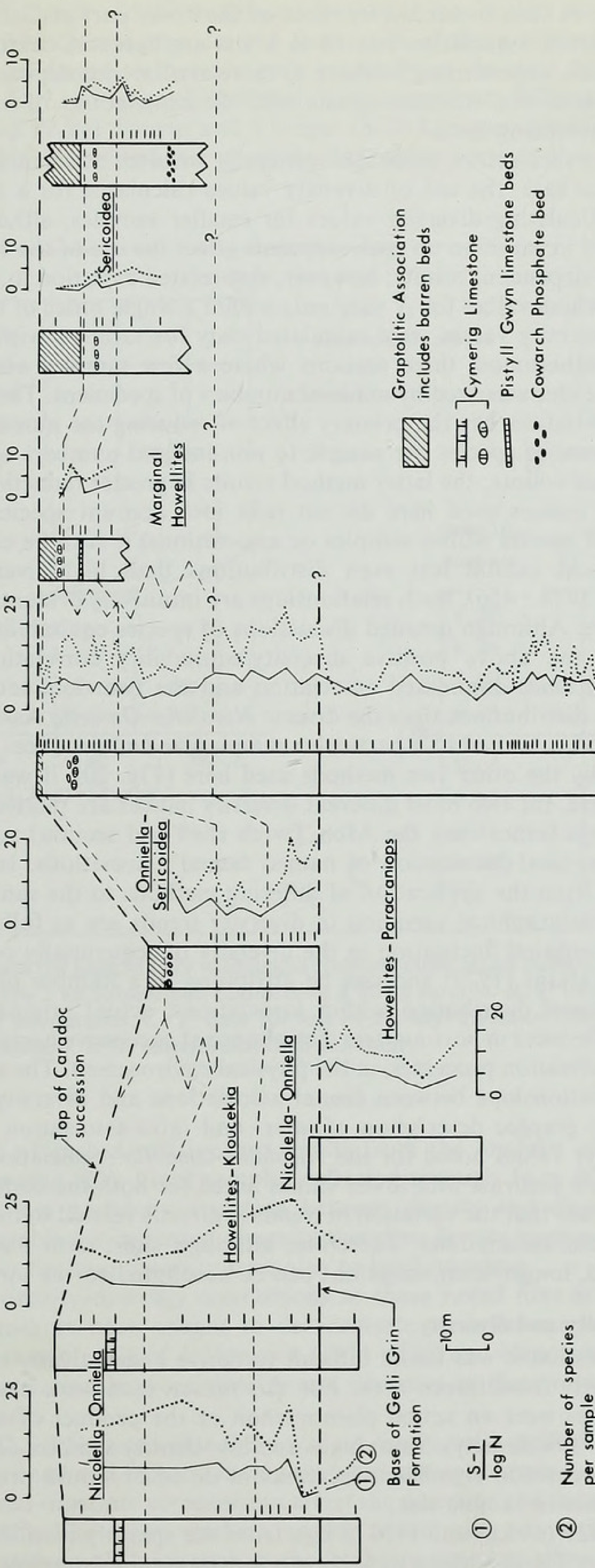


Fig. 21 Faunal diversity patterns and their relationship to faunal associations.

formation; these beds are in turn succeeded by those of the lower part of Gelli-grîn Formation which contain a high-diversity association related to a less argillaceous, calcareous facies. The middle part of the formation, representing a return to more argillaceous deposition, is characterized by a low-diversity association which contrasts with the associations of higher diversity of both the preceding and succeeding beds.

The use of the Sanders rarefaction technique generally involves adherence to a particular, chosen sample size. In this case, the use of diversity values calculated for a sample size of 50 avoids the necessity of calculating diversity values for smaller samples, although this may be done if desired. When used in isolation no such restraints affect the use of the Margalef diversity index which produces size-dependent results; however, size-related variation in diversity values is not excessive in this case where values for N vary only within a single order of magnitude. In the present study Margalef diversity values were calculated only for samples with at least 20 individuals, except in the southernmost three sections where a few samples associated with the Graptolitic Association are characterized by minimal numbers of specimens. The estimation of the Sanders and the Margalef indices has the primary effect of reducing the numerical value of the original whole-number count of species per sample to non-integral numbers of little more than 50% of the value of original counts; the latter method results in greater reductions (Fig. 20).

Although the diversity indices used here do not take into account species equitability (or evenness of distribution of species within samples or associations) it is to be expected that low-diversity associations would exhibit less even distributions than high-diversity associations (Pielou 1969 : 233; Krebs 1978 : 456). Such relationships are intuitively evident in the case of the associations discussed here. Although detailed discussions of species equitability are outside the present scope, following the above positive diversity/equitability correlation we may say, for example, that the *Sericoidea*-dominated association and the two dominated by *Howellites* have less equitable species distributions than the diverse *Nicolella–Onniella* Association.

Since the Sanders method is limited to a particular sample size and produces values which fall between those calculated by the other two methods used here (Fig. 20), it was not used in the compilation of Fig. 21. Here, the two most different diversity indices are plotted for all the main thoroughly-sampled sections (other than the Afon Twrch shell bed section) and shown in conjunction with the stratigraphical distribution of named faunal associations. In addition to the parallel patterns resulting from the application of differing methods to the same data, the most striking features of the stratigraphical variation in diversity trends are as follows. Firstly, it is apparent that there is a continual fluctuation in the diversity of sequentially collected samples; this has been noted by Watkins (1979) and can be attributed to a number of possible factors including patchiness of faunal distribution within associations, actual original fluctuations of diversity with time and differences in *post-mortem* disturbance at successive horizons or variations, including variations in fossilization processes, in the physical environment. The second distinctive pattern pertains to the relationships between faunal associations and diversity trends; Fig. 21 serves as a comprehensive graphic description of inter- and intra-association diversity trends. The relatively high diversity values noted for the *Nicolella–Onniella* Association from the lower part of Gelli-grîn Formation contrast with lower values noted for both the underlying and overlying associations and indicate that the variation in trends is directly related to original differences in the composition of these associations. Therefore, although short-term fluctuations cannot be unequivocally explained, longer-term variations can be accounted for to some degree.

Relationships between density and diversity

In lower parts of the succession it was found difficult to derive a statistically-valid sample (e.g. 50 individuals) from sparsely fossiliferous rock. For this reason tests were devised to establish whether low diversity values were an actual phenomenon or the product of small numbers of individuals in a sample (i.e. low density). Since high- and low-density samples often show similar patterns of taxonomic composition significant increases in diversity would probably not result from corresponding increases in sample size.

Two large collections, H29 (10 kg) and H26 (8 kg), from the sparsely fossiliferous lower Allt-Ddu Mudstones of the Afon Twrch section were chosen for testing. Each sample was divided into

2 kg 'sub-samples' of rock and the total fauna from each was broken out and identified separately. A consistent number of taxa was derived from each of these sub-samples and the cumulative number of taxa was found to increase only gradually as the data from each sub-sample were pooled (Fig. 22). A χ^2 test revealed that there is no significant difference between the taxonomic diversity in a small (2 kg) sample and a larger (8–10 kg) one; for H29 $98\% > P > 95\%$ and for H26 $95\% > P > 90\%$. This implies a positive relationship between low density and low diversity.

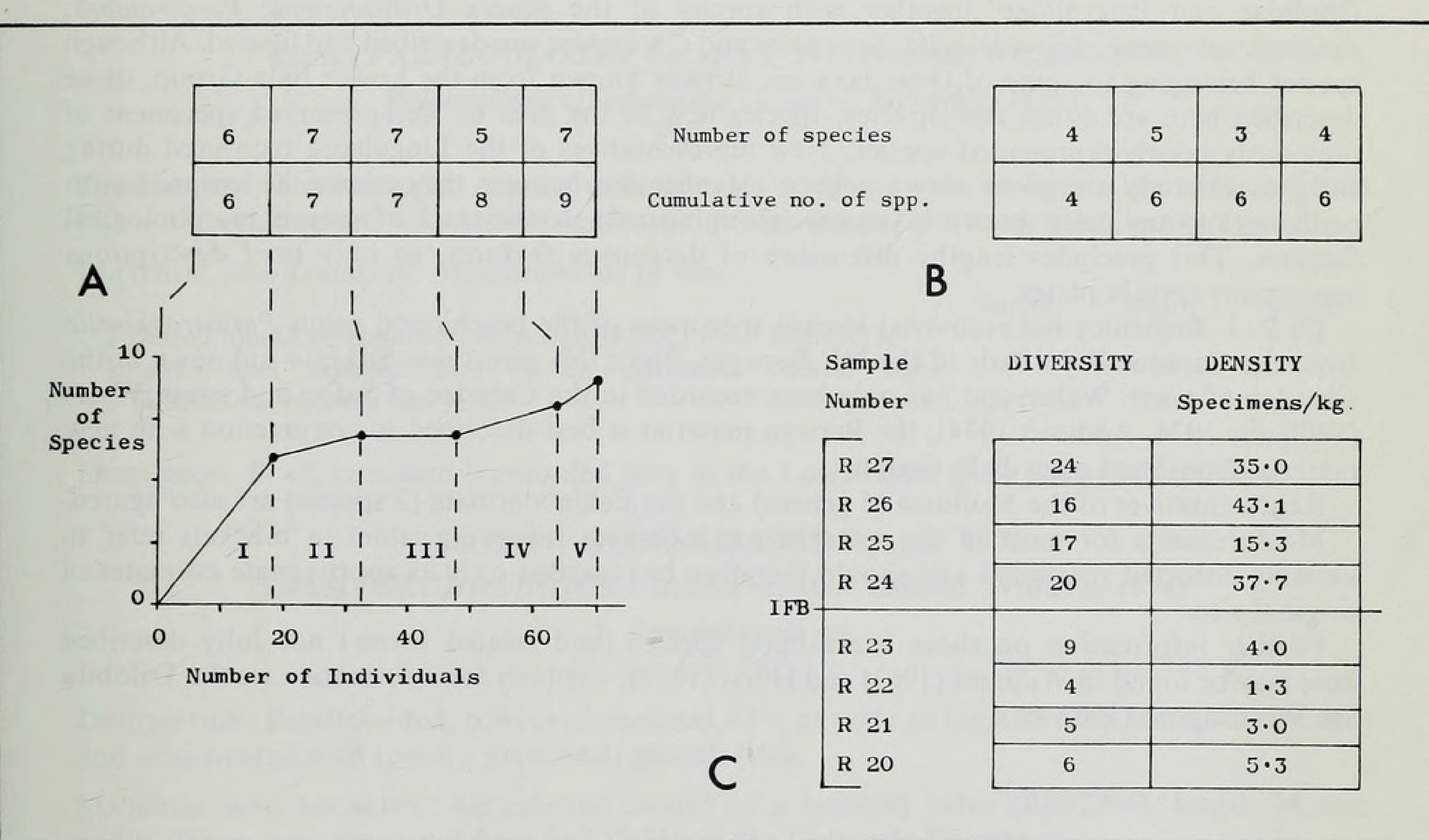


Fig. 22 A, χ^2 data for sample H29 with graph showing cumulative number of species and individuals derived from five 2 kg subsamples comprising a 10 kg sample. B, χ^2 data for sample H26, divided into four 2 kg subsamples. C, χ^2 data for test of density–diversity relationships in a part of the Rhiw March section. IFB: interformational boundary.

Further evidence of such a relationship results from the analysis of a series of samples from contrasting facies (Fig. 22). Eight samples collected through 16 m of strata and across a facies boundary all show a positive correlation between density and diversity (χ^2, $50\% > P > 20\%$). Conditions favourable for increased diversity therefore favour increased numbers of individuals; conversely, factors limiting diversity tend also to limit numbers.

Such positive density–diversity correlations as those noted here are by no means universally evident; many authors have sought to demonstrate an inverse relationship between the two parameters. For example, Calef & Hancock (1974 : 779) and Hancock *et al.* (1974 : 151) referred to a negative correlation between density and diversity in their respective analyses of Silurian benthic communities.

Valentine (1972 : 195) stated that there was no single, well-verified theory of diversity regulation. Many environmental factors, including temperature, temperature stability, depth, salinity, current activity and substrate composition affect the diversity and density of benthic associations. The present author, like many workers, avoids considering any single factor in isolation and tends to favour unifying theories such as the 'stability-time hypothesis' (Sanders 1969).

Taxonomic descriptions

The main aim of this section is to describe and figure genera and species hitherto unknown in the Lower Bala Group. Amongst these are representatives of the trilobite genera *Cyphoproetus*, *Lonchodomas*, *Phillipsinella* and *Sphaerocoryphe*. Species of the brachiopod genera *Bimuria* and *Protozyga* are recorded in Wales for the first time. Excluding *Cyphoproetus*, the above-mentioned genera are from the Gelli-grîn Formation (at Rhiw March) and current evidence suggests that their distribution elsewhere is very restricted. Representatives of the brachiopod families Obolidae and Paterulidae, together with species of the genera *Orthisocrania*, *Paracraniops*, *Palaeostrophomena*, *Anisopleurella*, *Sericoidea* and *Cyclospira*, are described and figured. Although species belonging to some of these taxa are already known from the Lower Bala Group, those described here are either new species, species new to the area or well-preserved specimens of previously poorly-represented species. New representatives of the Lingulacea recovered during the present study are given only a generic classification because they cannot be assigned with confidence to any more specific taxonomic grouping owingto their lack of internal morphological features. This precludes lengthy discussion of diagnostic features, so only brief descriptions accompany certain plates.

Dr P. J. Brenchley has recovered several specimens of the brachiopod genus *Parastrophinella* from the Caradoc Bryn Beds of the NE Berwyns. Since this genus was hitherto unknown in the Caradoc of north Wales, and has only been recorded in the Caradoc of Salop and south Wales (Williams 1974, Addison 1974), the Berwyn material is best described in conjunction with new material from the Lower Bala Group.

Representatives of the Mollusca (6 genera) and the Echinodermata (2 species) are also figured.

Measurements for most of the material are included; however, values in brackets refer to variably distorted specimens and should therefore be regarded only as approximate estimates of original size.

Further information on those brachiopod species (and related forms) not fully described here may be found in Williams (1963) and Hurst (1979); similarly for information on the Trilobita see Whittington (1962–68).

Phylum **BRACHIOPODA** Dumeril, 1806
Class **INARTICULATA** Huxley, 1869
Order **LINGULIDA** Waagen, 1885
Superfamily **LINGULACEA** Menke, 1828
Family **OBOLIDAE** King, 1846
Subfamily **LINGULELLINAE** Schuchert, 1893

Genus ***LINGULELLA*** Salter, 1866

? ***Lingulella*** sp.
Fig. 24

DESCRIPTION. Suboval, convex specimen of exfoliated *Lingulella*, with pedicle valve 80 % as wide as long and an acute beak (< 90°); ornamented with concentrically-arranged growth lines numbering at least four per mm at 3 mm anterior of the umbo, with fine fila between growth lines.

MATERIAL AND LOCALITY. Complementary internal and external parts (BB92200a, b) of exfoliated pedicle valve (length 8 mm, width 6·5 mm, depth at umbo 0·7 mm) from fossiliferous shales at Pont Aber Derfel (SH 850395), the type locality for the Derfel Limestone.

DISCUSSION. This is the first record of a genus belonging to the Inarticulata in this oldest member of the Lower Bala Group.

Lingulella* cf. *ovata (M'Coy, 1846)
Fig. 25

Description. Suboval, convex specimen of a pedicle valve 70% as wide as long and with an acute beak (<90°). Ornamented with fine concentric growth lines seen only at anterior commissure (spacing 0·3 mm).

Material and locality. Complementary internal and external parts (BB92201a, b) of exfoliated pedicle valve from bed R36 in the Gelli-grîn Formation at Rhiw March.

Genus ***PALAEOGLOSSA*** Cockerell, 1911 (emend. Williams 1974)

Palaeoglossa* cf. *attenuata (J. de C. Sowerby, 1839)
Figs 26, 27

Description. Subtriangular convex pedicle valve 65% as wide as long with an acute beak (60° ± 5°), ornamented with strong concentric growth lines (2 per mm) in addition to fine fila.

Material and locality. Measurements in mm.

	length	width	depth
External mould of conjoined valves (BB92202) from bed GG1d .	14	9	1·5
Internal and external part of an exfoliated pedicle valve (BB92203a, b) from bed R52	10	6.5	–

Discussion. *P.* cf. *attenuata* is recorded here in the Lower Bala Group for the first time.

Subfamily **GLOSSELLINAE** Cooper, 1956

Genus ***PSEUDOLINGULA*** Mickwitz, 1909 (emend. Williams 1974)

? ***Pseudolingula*** sp.
Fig. 28

Description. Parallel-sided, convex glossellinid 42% as wide as long with an acute beak (<90°) and ornamented with (poorly preserved) growth lines.

Material and locality. An external mould of a brachial valve (BB92204), length 24 mm, width 10 mm, was recovered from bed GG1b in the Gelli-grîn Formation.

Discussion. *Pseudolingula* is recorded here in the Lower Bala Group for the first time.

Family **PATERULIDAE** Cooper, 1956

Genus ***PATERULA*** Barrande, 1879

Paterula sp.
Figs 29a, b, 30

Description. Smooth oval *Paterula* with rounded posterior and anterior margins. 76–84% as wide as long, beak poorly defined. Well-developed marginal limbus.

Material and locality. Single specimens of the external and internal moulds of convex pedicle (?) valves (BB92205, BB92206) respectively from beds R52 and R53 in the Cymerig Limestone at Rhiw March.

Discussion. *Paterula* is recorded here in the Lower Bala Group for the first time.

Family **CRANIOPSIDAE** Williams, 1963

Genus ***PARACRANIOPS*** Williams, 1963

Paracraniops* cf. *macellus Williams, 1963
Figs 32a, b

Description. Elongately oval and subequivalve *Paracraniops*, with flattened posterior margin and strong concentric ornamentation consisting of 7–8 irregularly-spaced growth lines per mm on the anterior part of valve.

Material and locality. Five well-preserved external moulds were obtained from beds GG2c (BB92208), R29 (BB92263), R46 (BB92264) and R47 (two specimens) in the Gelli-grîn Formation.

Discussion. Williams (1963 : 347–348) discussed the problems of differentiating between pedicle and brachial valves belonging to this genus and revised his earlier diagnosis (1962 : 88–89) of which valve was which, concluding that the pedicle valve bears the shield-shaped muscle scars while the brachial valve bears posterior adductor and oblique scars extending anterolaterally for about a quarter of the valve length. Mitchell (1977 : 22–23) apparently ignored Williams' later proposals, preferring to adhere to his earlier definitions. However, the more recently proposed orientation is adhered to here and it is noted that *P. glaber* sp. nov. has distinctive posterior adductor (?) scars (Figs 33–36).

When describing *P. macellus*[1] (Williams 1963 : 348; pl. 1), insufficient material was available to illustrate the external morphology adequately and the reader was referred to descriptions of *P. pararius* Williams (1962), emend. Williams (1963) for additional information. Material obtained during this study shows the close resemblance between the exterior morphology of *P.* cf. *macellus* and *P. pararius*.

Paracraniops glaber sp. nov.
Figs 33–36

Diagnosis. Large, externally smooth, oval, dorsibiconvex (?) *Paracraniops* with well-developed limbus, slightly convex to asymmetrically conical dorsal (?) valve and slightly convex ventral (?) valve.

Name. 'Smooth'.

Description. Oval *Paracraniops* 66–84% as wide as long in populations with smaller and larger mean size respectively. Dorsal (?) valve with pair of variably-developed faint posterior adductor scars (?) arising anterior to the posterior margin (10% of valve length) and extending for 20–30% of valve length, only known in large specimens (Figs 33, 34). External ornament smooth except for well-developed marginal limbus. (Rare development of concentric growth lines seen on some internal moulds.)

Type material. Measurements in mm.

	length	width
Holotype, internal mould of brachial (?) valve, BB92209 . .	5·5	4·8
Paratype, internal mould of pedicle (?) valve, BB92210 . .	5·0	4·2
Paratype, internal mould of brachial (?) valve, BB92211 . .	(4·5)	(4·1)
Paratype, internal mould of brachial (?) valve, BB92212 . .	3·4	3·0

Type horizon and localities. Fig. 23 gives biometric parameters of specimens of *P. glaber* sp. nov. from sample loc. 55 near Fedw Farm (9089 2975) and from the Rhiw March section (Fig. 9, p. 180). The former locality, on the south side of Nant Rhyd Wen (opposite the cliffs of Craig y Gath), is the 'alternative' type locality for the Allt Ddu Formation (p. 178). Fig. 45A, p. 208, gives statistics of two small populations of *P. glaber* from beds R093 and R096 in the Rhiw March section.

Discussion. The morphology of most of the specimens belonging to this common Allt Ddu species is so featureless that previous studies have disregarded them owing to uncertainty about their taxonomic affinity (Williams, personal communication 1976). However, a fortuitous discovery of a small population of well-preserved, large *Paracraniops* specimens in a partially decalcified calcareous nodule has revealed that a few of these normally featureless valves have internal muscle scars preserved. The internal morphology of the dorsal (?) valve closely resembles

[1] Called by Williams *P. macella*; however, a ruling of the I.C.Z.N. (1974, *Bull. zool. Nom.*, London, **31** : 81–83) is that generic names in *-ops* shall be regarded as masculine in all cases.

that of *P. pararius* Williams, but the lack of external ornament on *P. glaber* distinguishes it from other related forms at least at the specific level. *P. glaber* appeared much earlier in the Lower Bala Group than the related form *P. macellus* Williams, which is only known from the Gelli-grîn Formation.

The mean length/width ratio of *P. glaber* varies allometrically with growth. Specimens from loc. 55 apparently grew to a relatively large size, increasing in width relative to length.

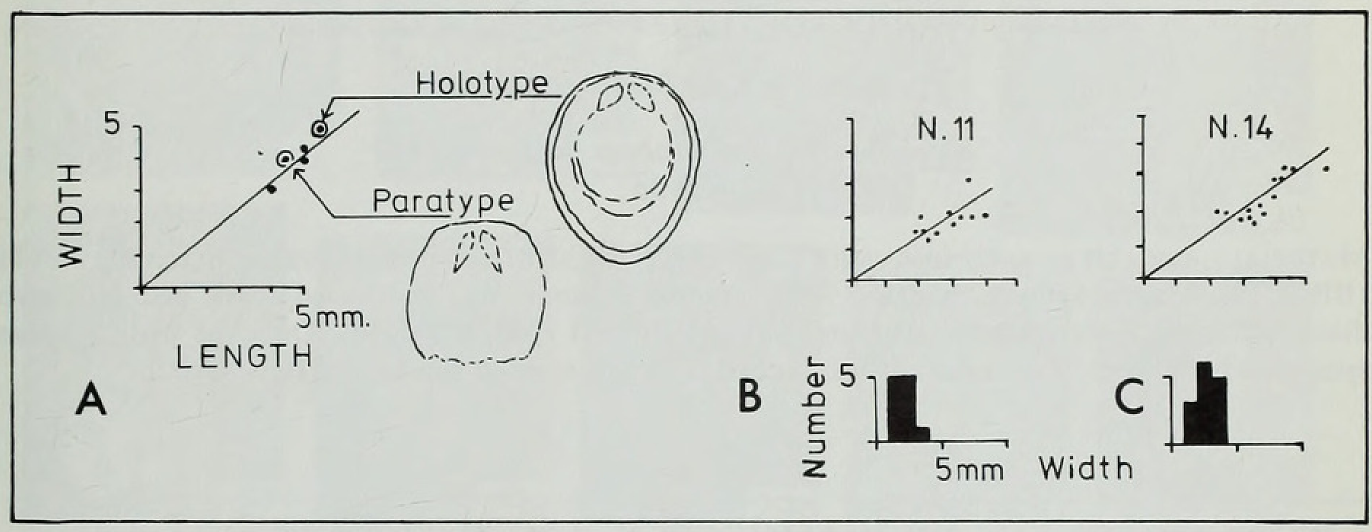


Fig. 23 Biometric parameters (length and width) of *Paracraniops glaber* sp. nov. A, specimens from sample 55 including two showing dorsal (?) muscle scars. B and C respectively represent specimens from samples R096 and R093; corresponding size frequency histograms are also shown.

Paracraniops cf. ***glaber*** Lockley, herein
Fig. 37

Material and locality. A single slightly distorted internal and external mould (BB92213a, b) of a specimen apparently conspecific with *P. glaber* recovered from bed H6 (9001 2305) is figured. The dorsal (?) posterior adductor scars and well-developed internal growth lines are seen. (Length of specimen 4·6 mm, width 3·1 mm.)

Suborder **CRANIIDINA** Waagen, 1885
Superfamily **CRANIACEA** Menke, 1828
Family **CRANIIDAE** Menke, 1828
Genus ***ORTHISOCRANIA*** Rowell, 1965

Orthisocrania sp.
Figs 31a, b

Description. Subcircular, convex brachial valve with elliptical anterior adductor scars.

Material and locality. Single internal mould of deformed brachial valve (BB92207) from bed H8 in Afon Twrch (9001 2305); see Fig. 4, p. 176.

Discussion. This is the first record of *Orthisocrania* from beds below the Gelli-grîn Formation. This Soudleyan occurrence, the earliest known in Britain, was predicted by Wright (1970 : 102).

Class **ARTICULATA** Huxley, 1869

Introduction. Systematic descriptions of members of this class are given for representatives of the Orders Strophomenida, Pentamerida and Spiriferida only. Although representatives of seven species in the Order Orthida are figured, they are all considered to be conspecific with those described by Williams (1963); they are included in order to illustrate well-preserved morphological features and, in the case of *Nicolella* cf. *actoniae obesa*, *Onniella ostentata* and *Salopia* sp., represent early occurrences of species previously known only from the Gelli-grîn Formation.

Order **ORTHIDA** Schuchert & Cooper, 1932
Superfamily **ORTHACEA** Woodward, 1852
Family **ORTHIDAE** Woodward, 1852
Subfamily **PRODUCTORTHINAE** Schuchert & Cooper, 1931

Genus *NICOLELLA* Reed, 1917

Nicolella cf. ***actoniae obesa*** Williams, 1963
Fig. 38

MATERIAL, LOCALITY AND DISCUSSION. A single undistorted pedicle valve external mould (BB92215), length 6·0 mm, width 8·5 mm, depth 1·2 mm, was recovered from bed H6; two distorted brachial valves were also found (beds H6 and H40, BB92214). Only the pedicle valve specimen is figured. This is the earliest record of this species in the Lower Bala Group.

Fig. 24 ? *Lingulella* sp. (p. 202). Derfel Limestone, Nant Aber Derfel. BB92200a. Internal part of exfoliated pedicle valve, ×4·5.

Fig. 25 *Lingulella* cf. *ovata* (M'Coy) (p. 203). Gelli-grîn Formation, Rhiw March, Llanymawddwy. BB92201a. Internal part of exfoliated pedicle valve, ×4.

Figs 26–27 *Palaeoglossa* cf. *attenuata* (J. de C. Sowerby) (p. 203). Fig. 26, Gelli-grîn Formation, near Gelli-grîn Farm, Bala. BB92202. Articulated valves, ×3. Fig. 27, Cymerig Limestone Member, Rhiw March, Llanymawddwy. BB92203a. Internal part of exfoliated pedicle valve, ×3.

Fig. 28 ? *Pseudolingula* sp. (p. 203). Gelli-grîn Formation, near Gelli-grîn Farm, Bala. BB92204. External mould of a brachial valve, ×2.

Figs 29–30 *Paterula* sp. (p. 203). Cymerig Limestone Member, Rhiw March, Llanymawddwy. Figs 29a, b, BB92206. External mould of a pedicle (?) valve and latex cast of the same, both ×7·5. Fig. 30, BB92205. Internal mould of a pedicle valve, ×6.

Figs 31a, b *Orthisocrania* sp. (p. 205). Llaethnant Formation, Afon Twrch, near Bwlch y Groes. BB92207. Internal mould of a brachial valve, ×4; latex cast of same, ×5.

Figs 32a, b *Paracraniops* cf. *macellus* Williams (p. 203). Gelli-grîn Formation, near Gelli-grîn Farm, Bala. BB92208. Latex cast (a) of external mould of valve (b), both ×9.

Figs 33–36 *Paracraniops glaber* sp. nov. (p. 204). Allt Ddu Formation; all internal moulds. Figs 33–35, near Fedw Farm, Llangower. Fig. 33, **Holotype,** BB92209. Brachial (?) valve, ×6. Fig. 34, Paratype, BB92211. Brachial (?) valve, ×6. Fig. 35, Paratype, BB92210. Pedicle (?) valve, ×4. Fig. 36, Rhiw March, Llanymawddwy. Paratype, BB92212. Brachial (?) valve, ×6.

Fig. 37 *Paracraniops* cf. *glaber* Lockley (p. 205). Llaethnant Formation, Afon Twrch, near Bwlch y Groes. BB92213a. Internal mould of a brachial (?) valve, ×6.

Fig. 38 *Nicolella* cf. *actoniae obesa* Williams (above). Llaethnant Formation, Afon Twrch, near Bwlch y Groes. BB92215. External mould of a pedicle valve, ×3.

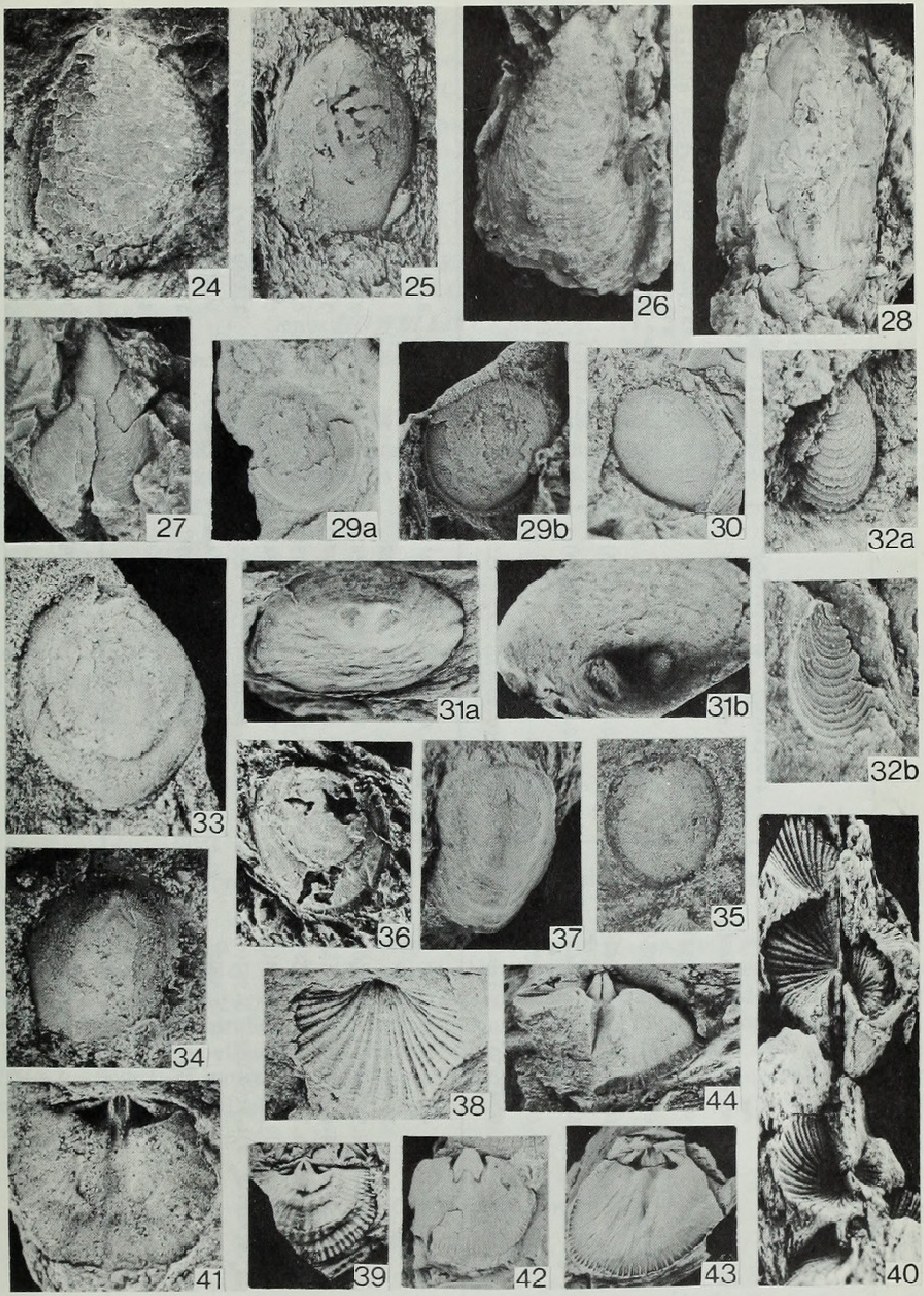
Fig. 39 *Rhactorthis crassa* Williams (p. 209). Nod Glas Formation, Rhiw March, Llanymawddwy. BB92216a. Internal mould of a brachial valve, ×3.

Fig. 40 *Howellites* cf. *ultimus* Bancroft (p. 209). Allt Ddu Formation, Rhiw March, Llanymawddwy. BB92217. External moulds of articulated valves, ×6.

Fig. 41 *Howellites* cf. *antiquior* (M'Coy) (p. 209). Ceiswyn Formation, Aber Cowarch, Dinas Mawddwy. BB92218a. Internal mould of a brachial valve, ×4.

Figs 42–43 *Onniella ostentata* Williams (p. 209). Llaethnant Formation, Afon Twrch, near Bwlch y Groes. Fig. 42, BB92219. Internal mould of a pedicle valve, ×3. Fig. 43, BB92220a. Internal mould of a brachial valve, ×3.

Fig. 44 *Salopia* sp. (p. 210). Llaethnant Formation, Afon Twrch, Bwlch y Groes. BB92222. Internal mould of a brachial valve, ×3.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29a
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32a
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31a
31b
32b
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A

	A	B
N	11	14
$\bar{l}$.mm(var.l)	2.827(0.522)	3.628(0.728)
$\bar{w}$.mm(var.w)	1.882(0.232)	2.443(0.359)
r	0.5996	0.8347
a(var.a)	0.666(0.032)	0.703(0.013)
$lg_e\bar{l}$(var.lg_el)	1.007(0.063)	1.262(0.054)
$lg_e\bar{w}$(var.lg_ew)	0.600(0.063)	0.864(0.058)
r_e	0.607	0.838
α (var.α)	1.000(0.70)	1.042(0.269)

C

	A	B
N	12	7
$\bar{l}$.mm(var.l)	4.00(1.453)	4.01(0.205)
$\bar{w}$.mm(var.w)	3.65(1.319)	4.14(0.503)
r	0.9627	0.7301
a(var.a)		
$lg_e\bar{l}$(var.lg_el)	1.343(0.087)	1.383(0.013)
$lg_e\bar{w}$(var.lg_ew)	1.247(0.094)	1.407(0.029)
r_e	0.9644	0.7326
α (var.α)	1.0423(0.0076)	1.5123(0.212)

A Statistics of length (l) and maximum width (w) for Paracraniops glaber sp. nov. from horizons RO96 (A) and RO93 (B) in the Allt Ddu Mudstone at Rhiw March.

B Statistics of length (l) and width (w) of pedicle valves of Sericoidea abdita complicata subsp. nov. from four horizons (A-D) in the Nod Glas; (E-H) statistics of brachial valves from same samples.

C Statistics of length (l) and width (w) of pedicle (A) and brachial (B) valves of Cyclospira aff. bisulcata (Emmons) from the Cymerig Limestone and associated beds in the Tan y Bwlch and Rhiw March sections.

B

Locality	R 47	R 48	R 52	R 53	R 47	R 48	R 52	R 53
N	38	54	59	48	32	29	15	15
$\bar{l}$.mm(var.l)	2.54(0.289)	2.70(0.343)	2.476(0.468)	2.631(0.440)	2.38(0.273)	2.80(0.369)	2.26(0.395)	2.19(0.301)
$\bar{w}$.mm(var.w)	4.61(0.905)	5.06(1.866)	4.442(1.837)	4.9.5(2.157)	4.72(1.227)	5.04(1.501)	3.93(1.342)	4.61(1.357)
r	0.7429	0.8358	0.8341	0.8496	0.7395	0.8911	0.8242	0.9350
$lg_e.\bar{l}$(var.lg_e.l)	0.91(0.044)	0.974(0.046)	0.869(0.074)	0.936(0.062)	0.84(0.047)	1.01(0.046)	0.78(0.075)	0.75(0.061)
$lg_e.\bar{w}$(var.lg_e.w)	1.51(0.042)	1.587(0.070)	1.447(0.089)	1.549(0.085)	1.53(0.054)	1.59(0.058)	1.33(0.084)	1.50(0.062)
r_e	0.7470	0.8402	0.8397	0.8496	0.7444	0.8937	0.8299	0.9369
α (var.α)	0.975(0.012)	1.239(0.008)	1.099(0.006)	1.177(0.008)	1.07(0.017)	1.12(0.009)	1.06(0.027)	1.01(0.010)
	A	B	C	D	E	F	G	H

Fig. 45 Statistics for: A, *Paracraniops glaber* sp. nov. B, *Sericoidea abdita complicata* subsp. nov. C, *Cyclospira* aff. *bisulcata* (Emmons).

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

Genus ***RHACTORTHIS*** Williams, 1963

Rhactorthis crassa Williams, 1963

Fig. 39

MATERIAL, LOCALITY AND DISCUSSION. Well-preserved, complementary internal and external moulds of a brachial valve (BB92216a, b) from bed R49 in the Rhiw March section; its length is 5·1 mm, width 7·0 mm.

Superfamily **ENTELETACEA** Waagen, 1884

Family **DALMANELLIDAE** Schuchert, 1913

Genus ***HOWELLITES*** Bancroft, 1945

Howellites cf. ***ultimus*** Bancroft, 1945 (emend. Williams 1963)

Fig. 40

MATERIAL, LOCALITY AND DISCUSSION. A group of at least seven articulated *Howellites* valves (BB92217) from bed R089 show attachment to an elongate strand of unknown material. The illustration of this specimen supplements descriptions of *Howellites* 'life assemblages' from the Berwyn area (Brenchley 1966).

Howellites cf. ***antiquior*** (M'Coy, 1852)

Fig. 41

MATERIAL, LOCALITY AND DISCUSSION. A well-preserved internal and external mould of a brachial valve (BB92218a, b), length 5·6 mm, width 7·0 mm, showing characteristic muscle scars, was recovered from bed AB07, associated with the Cowarch Phosphate Bed at Aber Cowarch.

Genus ***ONNIELLA*** Bancroft, 1928

Onniella ostentata Williams, 1963

Figs 42, 43

FIGURED MATERIAL. Representative internal moulds of a pedicle (BB92219) and a brachial valve (BB92220a) are shown.

HORIZON, LOCALITY AND DISCUSSION. Several populations of *O. ostentata* were recovered from beds H4–H7 and H38–H40 in Afon Twrch. The H4 population was compared with a population from bed GG1b at Gelli-grîn (type locality); no significant differences could be observed in the three allometrically controlled morphological features that were tested, the outline of the pedicle valve ($P > 10\%$), the outline of the brachial valve ($P > 10\%$) and the shape of the cardinalia ($10\% > P > 5\%$). (For statistics see Lockley 1977 : fig. 12.2). For a full description of this species see Williams (1963 : 405); it is discussed here to draw attention to its early appearance in pre-Frondderw beds.

Genus ***BANCROFTINA*** Sinclair, 1946

Bancroftina sp.

Figs 46a, b

MATERIAL, LOCALITY AND DISCUSSION. A well-preserved internal mould of a *Bancroftina* brachial valve (BB92221, length 13 mm, width 18 mm; cardinalia length 2·5 mm, width 5·5 mm) was recovered from bed GG1h above the Cymerig Limestone. This form is poorly represented in the Lower Bala Group.

Family **LINOPORELLIDAE** Schuchert & Cooper, 1931

Genus ***SALOPIA*** Williams, 1955

Salopia sp.

Fig. 44

MATERIAL, LOCALITY AND DISCUSSION. This internal mould of a brachial valve (BB92222), from bed H6 below the Frondderw Ash, is one of several found in association with species which make an early appearance in the Lower Bala Group at about this horizon.

Suborder **TRIPLESIIDINA** Moore, 1952
Superfamily **TRIPLECIACEA** Schuchert, 1913
Family **TRIPLECIIDAE** Schuchert, 1913

Genus ***TRIPLESIA*** Hall, 1959

Triplesia maccoyana Davidson, 1869, emended

1852 *Hemithyris depressa* (J. de C. Sowerby); M'Coy *in* Sedgwick & M'Coy: 201.
1869 *Triplesia ? Maccoyana* Davidson: 199; pl. 24, fig. 29.
1978 *Triplesia*? *maccoyana* Davidson; Cocks: 86, 187.

DESCRIPTION. Small dorsibiconvex, globular, plicate *Triplesia* with pedicle valve averaging 96% as long as wide in 5 specimens (range 80–108%) and 22% as deep as long in 4 specimens (range 15–27%); dorsal valve averaging 87% as long as wide in 13 specimens and 45% as deep as long in 12 specimens; ventral sulcus and corresponding dorsal fold arising between the 2 and 3 mm growth stages and averaging 62% as wide (wavelength) as valve (range 56–67%) and 30% as high (amplitude) as wavelength (range 21–40%) at the commissure of 4 smaller valves between 3·6 and 5·0 mm in width, deepening to respective average width : wavelength and amplitude : wavelength ratios of 59% (range 55–63%) and 44% (range 39–47%) at the commissure of 4 larger valves between 5·5 and 7·2 mm in width; ventral umbo pointed, overhanging incurved dorsal umbo and with short narrow curved apsacline interarea divided by elongate pedicle groove; surface smooth except for fine concentric growth lines numbering about 10 per mm beyond the 3 mm growth stage. Interior of both valves unknown.

MATERIAL AND LOCALITY. Lectotype (selected Cocks 1978: 86) articulated valves (SMA.42436), length 5·6 mm, width 7·0 mm, and 19 other paralectotypes (SMA.42437–48) from a limestone lens in the Allt Ddu Mudstones, Bryn Bedwog Quarry, near Bala, Gwynedd (grid. ref. SH 931329).

DISCUSSION. The species is known only from M'Coy's original material and its importance as an element of the Lower Bala Group fauna is difficult to evaluate. It is, however, the first *Triplesia* species recorded in the Ordovician of north Wales; Williams (1974) recorded a contemporary *Triplesia* sp. from the Soudleyan of Salop. There is also an earlier species, *Triplesia edgelliana* (Davidson), from the Upper Llanvirn of the Llandeilo area (Lockley & Williams, in press); *T. maccoyana* compares most closely with this, differing only in respect of its significantly deeper dorsal valve ($0{\cdot}05 < P < 0{\cdot}02$). Relevant statistics for the dorsal valve length (l), width (w) and depth (th) are as follows: (n = 13) $\bar{l}$ mm (var. l) 5·14 (1·273), $\bar{w}$ mm (var. w) 5·91 (2·185), r = 0·9077, a (var. a) 1·3103 (0·0275); (n = 12) $\bar{l}$ mm (var. l) 5·32 (0·938), $\overline{th}$ (var. th) 2·42 (0·552), r = 0·8066, a (var. a) 0·7675 (0·0206).

Order **STROPHOMENIDA** Öpik, 1934
Superfamily **PLECTAMBONITACEA** Jones, 1928
Family **LEPTESTIIDAE** Öpik, 1933
Subfamily **LEPTESTIINAE** Öpik, 1933

Genus ***PALAEOSTROPHOMENA*** Holtedahl, 1916

Palaeostrophomena canalis sp. nov.

Figs 47a, b, 48–52

DIAGNOSIS. Subquadrate, gently biconvex to biplanate *Palaeostrophomena* with pedicle valve characterized by well-developed mantle canal system arising anteromedially and restriction of genital markings to posterolateral part of valve.

NAME. With reference to the mantle canal system.

DESCRIPTION. Pedicle valve 85–90% as long as wide with interior characterized by elongate, narrow, divergent diductor scars flanking narrow, small anterior median adductor scars. Musculature otherwise poorly defined and intricately related to well-defined mantle canal system.

Interarea long apsacline, dental lamellae absent, but divergent false dental plates present. Narrow delthyrium open medially but covered laterally by pseudodeltidium. Up to 12 mantle canals branching radially into at least 30 tributary canals at the commissure. At least seven concentric rugae (wavelength 0·2 mm) developed posterolaterally at an acute angle to the hinge. Ornament very fine, unequally parvicostellate; at least seven ribs arise in umbonal area defining sectors bisected by ribs arising 3–4 mm from umbo, and these in turn define sectors bisected by ribs arising 5–6 mm from umbo. Brachial valve unknown.

TYPE MATERIAL. Measurements in mm.

	length	width
Holotype, internal mould of pedicle valve, BB92223 . . .	(15)	(16·5)
Paratype, internal mould of pedicle valve, BB92224 . . .	(13)	(18)
Paratype, internal mould of pedicle valve, BB92225 . . .	(12)	(12)
Paratype, internal mould of pedicle valve, BB92226 . . .	(9)	(12)
Paratype, internal mould of pedicle valve, BB92227 . . .	(9)	(15)
Paratype, external mould of pedicle valve, BB92228 . . .	(9)	(11)

TYPE HORIZON AND LOCALITIES. Holotype from sample GG1b in the Gelli-grîn type section; paratypes from samples R27 and R28 in the Rhiw March section.

DISCUSSION. This species is quite distinct from *P. magnifica* Williams, which is known from the Derfel Limestone. The lack of well-developed genital markings and the closely-spaced mantle canals are its most distinctive features. Cooper (1956 : 703) noted the complete absence of well-preserved brachial valves in a large population of *P. angulata* and attributed this to their fragility. Although similar absence of brachial valves of *P. canalis* is noted here, explanations are not proposed.

Family **SOWERBYELLIDAE** Öpik, 1930
Subfamily **SOWERBYELLINAE** Öpik, 1930
Genus ***ANISOPLEURELLA*** Cooper, 1956
Anisopleurella cf. ***multiseptata*** (Williams, 1955)
Fig. 53

DISCUSSION. A well-preserved specimen of a pedicle valve internal mould (BB92229) from bed GG2b represents the first record of *Anisopleurella* in the Gelli-grîn Formation. The large, paired diductor scars are well displayed and the fragmentary remains of external moulds which were also recovered reveal the essentially smooth exterior of the shell which is ornamented only by widely-spaced primary costae. The specimen compares closely with *A. multiseptata* Williams from the Derfel Limestone (Williams *in* Whittington & Williams 1955 : 416).

Subfamily **AEGIROMENINAE** Havlíček, 1961
Genus ***SERICOIDEA*** Lindström, 1953
Sericoidea abdita Williams, 1955, emend. herein

DIAGNOSIS. *Sericoidea* with variable arrangement of paired or single strong lateral septules and a well-defined median septum all extending into the anterior half of the valve; dorsal muscle platform bilobed.

Sericoidea abdita complicata subsp. nov.
Figs 54–59

DIAGNOSIS. Differs only from the nominate subspecies in the variable development of septules and the presence of dorsal muscle scars.

NAME. 'Complicated'.

DESCRIPTION. Semicircular, planoconvex *Sericoidea* with mean length/width ratio of 54·4% and 52·7% for pedicle (N = 199) and brachial (N = 91) valves respectively. Ornamentation consisting of fine, differentially thickened, radial costae and costellae with a mean of 12·4 per mm (N = 56) found anteromedially. Dorsal septules arranged in arcs over two-thirds of the length of the brachial valve anterior of the umbo. Septules are generally but not invariably arranged in arcuate, single or double rows, or both, on either side of the median septum. The mean number of septules per row (as counted for the longest row) is 5·8 (N = 25). Dorsal adductor scar bilobed, extending anteriorly for less than half the length of the valve and laterally for over one-third the width of the valve.

TYPE MATERIAL. Measurements in mm.

	length	width
Holotype, internal mould of brachial valve, BB92231 . . .	5·0	2·8
Paratype, internal mould of brachial valve, BB92230 . . .	–	–
Paratype, exterior of pedicle valve, BB92232	5·3	3·5
Paratype, exterior of pedicle valve, BB92233	4·6	3·0
Paratype, internal mould of brachial valve, BB92234 . . .	–	–
Paratype, internal mould of brachial valve, BB92235 . . .	5·0	3·2
Paratype, exterior of pedicle valve, BB92236	7·0	4·0

TYPE HORIZON AND LOCALITY. Nod Glas Formation, Rhiw March: holotype from bed R47 and paratypes from beds R52 and R53.

DISCUSSION. The genus *Sericoidea* is abundantly represented in the Nod Glas. The largest populations were recovered from beds R47, R48, R52 and R53; full statistical details are given in Fig. 45B. Estimates of α, the growth ratio for samples affected by allometry, have been derived from the data in Fig. 45B and tests show that none of the populations differs significantly from any other ($P > 0·1$). Furthermore, they do not differ significantly from *S. restricta* from the Sulårp Shale and from *S.* aff. *restricta* from the Craighead Limestone; nor do they differ significantly from *S.* aff. *abdita* from the Balclatchie Mudstones either at Laggan Burn or Byne Hill ($P > 0·1$, for all tests). Even when using growth ratios not corrected for allometry, no significant difference

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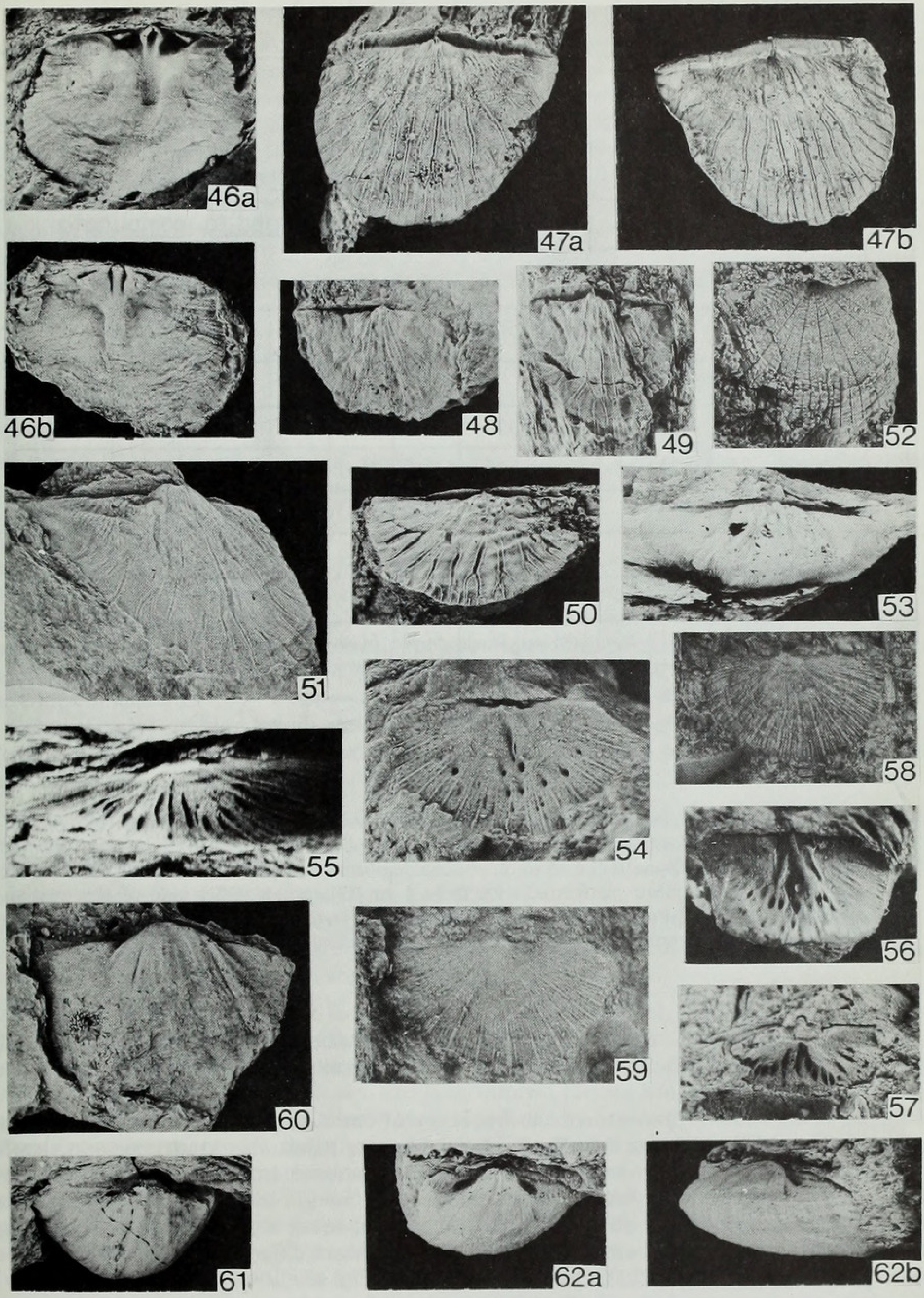
Figs 46a, b *Bancroftina* sp. (p. 209). Gelli-grîn Formation, Gelli-grîn Farm, Bala. BB92221. Internal mould and latex cast of a brachial valve, both ×2·5.

Figs 47–52 *Palaeostrophomena canalis* sp. nov. (p. 210). Gelli-grîn Formation. Figs 47a, b, Gelli-grîn Farm, Bala. **Holotype,** BB92223. Internal mould and latex cast of a pedicle valve, ×2·5. Figs 48–52, Rhiw March, near Llanymawddwy. Figs 48–50, Paratypes, BB92226, BB92225, BB92227. Internal moulds of pedicle valves, all ×2. Fig. 51, Paratype, BB92224. Internal mould of a pedicle valve, ×2·5. Fig. 52, Paratype, BB92228. External mould of a pedicle valve, ×2·5.

Fig. 53 *Anisopleurella* cf. *multiseptata* (Williams) (p. 211). Gelli-grîn Formation, Maes-Meillion, near Llangower. BB92229. Internal mould of a pedicle valve, ×2·5.

Figs 54–59 *Sericoidea abdita complicata* subsp. nov. (above). Nod Glas Formation, Rhiw March, Llanymawddwy. Fig. 54, **Holotype,** BB92231. Internal mould of a brachial valve, ×7·5. Figs 55–57, Paratypes, BB92230, BB92235, BB92234. Internal moulds of brachial valves, ×12, ×6 and ×7·5 respectively. Figs 58–59, Paratypes, BB92233, BB92232. Exteriors of pedicle valves, both ×6.

Figs 60–62 *Bimuria dyfiensis* sp. nov. (p. 215). Gelli-grîn Formation, Rhiw March, near Llanymawddwy. Figs 60–61, internal moulds of pedicle valves, ×2·5. Fig. 60, **Holotype,** BB92237. Fig. 61, Paratype, BB92239a. Figs 62a, b, Paratype, BB92238a. Posterior and lateral views of a pedicle valve, both ×2·5. See also Figs 64–65.


46a
47a
47b
46b
48
49
52
51
50
53
58
55
54
56
60
59
57
61
62a
62b

A

costellae per mm	9	10	11	12	13	14	15	16	17	18	19
N	-	5	6	15	6	13	6	2	2	1	-

B

costellae per mm.	9-11	12	13-18	N
S. aff. abdita	5	16	41	62
S. abdita complicata	11	15	30	56

C

	MS	1	2	3	4	5	6	7	8	9	10	
0·6 - 1·0	-(3)											- (3)
1·1 - 1·5	-(1)	1(1)				2(-)						3 (2)
1·6 - 2·0		-(2)	1(-)	-(4)	1(-)	2(-)	1(-)	1(-)				6 (6)
2·1 - 2·5		-(2)		-(3)	1(-)	1(-)	3(-)	4(-)				9 (5)
2·6 - 3·0				-(4)		1(-)	2(-)	2(-)			1(-)	6 (4)
3·1 - 3·5				-(3)						1(-)		1 (3)
	-(4)	-(5)	1(-)	-(16)	2(-)	6(-)	6(-)	7(-)	--	1(-)	1(-)	24(25)

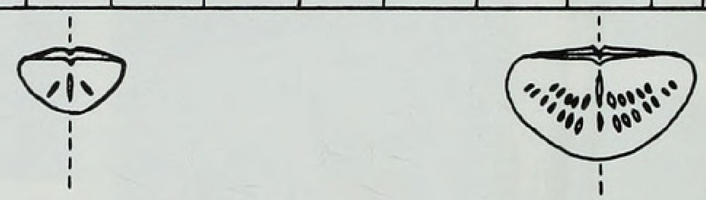


Fig. 63 A, frequency of counts of costellae per mm occurring at the anteromedian margins of *Sericoidea abdita complicata* subsp. nov. B, pooled data for costellae frequency in *S.* aff. *abdita* from Laggan Burn and Byne Hill and in *S. abdita complicata* subsp. nov. C, the distribution of various types of lophophore platforms, with from 1 to 10 septules either side of the median septum (MS) in *S.* aff. *abdita* from Laggan Burn (number of individuals in brackets) and *S. abdita complicata* subsp. nov. from the Nod Glas (number of individuals not in brackets).

can be detected between *S. abdita complicata* and *Chonetoidea radiatula* (Barrande) from the Ashgill of Pomeroy ($P > 0{\cdot}1$). This evidence highlights the similarity in the shape of these related aegiromeninids.

Williams (1963 : 188–190) measured the frequency of costellae per mm at the anteromedian margins of *Sericoidea* and found that *S.* aff. *abdita* from the Balclatchie Mudstones was significantly different from S. aff. *restricta* from the Craighead Limestone. In this study similar measurements on the frequency of costellae at the anteromedian margin in *S. abdita complicata* were compared with measurements obtained for *S.* aff. *abdita*, using a χ^2 test with cell groupings identical to those used by Williams (1963 : 189). No significant difference was detected between the two populations ($0{\cdot}2 > P > 0{\cdot}1$); the data are given in Fig. 63.

However, a comparison between the different types of septule arrangement in *S.* aff. *abdita* and *S. abdita complicata* reveals that the latter subspecies was significantly different (χ^2 test, $P < 0{\cdot}001$) in having longer rows of single and paired septules of comparable size; see Fig. 63.

Since there is a high degree of variability in the disposition of septules in the *S. abdita complicata* population the differences are considered subspecific.

Although attempts have been made by Williams (1962) and the author to define *Sericoidea* populations quantitatively, a certain element of qualitative judgement attaches to whether smaller or larger septules are considered important as representatives of well-defined or less well-defined rows. According to Williams (1962 : table 46) septule rows never contain more than three septules (either in *S. restricta* or in *S.* aff. *abdita*). Similarly, *S. abdita* was diagnosed as having 'up to three pairs of strong lateral septules' (Williams *in* Whittington & Williams 1955 : 418). However, whilst acknowledging that palaeontologists might differ as to what constitutes a septule rather than a tubercle (the specimens in Williams 1974 : pl. 24, figs 8, 9 and Williams 1962 : pl. 18, fig. 8 might for example be considered to display at least four septules in each lateral row) the differences between *S.* cf. *abdita*, S. aff. *abdita* and *S. abdita complicata* are considered significant because all measurements and counts of morphological features were estimated in the same way.

Family **BIMURIDAE** Cooper, 1956

Genus ***BIMURIA*** Ulrich & Cooper, 1942

Bimuria dyfiensis sp. nov.

Figs 60, 61, 62a, b, 64a, b, 65

Diagnosis. Concavo-convex, small, slightly sulcate *Bimuria* with pedicle valve umbo strongly incurved and overlapping dorsal interarea, teeth simple.

Name. From the Dyfi river.

Description. The pedicle valve interior morphology is well defined. Variably developed, narrow, divergent diductor scars extend anterolaterally for approximately three-quarters of the length of the valve, enclosing less well defined, radial adductor and mantle canal impressions postero-medially. Simple teeth developed laterally for about one-third of the width of the valve but short anteromedially. Slight development of pedicle valve sulcus evident from broad indentation of anterior commissure.

Brachial valve interior unknown; exterior essentially smooth in the only known specimen. Ventral exterior poorly known, essentially smooth, comae absent or very indistinct, resembling faint concentric growth lines where present.

Type material, horizon and locality. Holotype, internal mould of pedicle valve (BB92237) from bed R28 (length 12 mm, width 16 mm). Paratypes, internal and external moulds of pedicle valves (BB92238a, b–BB92241a, b) and internal moulds of pedicle valves (BB92242 and BB92243) and a brachial valve (BB92244), all from bed R28.

The above specimens, all from bed R28 in the Gelli-grîn Formation at Rhiw March, are distorted so that measurements are inaccurate; but the mean size of this population was clearly small, only two specimens being slightly wider than 12 mm.

Discussion. The morphological features described above suggest that this species cannot be assigned to any of the Scoto-Irish species (*B.* cf. *buttsi* Cooper, *B. youngiana* Davidson, *B. youngiana recta* Williams and *B.* cf. *youngiana recta*). The Welsh specimens apparently belonged to a population with a smaller mean size than the two former Scoto-Irish species populations (and the latter subspecies population). More significantly, however, the lack of any comae or other distinctive concentric ornamentation must be regarded as an important morphological difference. This lack of ornamentation is not simply the result of the small size of the Welsh specimens; Williams (1962 : 174–175) reported comae originating at 4–6 mm from the ventral umbo in all three of the Scottish species he described. Although the length of the Welsh specimens is not determined precisely, if one can assume, following Williams (1962) and Mitchell (1977), that *Bimuria* is at least two-thirds to three-quarters as long as wide, then all the Welsh specimens must be 6 mm or more in length. *B. dyfiensis* represents the first known occurrence of the genus *Bimuria* in Wales; since it is morphologically distinct, in respect of its essentially smooth external ornament, from all other known species in Britain, it is given specific recognition.

Order **PENTAMERIDA** Schuchert & Cooper, 1931
Suborder **SYNTROPHIIDINA** Ulrich & Cooper, 1936
Superfamily **PORAMBONITACEA** Davidson, 1853
Family **PARASTROPHINIDAE** Ulrich & Cooper, 1938

Genus *PARASTROPHINELLA* Schuchert & Cooper, 1931

Parastrophinella brenchleyi sp. nov.
Figs 66–69

DIAGNOSIS. Large, subpentagonal, biconvex *Parastrophinella* with vestigial fold and sulcus and commonly 12 costae, with a wavelength of 1·0–1·5 mm, ornamenting anteromedian part of the shell.

NAME. For Dr P. J. Brenchley.

DESCRIPTION. Unequally biconvex, rostrate *Parastrophinella* with a subpentagonal outline. 80% as long as wide with pedicle valve about 30% as deep as long. Transverse profile convex with steep lateral slopes; longitudinal profile unevenly convex to anteriorly geniculate in larger specimens. Faintly and sporadically developed low dorsal fold with at least 4 costae and shallow ventral sulcus with 3 costae. Twelve variably developed ventral costae are characteristically angular and well developed anteromedially (being 1·0–1·5 mm in width and amplitude) but are rounded and indistinct posterolaterally. Variably developed concentric corrugations up to 4 per mm anteromedially and anterolaterally are faint or absent in posteromedian part of shell.

Ventral interior with spondylium which is sessile posteriorly but supported anteriorly by sporadically developed medium septum extending forward for an average of 49% of the length of three pedicle valves. Muscle scars very faint or absent. Dorsal interior unknown.

TYPE MATERIAL. Measurements in mm.

	length	width
Holotype. Internal mould of a pedicle valve, NMW 77.11G.24 .	(10·0)	(15·0)
Paratype. Internal mould of a pedicle valve, NMW 77.11G.25 .	(7·0)	(9·0)
Paratype. Internal mould of a pedicle valve, NMW 77.11G.26 .	(10·5)	(10·5)
Paratype. Internal mould of a pedicle valve, NMW 77.11G.27 .	(9·0)	(11·0)
Paratype. Internal mould of a pedicle valve, NMW 77.11G.28 .	–	–

(Measurements given here indicate respective mean length and width values of 9·12 and 11·37 mm)

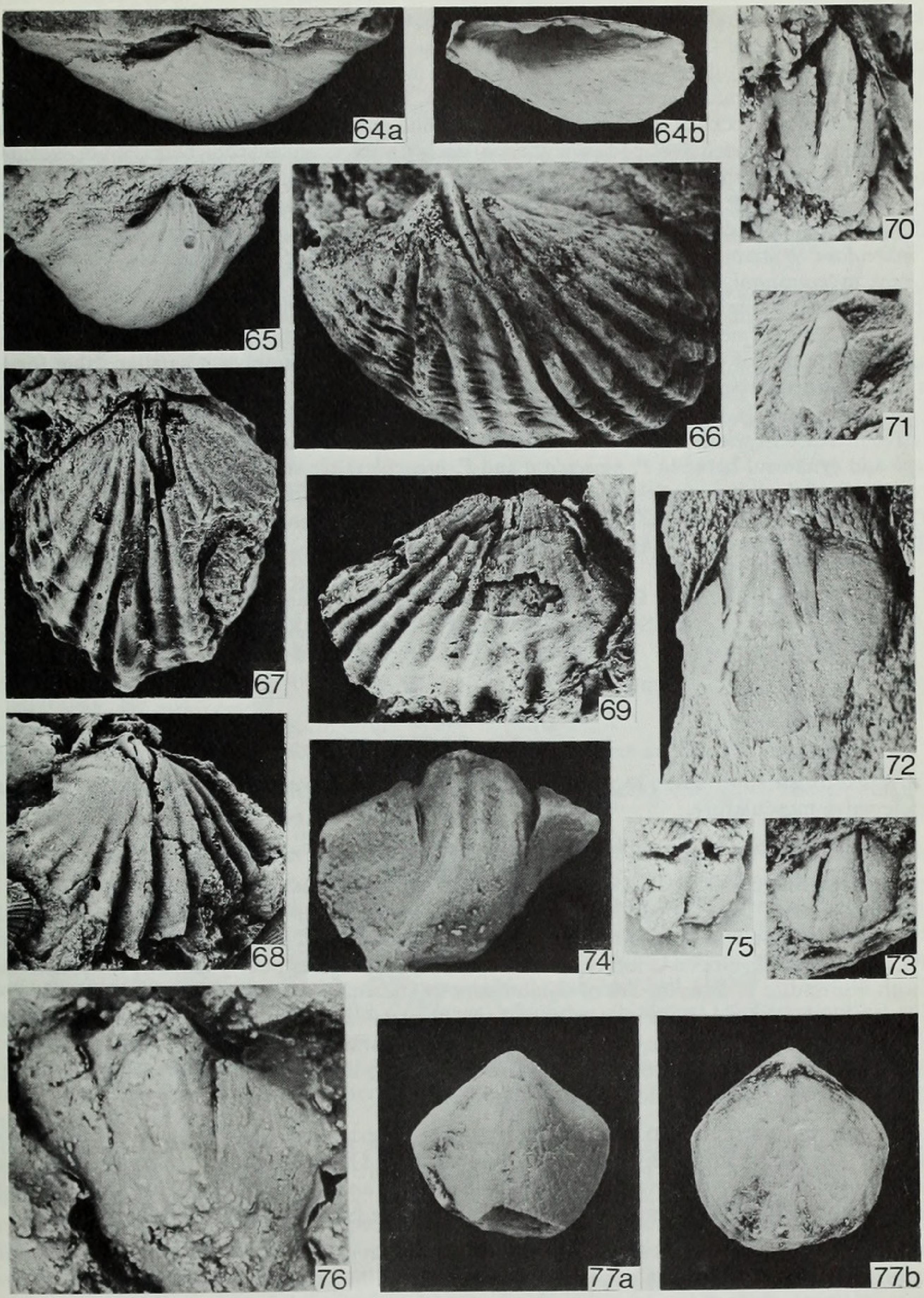
TYPE HORIZON AND LOCALITY. Bryn Beds (Lower Longvillian) exposed in small overgrown quarry 55 m east of Pandy Quarry (SJ 202363).

Figs 64–65 *Bimuria dyfiensis* sp. nov. (p. 215). Gelli-grîn Formation, Rhiw March, near Llanymawddwy. Figs 64a, b, Paratype, BB92241a. Internal mould of a pedicle valve, ×4; corresponding latex cast, ×2·5. Fig. 65, Paratype, BB92240a. Internal mould of a pedicle valve, ×4. See also Figs 60–62.

Figs 66–69 *Parastrophinella brenchleyi* sp. nov. (above). Bryn Beds, Pandy Quarry, near Glyn Ceriog. Fig. 66, **Holotype**, NMW.77.11G.24. Internal mould of a pedicle valve, ×4. Figs 67–69, Paratypes, NMW.77.11G.26, NMW.77.11G.25 and NMW.77.11G.27 respectively. Internal moulds of pedicle valves, all ×4.

Figs 70–76 *Protozyga musculosa* sp. nov. (p. 218). Nod Glas Formation; all internal moulds. Figs 70, 74–76, Rhiw March, near Llanymawddwy. Fig. 70, Paratype, BB92249. Pedicle valve, ×8. Fig. 74, Paratype, BB92246. Pedicle valve, ×16. Fig. 75, Paratype, BB92252. Brachial valve, ×10. Fig. 76, Paratype, BB92247. Pedicle valve, ×16. Figs 71–73, Nant Tan y Bwlch, near Bwlch y Groes. Fig. 71, Paratype, BB92253. Pedicle valve, ×9. Fig. 72, **Holotype**, BB92245. Pedicle valve, ×12. Fig. 73, Paratype, BB92254. Pedicle valve, ×9.

Figs 77a, b *Cyclospira* aff. *bisulcata* (Emmons) (p. 219). Cymerig Limestone Member, Rhiw March, near Llanymawddwy. BB92255. Ventral and dorsal views of the exterior of an articulated specimen, both ×6. See also Figs 78–82.



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DISCUSSION. This material, collected by Dr P. J. Brenchley from a single locality, has hitherto been described only briefly and informally (Brenchley 1966 : 242; figs 161–162). *Parastrophinella* is known from Scotland (Williams 1962), from Wales (MacGregor 1961, Addison 1974) and from the Welsh Borderland (Williams 1974). The Scottish species *P. youngi* (Reed) from the Craighead Limestone (Caradoc) differs from *P. brenchleyi* in being characteristically tumid with poorly-developed costae primarily associated with plication. Similarly, *P. parva* MacGregor (1961 : 197) from the Llandeilo rocks of the Berwyns is small, tumid and lacks well-developed costae; Addison (1974 : 47) also recorded this species in rocks of early Caradoc age near Narbeth (Pembrokeshire). However, the other smaller species, *P. costata* MacGregor (1961 : 199) from the Llandeilo of the Berwyns, resembles *P. brenchleyi* in outline, length/width ratio and spondylial arrangement, but differs in being considerably smaller (mean size) and having a larger number of costae (13–22). *P. musculosa* Williams (1974 : 151) from the Spy Wood Grit, Salop, resembles *P. brenchleyi* sp. nov. in 'commonly' having 11–13 costae (mean *c.* 12) and exhibiting a poorly-developed fold and sulcus and a similar spondylial arrangement; however, it differs in being smaller than *P. brenchleyi* (55% of mean width) and relatively but not significantly wider ($25 > P > 10$). A mean width/length ratio of 0·93 for 4 brachial valves of *P. musculosa* implies a smaller value for the corresponding, relatively longer pedicle valves (say $< 0{\cdot}90$); this differs considerably from the ratio of 1·25 for 4 pedicle valves of *P. brenchleyi*. Although allometric growth might account for a relative increase in width with size, even in the absence of more material the differences in size, shape and ornament between *P. musculosa* and *P. brenchleyi* are sufficient to merit the systematic recognition of the latter species. Williams (1974 : 152) also described *Parastrophinella* sp. from the Hagley Volcanics; although resembling *P. brenchleyi* in its sub-pentagonal outline and large size it differs from this form in having about 20 well-developed costae.

Order **SPIRIFERIDA** Waagen, 1883
Superfamily **ATRYPACEA** Gill, 1871
Family **ATRYPACEA** Gill, 1871

Genus ***PROTOZYGA*** Hall & Clarke, 1893

Protozyga musculosa sp. nov.
Figs 70–76

DIAGNOSIS. Small subcircular to subspherical *Protozyga* with well-developed dental plates and pedicle valve musculature.

NAME. With reference to the well-developed musculature.

DESCRIPTION. Small subcircular to subeliptical or subpentagonal ventribiconvex *Protozyga* as wide as long, with long subparallel to slightly divergent dental plates extending anteromedially for between half and two-thirds the length of the pedicle valve and enclosing equally long diductor muscle scars best developed in larger specimens. External features poorly known; ornamentation smooth but nature of anterior arc of commissure unknown.

Brachial valve interior with posterolateral socket plates and long median septum arising at a point anterior to the hinge line and extending anteriorly for most of the length of the valve.

Statistics for three measured pedicle valve paratypes; mean length (2·73 mm), mean width (2·73), r (0·9736), a (1·077) and b (−0·1415).

TYPE MATERIAL, HORIZON AND LOCALITIES. Holotype, internal mould of pedicle valve, BB92245 (length 3 mm, width 3 mm). From bed TB19 in the Nod Glas at Nant Tan y Bwlch. Paratypes, internal moulds of pedicle valves, BB92246–BB92251 and BB92253–BB92254, and a single brachial valve, BB92252. From beds TB19 and R54 in the Nod Glas at Rhiw March.

DISCUSSION. This occurrence is the first record of *Protozyga* in Wales; related forms including *P. diversa* (Reed), *P. rotunda* Cooper and *P. perplexa* Williams from Girvan and *P.* cf. *perplexa* and *P.* cf. *diversa* from Pomeroy are unlike the Welsh species both in the ventral arrangement of dental plates and diductor muscle scars and in the posterior origin of the brachial valve median septum.

Superfamily **DAYIACEA** Waagen, 1883
Family **DAYIIDAE** Waagen, 1883
Subfamily **CYCLOSPIRINAE** Schuchert, 1913

Genus ***CYCLOSPIRA*** Hall & Clarke, 1893

Cyclospira aff. ***bisulcata*** (Emmons, 1842)
Figs 77–82

DIAGNOSIS. Unequally biconvex, subpentagonal *Cyclospira* with rounded anterior margin.

DESCRIPTION. Unequally biconvex *Cyclospira* with pedicle valve nine-tenths as wide as long and brachial valve about as wide as long. Pedicle valve strongly convex in median part of valve with slight development of anteromedian sulcus and flat or concave posterolateral flanks or 'wings' subparallel to commissural plane.

External ornament mainly smooth but with fine concentric growth lines developed anteriorly and fine radial striations emphasized by slight exfoliation of shells. Pedicle interior characterized by well-developed 'shoelifter process' partly anterior to ventral muscle field.

Brachial valve sulcate with slight development of median plication dividing anterior part of sulcus. Interior characterized by median septum originating just anterior of medially cleft hinge line and extending anteriorly for at least three-quarters of the valve length. Thin socket plates present.

MATERIAL. Measurements in mm.

	PV		BV	
	length	width	length	width
Complete articulated specimen, BB92255	5·0	5·5	4·5	5·5
Complete articulated specimen, BB92256	4·0	3·5	3·9	3·5
External of pedicle valve, BB92257	5·6	5·0	–	–
Latex cast of articulated specimen, BB92258	4·6	4·4	4·2	4·4
Complete articulated specimen, BB92259	4·7	4·6	4·1	4·6
Internal and external mould of pedicle valve, BB92260a, b	(5·0)	(4·2)	–	–
Internal mould of brachial valve, BB92261	–	–	–	(3·0)

Statistics of length and width for 12 pedicle and 7 brachial valves are given in Fig. 45C.

HORIZON AND LOCALITIES. From bed R53 in the Cymerig Limestone at Rhiw March and bed TB20 in the Tan y Bwlch section.

DISCUSSION. The material recovered in this study affords an excellent opportunity to elaborate on the description of the *Cyclospira* sp. which Williams (1963 : 469) described as 'reminiscent' of *C. bisulcata* (Emmons). *C. bisulcata* is one of six species described by Cooper (1956); of these only a form related to *C.* ? *longa* (Cooper) has previously been described from British successions (Williams 1962 : 251; pl. 23). *C. carrickensis* (Reed) and *C. nana* (Davidson) have also been described from Ordovician rocks by Williams (1962) and Mitchell (1977) respectively. The specimens from north Wales are unlike *C.* ? *longa*, which has an almost triangular outline with incipient plication of the anterior commissure (Cooper 1956 : pl. 142.I). They are also unlike *C. nana* in having a longer median septum and thinner socket plates. They differ from *C. carrickensis* in not having an emarginate anterior commissure (Williams 1962 : 250) but are otherwise similar in exterior morphology.

The present *C.* aff. *bisulcata* bears a general resemblance to both *C. quadrata* Cooper and *C. preciosa* Cooper, but these two American species lack any median plication in the dorsal sulcus and show little or no ventral sulcation. *C. parva* Cooper and particularly *C. sulcata* Cooper are considerably more elongate than the present form. The species described by Cooper are hard to differentiate on external morphology; internal features are not illustrated, though *C. parva*, *C. quadrata* and *C.* ? *longa* are all known to have a dorsal median septum. The species based on British specimens (including *C.* aff. *bisulcata*) are probably better known in their internal morphology. The designation of this species as *C.* aff. *bisulcata* supports the suggestion of Williams (1963) that the Welsh Cyclospiridae belong to a group closely related to *C. bisulcata*.

Superfamily unknown

? Spiriferide, gen. indet.
Fig. 83

Description and discussion. Pedicle valve about as wide as long, with well-defined 'shoelifter process', which differs from *C.* aff. *bisculcata* in having paired raised scars in median part of valve between flanks of anterior part of process. External ornament of (unfigured) counterpart smooth. Posterior lateral flanks of valves show more 'wing-like' extension than in *C.* aff. *bisulcata*, but the possibility that this specimen is closely related to that form cannot be ruled out.

Material and locality. Pedicle valve internal and external moulds (BB92262a, b), from loc. 615a in beds above the Cymerig Limestone on Pen y Cefn Coch.

Other phyla

In addition to the brachiopod taxa described above, representatives of other phyla, notably the Arthropoda (Trilobita) and Mollusca (Bivalvia), are also recorded in the Lower Bala Group for the first time. These include four trilobite genera and five bivalve genera which are figured below but not accompanied by full systematic descriptions. Brief discussion on the significance of these newly recorded genera is included where appropriate.

Phylum **ARTHROPODA** Siebold & Stannius, 1845
Class **TRILOBITA** Walch, 1771
Family **PHILLIPSINELLIDAE** Whittington, 1950
Genus ***PHILLIPSINELLA*** Novak, 1886

Phillipsinella sp.
Figs 84–87

Material and locality. Three pygidia (It.14294–6) and four cephalic (glabellar) fragments (It.14297–300) from bed R53 in the upper part of the Cymerig Limestone at Rhiw March.

Discussion. These specimens, from beds of 'presumed' Upper Longvillian age, are the oldest known *Phillipsinella* specimens in Britain (Ingham, personal communication 1977); they are the first record of this genus in the Caradoc Series of north Wales. The phylogeny of the genus is discussed in Bruton (1976).

Figs 78–82 *Cyclospira* aff. *bisulcata* (Emmons) (p. 219). Figs 78–81, Cymerig Limestone Member, Rhiw March, near Llanymawddwy. Fig. 78, BB92258. Posterodorsal view of latex cast of an articulated specimen, ×7·5. Fig. 79, BB92257. Exterior of a pedicle valve, ×5. Fig. 80, BB92261. Internal mould of a brachial valve, ×8. Figs 81a, b, BB92256. Ventral and dorsal views of the exterior of a broken articulated specimen, both ×5. Fig. 82, Nod Glas Formation, Nant Tan y Bwlch, near Bwlch y Groes. BB92260. Internal mould of a pedicle valve, ×5. See also Figs 77a, b.

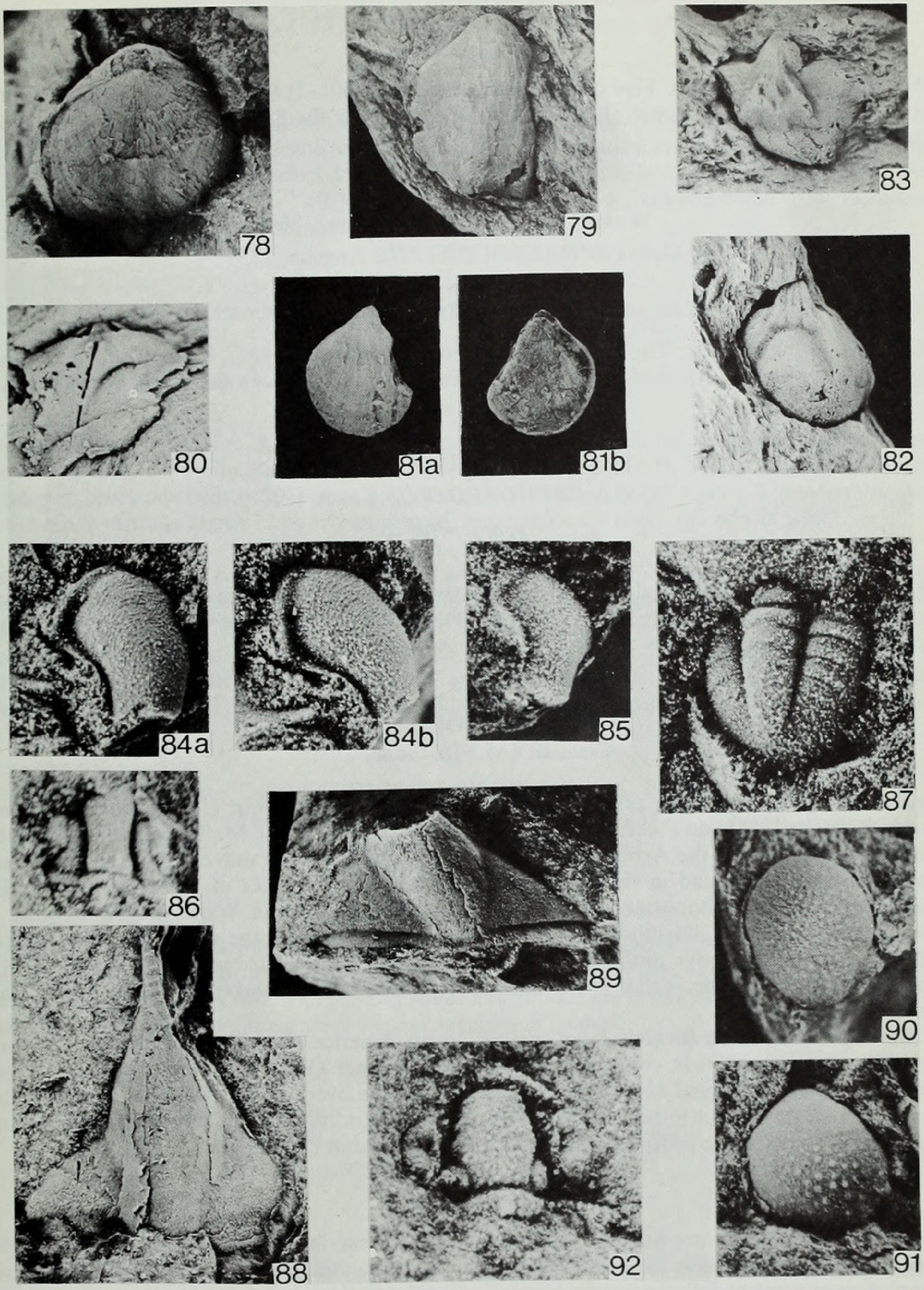
Fig. 83 ? Spiriferide, gen. indet. (above). Gelli-grîn Formation, Pen y Cefn Coch. BB92262a. Internal mould of a pedicle valve, ×5.

Figs 84–87 *Phillipsinella* sp. (above). Cymerig Limestone, Rhiw March, near Llanymawddwy. Figs 84a, b, It.14297. Oblique left-lateral and left-lateral views of a cranidium, ×16. Fig. 85, It.14298. Oblique left-lateral view of a cranidium, ×16. Fig. 86, It.14299. Dorsal view of a small cephalon, ×15. Fig. 87, It.14294. Dorsal view of a pygidium, ×16.

Figs 88–89 *Lonchodomas* sp. (p. 222). Cymerig Limestone Member, Rhiw March, near Llanymawddwy. Fig. 88, It.14301. Dorsal view of plasticine cast of cranidium, ×3. Fig. 89, It.14302. Dorsal view of cranidium, ×4.

Figs 90–91 *Sphaerocoryphe* sp. (p. 222). Cymerig Limestone Member, Rhiw March, near Llanymawddwy. Dorsal views of cranidia, both ×6. Fig. 90, It.14307. Fig. 91, It.14308.

Fig. 92 *Cyphoproetus* sp. (p. 222). Derfel Limestone, Nant Aber Derfel. It.14309. Dorsal view of cranidium, ×15.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Family **RAPHIOPHORIDAE** Angelin, 1854

Genus ***LONCHODOMAS*** Angelin, 1854

Lonchodomas sp.
Figs 88–89

MATERIAL AND LOCALITIES. Five cephalic specimens (It.14301–5) from bed R52 at Rhiw March and a single cephalic specimen (It.14306) from bed R49 are the first record of this genus in the Lower Bala Group.

Family **CHEIRURIDAE** Salter, 1864

Genus ***SPHAEROCORYPHE*** Angelin, 1854

Sphaerocoryphe sp.
Figs 90–91

MATERIAL AND LOCALITY. Two spherical, pustulose glabellae (It.14307–8) from bed R52 in the Cymerig Limestone at Rhiw March are the first record of this genus in the Lower Bala Group.

Family **PROETIDAE** Salter, 1864

Genus ***CYPHOPROETUS*** Kegel, 1927

Cyphoproetus sp.
Fig. 92

MATERIAL AND LOCALITY. The internal and external mould of a cranidium (It.14309) from the type Derfel Limestone at Nant Aber Derfel (SH 850395) is the first record of this genus in the Ordovician of Wales.

Phylum **MOLLUSCA**

Class **BIVALVIA** Linné, 1758

Introduction

Recent studies by Brenchley (1966), Pickerill (1974), Hurst & Hewitt (1977), Hurst (personal communication 1978) and Pickerill & Brenchley (1979) show that the Mollusca, and in particular the Bivalvia, are, after the Articulata (Brachiopoda) and Trilobita, one of the most important classes of organism found in the shelly facies of the Caradoc Series in Wales and the Welsh Borderland. But their importance has not been emphasized, and in Wales, largely because of poor preservation and indistinctive, mainly external morphology, the class has received little attention. Since the above authors record the occurrence and distribution of various bivalve genera in Wales and the Welsh Borderland, distinctive forms recovered from the Lower Bala Group are noted here.

Although Ordovician Bivalvia from eastern North America (Bretsky 1970, Pojeta 1971) are generally more common in contemporary Middle to Upper Ordovician deposits of the Appalachians (Bretsky, personal communication 1977), and the overall distribution of Anglo-Welsh Caradoc Bivalvia has yet to be outlined in any detail, the occurrence of congeneric taxa in both areas implies reasonable prospects for future correlations and comparisons.

Figured material

The forms figured here are assigned to genera but not described in any detail. In general the material from the Bala area is less abundant and well-preserved than that from the Berwyns and Salop. Any attempt at full systematic description of the Bala material would prove unrewarding without detailed consideration of other, more abundant material in other parts of the Anglo-Welsh region, but full locality details are given for the material discussed.

Order **NUCULOIDA** Dall, 1889
Family **PRAENUCULIDAE** McAlester, 1969
Genus ***CARDIOLARIA*** Munier-Chalmas, 1876
? ***Cardiolaria*** sp.
Figs 93–95

Material and localities. Internal moulds of nuculoid bivalves from beds AD A (PL 4441–3) and loc. 35 (PL 4440) in the middle part of the Allt Ddu Formation are provisionally assigned to ? *Cardiolaria* sp. The four numbered specimens have respective height and length measurements (mm) as follows: 2·5 and 4·0; – and 3·5; 3·0 and 5·0; 3·5 and 5·5 (means 3·0 and 4·5). Dentition is observed in the first two specimens.

Family **MALLETIIDAE** Adams & Adams, 1858
Genus ***NUCULITES*** Conrad, 1841
Nuculites sp.
Fig. 96

Material and locality. A single phosphatized internal mould of an articulated specimen (PL 4444), height 5·0 mm, length 8·0 mm, was recovered by Mr P. Magor from the locally-developed limestone beds in the lower part of the Nod Glas at Pistyll Gwyn. The posterior part of the hinge exhibits about 12 poorly-preserved, fine teeth each about 0·2 mm in width.

Discussion. The above two nuculoids, though uncommon in most of the succession, are the only sessile benthos recovered from parts of the 'faunal depletion zone' in the middle part of the Allt Ddu Formation. They are considered to be infaunal deposit feeders. In the absence of better-preserved material Dr N. J. Morris, who has helped the author with the identification of bivalve taxa, has suggested that forms resembling the genera *Praenucula* and *Palaeosolen* are also present amongst the unfigured material collected from the middle part of the Allt Ddu Formation.

Order **MODIOMORPHOIDA** Newell, 1965
Family **MODIOMORPHIDAE** Miller, 1877
Genus ***MODIOLOPSIS*** Hall, 1847
Modiolopsis sp.
Figs 97, 98

Material, localities and discussion. Specimens (PL 4445 and PL 4446a, b) from beds at loc. 928 (8990 2234) and from bed AD 3J, respectively, in the upper part of the Allt Ddu Formation are assigned to the genus *Modiolopsis*. The Modiomorphidae are usually considered to have been byssally attached, semi-infaunal or epifaunal suspension feeders.

Order **ARCOIDA** Stoliczka, 1871
Family **CYRTODONTIDAE** Ulrich, 1894
Genus ***CYRTODONTA*** Billings, 1858
Cyrtodonta sp.
Figs 99–101

Material, localities and discussion. Specimens from beds GG 1X (PL 4447), AD 0 (PL 4448) and H13 (PL 4449) are assigned to this genus. The former, an articulated specimen, was found in presumed life position with the umbones pointing downwards. Another specimen, PL 4450 from bed CYG 5 (see Fig. 8, p. 179), is assigned to ? *Cyrtodonta* sp.

Order **PHOLADOMYOIDA** Newell, 1965
Family **GRAMMYSIIDAE** Miller, 1877
Genus *CUNEAMYA* Hall & Whitfield, 1875
Cuneamya sp.
Figs 102a–c

MATERIAL, LOCALITY AND DISCUSSION. A single, well-preserved specimen (PL 4451) of an articulated *Cuneamya* was recovered from bed AD 3H in the Allt Ddu Formation. This genus is commonly regarded as having had a burrowing, infaunal mode of life.

Discussion of the Bivalvia

Brenchley (1966), Pickerill (1974) and Pickerill & Brenchley (1979) record *Modiolopsis*, *Goniophorina*, *Arca*, *Psilonychia* and *Vlasta* in their *Howellites* Community, *Byssodesma*, *Psilonychia* and a pteriacean in the *Dinorthis* Community and *Colpomya* in the *Dalmanella* Community. Pickerill (1974) also referred to *Ambonychia*, *Ctenodonta* sp. and *M. modiolaris* in the Berwyn area. Most of the bivalves in the Caradoc Series of north and central Wales are confined to the Soudleyan Stage.

Dr J. M. Hurst has collected a large number of bivalves from the Caradoc Series of Shropshire, many of which are congeneric with, or otherwise closely related to, bivalves from Wales. The author, who is currently examining some of this material, has collected *Cyrtodonta* from the lower part of the Chatwall Flags (Soudleyan) and has also examined faunas rich in nuculoid bivalves from the Acton Scott Beds. In the light of forthcoming publications on the Shropshire faunas, however, further comment on the known and recently-discovered bivalvia is considered premature.

Class **GASTROPODA** Cuvier, 1797

Elles (1922) recorded the gastropod genera *Cyclonema*, *Bellerophon* (*Sinuites*), *Lophospira* and *Murchisonia* in the Caradoc Series at Bala. In the present study representatives of the three former genera have been recorded in 55 of the 196 samples corresponding to the main sections (Figs 2, 8, 12–15). Dr J. S. Peel confirmed the identifications and noted that two distinct species of

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Figs 93–95 ? *Cardiolaria* sp. (p. 223). Allt Ddu Formation, south side of Pen y Cefn Coch. Figs 93a, b, PL 4440. Left-lateral and anterior views of internal mould of an articulated specimen, both ×7·5. Fig. 94, PL 4442. Internal mould of a right valve, ×6. Fig. 95, PL 4443. Internal mould of a right valve, ×9.

Fig. 96 *Nuculites* sp. (p. 223). Limestone beds beneath the Cymerig Member in the Nod Glas Formation at Pistyll Gwyn, near Llanymawddwy. PL 4444. Right-lateral view of internal mould of an articulated specimen, ×5.

Figs 97–98 *Modiolopsis* sp. (p. 223). Allt Ddu Formation. Fig. 97, Craig y Gath, near Llangower. PL 4445. Right-lateral view of external mould of an articulated specimen, ×1·5. Fig. 98, north of Graig Ty nant, near Llanymawddwy. PL 4446a. External view of a right valve, ×1·5.

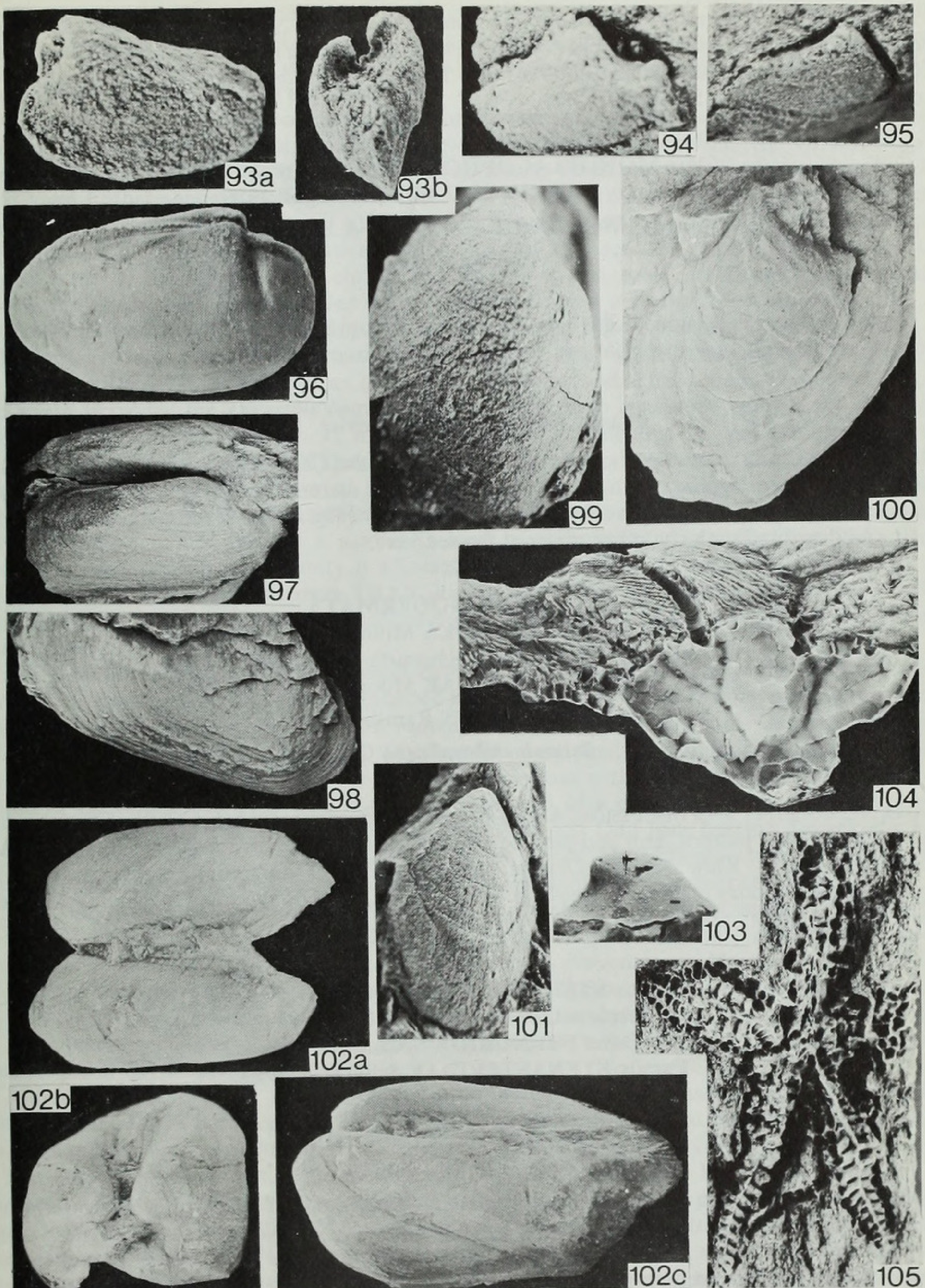
Figs 99–101 *Cyrtodonta* sp. (p. 223). Figs 99–100, Allt Ddu Formation. Fig. 99, west of Gelli-grîn Farm, Bala. PL 4448. Left-lateral view of an articulated specimen, ×2. Fig. 100, Craig y Gath, near Llangower. PL 4447. External mould of a left valve, ×4·5. Fig. 101, Llaethnant Formation, Afon Twrch, near Bwlch y Groes. PL 4449. External mould of a left valve, ×4·5.

Figs 102a–c *Cuneamya* sp. (above). Allt Ddu Formation, Craig y Gath, near Llangower. PL 4451. Dorsal, anterior and left lateral views of the external mould of an articulated specimen, all ×2.

Fig. 103 ? *Archinacella* sp. (p. 226). Nod Glas Formation, Rhiw March, Llanymawddwy. PG 5022. Left-lateral view of an internal mould of a complete specimen, ×6.

Fig. 104 *Balacrinus basalis* (M'Coy) (p. 226). Allt Ddu Formation, Rhiw March, Llanymawddwy. E 67750. External mould of cup remains and attached arm and pinnule remains, ×2.

Fig. 105 *Stenaster obtusus* (Forbes) (p. 226). Allt Ddu Formation, Ty nant Farm, south of Llanuwchllyn. E 53698. Internal mould of a complete specimen, ×4.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102a
102b
102c
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Cyclonema are found, in the Allt Ddu and Gelli-grîn formations respectively. Material from this study is not figured here.

Pickerill & Brenchley (1979) record *Cyclonema*, *Cyrtolites*, ? *Seelya*, *Sinuites* and *Bucanopsis* from the *Howellites* Community, and *Lophospira* and *Murchisonia* in the *Dinorthis* and *Dalmanella* Communities respectively. Pickerill (1974) also referred to *Bucania* sp. and *Kokenospira* in the Lower Cwm Rhiwarth Siltstones.

Class **MONOPLACOPHORA** Wenz *in* Knight, 1952
Family **ARCHINACELLIDAE** Knight, 1956

Genus ***ARCHINACELLA*** Ulrich & Scofield, 1897

? ***Archinacella*** sp.
Fig. 103

A single asymmetrically conical shell mould (PG 5022) from bed R45 at the base of the Nod Glas Formation resembles *Archinacella* and is provisionally assigned to this genus.

Class **CEPHALOPODA** Cuvier, 1797

MATERIAL AND DISCUSSION. Although representatives of the Cephalopoda are recorded in 33 of the 196 samples corresponding to the main sections, most material is poorly preserved. However, a single well-preserved specimen (C 81324) from bed H40 (Fig. 4, p. 176) is assigned to ? *Orthoceras* and deposited with the other material figured here.

Phylum **ECHINODERMATA**
Class **CRINOIDEA** Miller, 1821
Subclass **CAMERATA** Wachsmuth & Springer, 1885
Family **ARCHAEOCRINIDAE** Moore & Laudon, 1943

Genus ***BALACRINUS*** Ramsbottom, 1961

Balacrinus basalis (M'Coy)
Fig. 104

MATERIAL, LOCALITY AND DISCUSSION. A well-preserved external mould (E 67750) of cup showing characteristic plate pattern, arm and pinnule remains was recovered from sample R14 in the Allt Ddu Formation at Rhiw March. Despite the occurrence of numerous fragmentary crinoid remains in the majority of samples (see Figs 4, 6–9, 12–15, 17) this specimen is the only complete one recovered during this study.

Class **STELLEROIDEA** Lamarck, 1816
Subclass **OPHIUROIDEA** Gray, 1840
Order **STENURIDA** Spencer, 1951
Family **STENASTERIDAE** Schuchert, 1914

Genus ***STENASTER*** Billings, 1858

Stenaster obtusus (Forbes)
Fig. 105

MATERIAL, LOCALITY AND DISCUSSION. A complete internal mould (E 53698) was recovered from beds immediately above the Frondderw Ash in the stream at Ty Nant (SH 906262); this is the same horizon from which sample 1022B was obtained (Fig. 6A, p. 178). The specimen is from a similar stratigraphical horizon (associated with the Frondderw Ash) to the Moel y Garnedd locality from which Salter recovered a specimen (Spencer 1927 : pl. 23). Elles (1922 : 138) recorded another ophiuroid *Protaster salteri* (Salter, *ex* Forbes) from immediately above the Cefn Gwyn Ash (Cefn Gwyn) (Spencer 1934 : pl. 31).

Faunal communities and associations

Unlike the Silurian faunas categorized by Zeigler (1965), Ziegler *et al.* (1968) and others into benthic 'communities', British Ordovician faunas have not, until recently, been classified in any such way, but elsewhere, e.g. in eastern North America, several Ordovician communities have been named by Bretsky (1969) and others.

Williams (1973 : 242–243) concluded that the Lower and Middle Caradoc faunas of Wales and the Welsh Borderland contained four facies-related 'faunal associations' (or 'communities'), named after *Dinorthis*, *Nicolella*, *Onniella* and *Howellites*, which are respectively characterized by 4, 5, 2 and 1 other named brachipod genera. He also named a fifth association, the '*Bicuspina* set', which is characteristic of the Upper Llandeilo and Lower Caradoc succession of the Shelve area (Williams 1976 : 39); the quantitative composition of this set (Williams 1974 : tables 7–11) allows it to be distinguished, by cluster analysis, from two other pre-Caradoc, inarticulate-dominated Shelve sets. The *Bicuspina* set is readily compared with the *Dinorthis* Association as they contain elements in common, in particular *Dalmanella*, *Heterorthis* and *Bicuspina* itself.

Pickerill (1974, 1977 : figs 3, 4) and Pickerill & Brenchley (1979) followed Williams (1973) by naming a *Dinorthis*, a *Nicolella*, an *Onniella*, a *Howellites* and a *Dalmanella* 'community' from the South Berwyns; the *Dinorthis* community is considered to consist of component *Dinorthis* and *Macrocoelia* 'sub-communities', which are essentially analogous to 'populations' referred to by Bretsky (1970). Unlike Williams they used quantitative measurements of ubiquity and average abundance to define four of these five communities; they referred only briefly to the fifth, *Onniella* community with associated genera. As the author, independently, chose to define the associations named here in a similar fashion to the quantitative method of Pickerill & Brenchley, an excellent opportunity is afforded for comparisons between the compositions of related associations in adjacent areas. Like Williams (1973, 1976) and Pickerill & Brenchley (1979) I use dominant genera in naming the associations described here; this permits the following direct comparisons.

The *Howellites* community of the South Berwyns is essentially similar to the contemporary *Howellites–Paracraniops* Association described here; both occur in a mudstone or silty mudstone facies and have *Howellites*, *Paracraniops*, *Macrocoelia*, *Reuschella*, *Bicuspina*, *Leptaena*, *Sowerbyella*, *Broeggerolithus* and *Brongniartella* amongst the more persistent (ubiquitous) and abundant elements. The main difference between the two associations is the relative importance of *Sowerbyella* in the South Berwyns. This is partly a reflection of a difference in the range of strata considered in the two areas; if the fauna of pre-middle Allt Ddu beds bearing *Sowerbyella* and *Heterorthis* were considered in conjunction with the upper Allt Ddu association the compositional resemblance of the associations in these two areas would be even more striking.

The composition of the *Howellites–Kloucekia* Association (and the closely related marginal *Howellites* association, Fig. 19, p. 193) is quite distinct, in detail, from the other *Howellites*-dominated associations referred to here. The brachiopods *Paracraniops*, *Macrocoelia*, *Reuschella*, *Bicuspina*, *Leptaena* and *Sowerbyella* and the trilobite *Brongniartella* are rare, absent or, like *Howellites* and *Broeggerolithus*, represented in this association by species distinct from those found in the older association(s) elsewhere. The association is further characterized by the relative persistence of *Skenidioides* and *Kloucekia*.

Although *Howellites* and *Broeggerolithus* are characteristic of all associations incorporating the name *Howellites*, it is clear that the Allt Ddu and Gelli-grîn associations of the area south of Bala are quite distinct and should not be considered jointly as Williams (1973) has done.

The *Dinorthis* Association, *sensu* Williams, although recognized by Pickerill & Brenchley in the South Berwyns, has not been identified in the Lower Bala Group south of Llanuwchllyn. Current evidence suggests that it is recognizable in parts of the Soudleyan succession in the Bala area (*sensu* Bassett *et al.* 1966) but not in equivalent beds to the south. For example, *Dinorthis* is a dominant element in sample GG1X (Fig. 12, p. 184) but is rare in equivalent beds at Craig y Gath (Fig. 8, p. 179) and unknown in the equivalent Rhiw March section (Fig. 9, p. 180). Williams (1973) states that the association is characterized by *Bicuspina*, *Dalmanella*, *Heterorthis* and *Leptaena;* this is confirmed by Pickerill & Brenchley (1979) who recognize these genera together with *Howellites*, *Reuschella*, *Sowerbyella*, *Paracraniops*, *Macrocoelia*, *Broeggerolithus* and *Brongniartella* amongst the dominant and persistent elements of the *Dinorthis* sub-community in the South Berwyns. It is significant that these latter seven genera are all of equivalent importance in the South Berwyn *Howellites* community and the *Howellites–Paracraniops* Association. However, in the *Dinorthis* sub-community (*sensu* Pickerill & Brenchley 1979) of south Salop, *Bicuspina* and *Reuschella* are not recorded whereas *Harknessella* and *Salopia* are considered important elements. At various specified horizons in the Salop, south Berwyns, Breidden Hills and Snowdonia successions, these authors consider the community to be represented by the *Macrocoelia* sub-community which, apart from being dominated by this genus, is essentially similar in composition to the *Dinorthis* sub-community. Similarly, their *Dalmanella* community, which is not recognized in the Bala area, is composed essentially of elements which characterize their *Howellites* and *Dinorthis* communities; its only very distinctive feature is the relative importance of *Dalmanella*.

The *Kullervo–Nicolella–Palaeostrophomena* Association (Williams *in* Whittington & Williams 1955), the *Nicolella* association/community *sensu* Williams (1973) and of Pickerill & Brenchley (1979) and the phases of the *Nicolella–Onniella* Association (defined here) are clearly closely related. The six brachiopod genera, including *Nicolella*, referred to by Williams as components of the association are not those which are most characteristic of the Welsh associations. Pickerill & Brenchley (1979) and the present study have shown, for their respective associations, that the most dominant and persistent elements are *Nicolella*, *Dolerorthis*, *Skenidioides*, *Eoplectodonta*, *Leptestiina*, *Onniella*, *Platystrophia*, *Bicuspina* and *Reuschella*. Of these *Platystrophia* is particularly abundant in the South Berwyns, but not at Bala, whilst *Onniella*, *Eoplectodonta*, *Reuschella* and *Bicuspina* are considerably more important in this latter area.

In the area considered here the importance of *Onniella* and *Eoplectodonta* in the *Nicolella–Onniella* Association cannot be overlooked. Not only are both forms considerably more abundant, at certain horizons, than any other brachiopod genera but they also represent a 'dalmanellid–plectambonitacean combination' noted in numerous Ordovician faunal associations in Britain and elsewhere. The so-called *Onniella* association/community referred to by Williams/Pickerill & Brenchley, although not quantitatively defined, appears to differ from the *Onniella* associations of this paper.

The *Onniella–Sericoidea* Association quantitatively outlined here is clearly related to the *Onniella* association/community referred to by Williams/Pickerill & Brenchley. Both the Pen y Garnedd Shale and Dyfi Mudstone associations contain *Onniella*, *Sericoidea* and *Paterula*. This particular dalmanellid–plectambonitacean association is typical of argillaceous parts of the Caradoc Series elsewhere in Britain. For example, Hurst (personal communication 1978) reports an *Onniella–Sericoidea* type of association in the Onny Shales. Similarly, Dean (1959) described Marshbrookian to Pusgillian faunas characterized by *Onniella* and *Chonetoidea* (and *Sericoidea*, A. D. Wright, personal communication 1975) from the Cross Fell area.

The *Sericoidea* Association of the Pistyll Gwyn, Y Ceunant and Aber Cowarch sections (Figs 17 & 19, pp. 190–193) is simply a diluted (low diversity, low equitability) marginal variety of the *Onniella–Sericoidea* Association. Between Bala and Dinas Mawddwy there is a pronounced lateral variation in the faunal associations (and facies) of the uppermost 20 m of the Caradoc succession. The *Nicolella–Onniella* Association (occupying coarse, calcareous clastic substrates) passes laterally into the *Onniella–Sericoidea* and *Sericoidea* Associations (calcareous mudstones), then into a graptolitic association (in black shales); see Fig. 18, p. 192.

Contemporary Scoto-Irish faunas described by Williams *et al.* (1962) and Mitchell (1977) have yet to be categorized into named associations. These faunas are fundamentally different from those of 'Anglo-Welsh' affinity; this is a reflection of the mid-Ordovician separation of northern and southern Britain by the Proto-Atlantic ocean (Smith *et al.* 1973). The discovery of *Bimuria* and *Protozyga* in Wales and the recognition of wider distributions for *Cyclospira*, *Palaeostrophomena* and *Anisopleurella* are evidence of more mixing of Scoto-Irish with Anglo-Welsh faunas than was hitherto supposed.

Despite the fact that Whittington & Williams (1955 : 398) and Williams (1962 : table 2; 1969 : 131–135) have shown that faunal associations with Scoto-American (or Scoto-Appalachian) affinities show little similarities to those known from the Anglo-Welsh region, recent studies by Bayer (1967), Fox (1968), Bretsky (1969, 1970), Bretsky & Bretsky (1975, 1976), Walker & Laporte (1970), Walker (1972), Walker & Alberstadt (1975), Walker & Parker (1976) and others have led to the naming of a number of associations or communities from the Mid- to Upper Ordovician of the Appalachians which show striking parallels with those named from the Anglo-Welsh region.

Among these 'American communities' are several named after familiar dalmanellid–plectambonitacean combinations including the *Onniella–Sowerbyella* community (Bretsky 1969), the *Eoplectodonta* (*Thaerodonta*)–*Onniella* community (Bayer 1967) of the mid-continent upper Ordovician and the *Resserella–Sowerbyella* assemblage (Fox 1968); similarly, data given by Titus & Cameron (1976 : 1216–1217) reveal that *Paucicrura* and *Sowerbyella* represent about two-thirds (mean relative abundance) of the total fauna in four out of five communities named after rarer elements.

Other communities named after or dominated by genera common to the Anglo-Welsh successions are as follows. The mid-Appalachian *Rafinesquina*, *Sowerbyella*, *Lophospira* Association and the *Onniella*–nuculoid bivalve Association named by Bretsky (1969) from siltstones and mudstones respectively, as component associations (or 'populations') in the *Sowerbyella–Onniella* community, are reminiscent of parts of the Berwyn and Salopian faunal successions respectively. Similarly, the succession dominated by *Onniella* and *Cryptolithus* outlined by Bretsky & Bretsky (1975 : 228) from the upper Ordovician of Quebec is shown subsequently by these authors (1976 : table 3) to be dominated at different horizons by combinations of genera including *Nuculites* with *Cryptolithus* and *Nuculites* with *Onniella* (cf. Bretsky 1969). Such combinations are again reminiscent of parts of the Anglo-Welsh Caradoc successions.

The upper Ordovician *Platystrophia–Leptaena* assemblage (Fox 1968) is comparable to the *Nicolella* community (*sensu* Pickerill & Brenchley 1979) which, in addition to occurring in a similar calcareous facies, contains these two former genera amongst its most important elements.

Walker & Laporte (1970) and Walker (1972) referred to *Strophomena* and *Dalmanella* respectively as 'major' taxa in inferred low intertidal and subtidal carbonate facies of the middle Ordovician of New York. Similarly, Walker & Alberstadt (1975) and Walker & Parker (1976) have named a *Rostricellula–Strophomena* community from the middle Ordovician of the southern Appalachians. All these genera represent important or dominant elements in parts of broadly contemporary Anglo-Welsh successions.

Although Williams (1969 : 133–137) referred to *Sowerbyella*, *Sericoidea*, *Macrocoelia*, *Rafinesquina*, *Strophomena*, *Platystrophia*, *Dalmanella*, *Howellites* and *Onniella* as widespread or pandemic genera in Caradoc to Ashgill times, there has hitherto been little comment on their importance as 'community dominants' in parts of both the American and north European provinces. In the Anglo-Welsh and Appalachian regions the importance of dalmanellid–plectambonitacean dominated associations cannot be overemphasized; combinations like *Dalmanella* with *Sowerbyella* (in the Upper Llanvirn–Llandeilo of south Wales) and the other Caradoc to Ashgill combinations mentioned above occupy a wide variety of facies including limestones, tuffs, sandstones, siltstones and fine mudstones.

Conclusions

The present study suggests that detailed local examination of (Caradoc) faunal successions can lead to the identification of distinct associations dominated by different species of the same, often ubiquitous, genera. Since associations are commonly named after such dominant forms, a paradoxical situation arises, where on the one hand local interassociation variation is easily demonstrated, yet on the wider provincial scale considerable uniformity appears to be the rule. Such a paradox is the result of a dual influence. Firstly, the use of generic rather than specific terminology in the naming of communities, although favouring brevity, masks important differences. Secondly, the widespread occurrence of various species of ubiquitous genera strongly suggests that 'parallel communities' (*sensu* Thorson 1957, 1966) characterized Ordovician marine benthic environments. For these reasons it is emphasized that the generic names employed in the classification of associations should refer unequivocally to particular species at particular horizons, as stated or implied here in all cases. This approach permits named communities to be specifically identified and distinguished from other local or distant, more or less contemporary parallel communities dominated by ubiquitous congeneric forms.

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New taxonomic names and the page numbers of the principal references are in **bold** type. An asterisk (*) denotes a figure.

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