

# BENTHIC PALAEOCOMMUNITIES REPRESENTED IN THE FFAIRFACH GROUP AND COEVAL ORDOVICIAN SUCCESSIONS OF WALES

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**ABSTRACT.** The study provides detailed quantitative analyses of faunal assemblages from various Upper Llanvirn shelly facies occurring with the Lower Ordovician successions of mid-Wales. In particular fifteen assemblages occur in about 90 m of varied sediments and bedded pyroclastics constituting the Ffairfach Group stratotype. The assemblages congregate into eleven distinct associations two of which recur five times. The lithological successions and taphonomic structure of the entombed assemblages indicate predominantly shallow-water, shoreface deposits dominated by benthos. The exoskeletal remains underwent only limited post-mortem disturbance and mixing and are assumed to represent a series of extinct palaeocommunities. The extent to which these palaeocommunities intergraded, or were entirely separate from one another, may be inferred from the taxonomic and quantitative structures of the associations. A basic distinction can be drawn between very restricted opportunistic palaeocommunities, such as those dominated by *Tissintia* and *Hesperorthis*, and diverse recurrent ones dominated by *Orderleyella*, *Dalmanella* and *Sowerbyella*. In each of the last three palaeocommunities it has been possible to infer the main changes which led to the climax in its maturation. The palaeocommunities can be identified in successions elsewhere in Wales and in Shropshire.

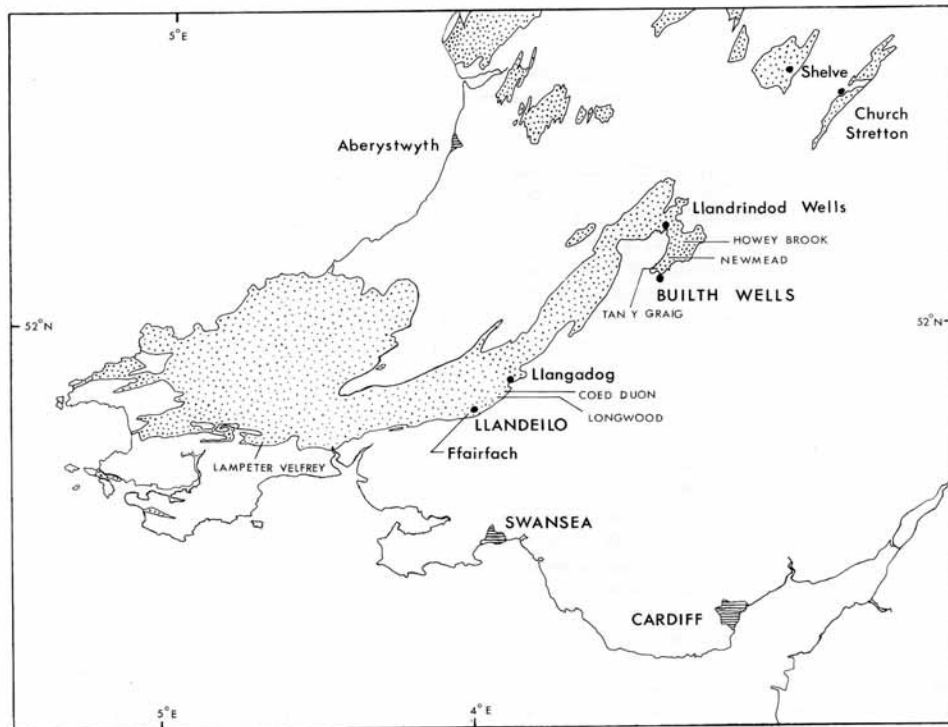
THE varied sediments immediately underlying the Llandeilo Flags of the type area are well exposed in the village of Ffairfach (Fig. 1), especially in the railway cutting south of the level-crossing (between Grid References SN 62782122 and 62802112). These exposures, which constitute the type section of the Ffairfach Group (Williams 1953a, p. 180), yield relatively diverse Lower Ordovician fossil assemblages (i.e. groups of fossils from specified localities and horizons). The fossils have attracted the attention of palaeontologists since the days of Phillips, Murchison and M'Coy; initially in the belief that they were coeval with those from the Caradoc 'sandstones' of Shropshire; more recently because the Llandeilo-Llanvirn Series boundary in relation to the Ffairfach Group is in dispute (Williams *et al.* 1972, p. 5; Bergstrom 1971, p. 109). The latter issue is not considered in this paper, although the nature of the faunal succession within the Group is relevant to its resolution. The main reason for the investigation is an acknowledgement that palaeontologists who first examined the fossil assemblages from the Group were right to be impressed by their similarity with those from the Caradoc rocks of Shropshire. This similarity is more than an expression of penecontemporaneity. A comparison of the stocks represented in the two faunas shows that, although they are rarely conspecific, long-lived genera tend to be associated in the same proportional frequency of occurrence.

The palaeoecological implications of such associations, by which is meant assemblages of taxa having definable recurrent relationships with one another, are obvious enough. Indeed some of the more striking generic associations, which are usually characteristic of distinctive sedimentary suites, have already been identified in the pre-Ashgill successions of Shropshire (Williams, 1976, p. 39) and the Caradoc rocks of north Wales (Williams 1963, p. 341), and further studied by Lockley (1978, p. 283) and Pickerill and Brenchley (1979, p. 229). These investigations suggested that similarly structured assemblages changed subtly from one geological horizon to the next, presumably by the evolution of some persistent stocks or by replacement of others, until the oldest associations bore little taxonomic resemblance to the youngest. Observations on the nature of these changes might, therefore, give some insight into the evolution of communities of interacting populations, assuming associations to be the fossil remnants of such organized units. Moreover, if a palaeoecosystem is

defined as a fossil community and its entombing lithofacies, it should eventually be possible to assess the relative importance of the biotic and physical components of such palaeoecosystems in determining the pace and nature of community evolution.

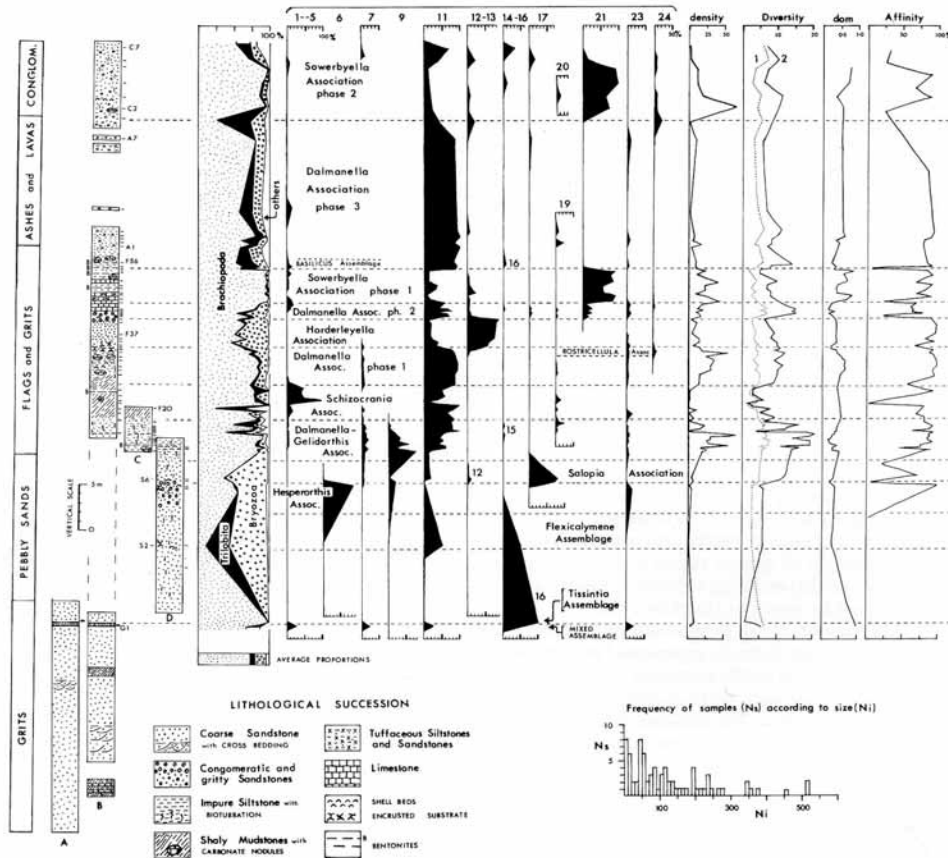
With this prospect in view, our attention turned to the Llanvirn and Llandeilo shelly facies of mid-Wales to seek out the antecedents of the Caradoc shallow water facies of south Britain. The study of which is still continuing. C. J. Wilcox and M. G. Lockley have also completed researches into assemblages of the Llandeilo shelly facies of Dyfed. The systematics of previously recorded Llanvirn species had to be revised and some new taxa described (Lockley and Williams 1981).

The Llanvirn successions of mid-Wales include fossil assemblages which occupied palaeoenvironments similar to those represented by the Caradoc shallow water facies of south Britain. Their stratigraphical relationships, however, are greatly complicated by rapid facies changes involving a wide range of sediments varying from pyroclastics and conglomerates to mudstones and limestones. These sediments form a variably developed apron around a volcanic complex of Llanvirn age, remnants of which are now exposed near Llangadog and in the Builth-Llandrindod Wells area, 12 and 60 km north-east of Llandeilo respectively (Williams 1969, p. 122). Accordingly, the sections from which material for census studies of fossils was retrieved had to be chosen with some regard for lithological variability as well as continuity of outcrop.



TEXT-FIG. 1. Map showing localities in the Llandeilo and Builth areas in relation to the outcrop of Ordovician rocks (stippled) in South West Wales.

The principal collections were obtained from the type section for the Ffairfach Group along the Cennen Valley railway-cutting. Here almost 100 m of steeply dipping strata are exposed between the underlying *Didymograptus bifidus* shales cropping out at the level-crossing and the overlying basal members of the Llandeilo Series also in their type section. Other collections were made from sections at Longwood (SN 693258) and Coed Duon (SN 279266) which are respectively 8 and 9 km north-east of the Ffairfach cutting. The shelly facies of the Builth-Llandrindod Wells area are less well-known than those of Ffairfach, but various exposures were sampled, particularly those near Howey Brook (SO 093592), south-east of Llandrindod Wells.



TEXT-FIG. 2. The lithological and faunal succession of the type Ffairfach section showing: percentage of main faunal groups and dominant brachiopod species (Inarticulata 1-5 and Articulata 6-24 as in Table 2); density estimated as specimens per kg; Diversity calculated (1) according to  $S - 1/\log N$  and (2) to species per sample; dom. = dominance (C) for whole assemblage; Index of Affinity estimated between successive stratigraphically adjacent samples. A = Grit exposures east of railway and river (Grid. Ref. SH 62972123), B = Main section along west bank of railway embankment, C and D respectively represent exposures in west and south-west sides of main embankment quarry.

This paper is presented in four sections. Having outlined the methods used to ensure that our samples and their scrutiny are adequate, we briefly discuss the lithological variation within the Ffairfach Group and the inferred succession of palaeoenvironments in which the sediments accumulated. The fossil assemblages recovered from the type section are then described, their associations identified and the palaeocommunities to which they belonged are inferred. Finally, we test the rock/fossil relationships of the type section against those found elsewhere before concluding with a review of the inferred palaeoecosystems.

In our discussion of the benthic palaeocommunities which we believe existed in the Anglo-Welsh Basin during mid-Ordovician times, we have attempted to use a number of ecological terms to convey the same meaning as they have in recent studies. We are well aware of the dangers of this practice since fossilized remnants of faunas and their entombing sediments can never adequately reflect the full relationship between organisms and their environments. The alternative, however, is to coin another terminology which would hinder communication between ecologists and those palaeontologists who want to know how far they can go in reconstructing extinct communities and past ecosystems. Communities evolve and the process can only be understood by identifying communities which existed in the past and studying the changes they underwent during significant segments of geological time. For this reason we describe our fossil material in such terms as: opportunistic species; pioneer, mature or climax palaeocommunities; ecotones; and edge species. The use of such terms may prove to be inappropriate, but it may at least prompt reappraisals of these and other data.

#### FIELD AND LABORATORY METHODS

Field collecting was based on the 'bulk census' method whereby samples were recovered from successive horizons at close intervals subject to accessibility. The nature of the rock type in determining the interval at which sampling occurred was important only in successions which were demonstrably unfossiliferous and uniform in lithology as is true of much of the basal formation of the Group, the Ffairfach Grit. In all, seventy-eight samples averaging 6.1 kg in weight were taken from the type section at a mean interval of 85 cm for the succession between the first occurrence of skeletal remains in the upper part of the basal Ffairfach Grit member and the top of the Group. The mean interval in the more fossiliferous formations above the Pebbly Sands was only half this (i.e. 42 cm). Orientated blocks for the study of the sedimentary fabric of the principal lithofacies were also collected. In the laboratory, the samples were broken up to provide a maximum yield of fossil remains. Much of the rock material is well-bedded so that estimates of the area as well as the volumetric density of distribution of fossils could be derived. We did, however, find that the simple relationship of: number of specimens/weight of sample (kgm) was a good index of the degree of dispersion of fossils throughout the succession; and that areal and volumetric density values showed the consistent relationship which had previously been observed by one of us (Lockley 1980).

The fossil counts for all samples were conducted according to the following criteria. The brachiopods are the dominant and most diversely represented phylum in the assemblages collected from all localities. They account for nearly 75% of all fossils recovered and almost 60% of the number of taxa composing the Upper Llanvirn faunas. Only 7% were preserved as complete shells; they occurred mostly as disarticulated valves or as fragments of indeterminate valves. The total number of individuals ascribed to a sample was therefore estimated by adding counts of all articulated and all brachial *or* pedicle valves, whichever occurred more frequently, and one-half of all identifiable fragments (cf. Lockley 1980). Bivalves were counted in the same way whilst gastropods, orthocones, machaeridians, conulariids, and graptolites were similarly treated by assuming fragments as well as complete skeletons to be the remains of individuals. The number of trilobite individuals recorded in a sample was estimated by dividing counts of the most numerous complete or relatively simple skeletal components, like pygidia or cephalae, by four (see Lockley 1980) as a compromise between extreme estimates of 10% (Harrington 1959, p. O111) and 100% (Hurst 1975, Table 2). The number of ostracode valves occurring in a collection were divided by eight which is a less arbitrary corrective for the effects of ecdysis in this class of arthropods (Anderson 1964). Bryozoan colonies, like those of the trepostome *Prasopora* or some branching trepostomes and cryptostomes, were often complete and counted as such. Counts of fragmentary remains of the ramose bryozoans were divided by four to provide an arbitrary estimate of the frequency of complete colonies. The siliceous rods of the problematic organism *Hyalostelia fascicula* (M'Coy) were counted wherever practicable, as were crinoid ossicles and other echinoderm fragments, but were assumed, except in the case of discrete *Hyalostelia* clusters, to represent only one individual in any given sample.

Fm.	TYPICAL FACIES	FAUNAL ASSEMBLAGES	ns	$\bar{d}$	$\bar{D}$ (range)	$\bar{C}$
CONG.	CONGLOMERATIC, GRITTY SANDSTONES.	SOWERBYELLA ASSEMBLAGES (Phase 2)	6	21.0	8.5 (6-11)	(0.601)
ASHES &c	TUFFACEOUS SILTSTONES AND SHALES (Poorly exposed)	DALMANELLA ASSEMBLAGES (Phase 3)	11	11.1	8.6 (5-14)	(0.437)
		Trilobite Assemblage			14	
GRITS & GRITS	CALCAREOUS, SHELLY SILTSTONES	SOWERBYELLA ASSEMBLAGES (Phase 1)	8	26.2	7.5 (5-10)	0.606
	MASSIVE LIMESTONES					
	PEBBLY SANDSTONES	DALMANELLA ASSEMBLAGES (Phase 2)	6	21.6	13.5 (10-15)	0.265
FLAGS & GRITS	SANDSTONES	HORDERLEYELLA / BRYOZOA ASSEMBLAGES	7	16.7	8.7 (6-10)	0.341
	CALCAREOUS, SHELLY SILTSTONES	ROSTRICELLULA / BRYOZOA ASSEMBLAGES	8	35.5	10.2 (9-12)	0.532
	SHALES	DALMANELLA ASSEMBLAGES (Phase 1)				
		? SCHIZOCHAMIA ASSEMBLAGES	9	3.9	4.9 (1-9)	(0.538)
SANDS	FINE, CALCAREOUS SILTSTONES	DALMANELLA / GELIDORTHIS ASSEMBLAGES	15	30.6	14.9 (11-20)	(0.422) - (0.320)
	PEBBLY SANDSTONES	SALOPIA / BRYOZOA ASSEMBLAGES	2	13.1	11.0 (10-12)	0.282
		HEPHEROTHIS / BRYOZOA ASSEMBLAGES	2	5.4	5.5 (5-6)	0.382
PEBBLY SANDS	BIOTURBATED FLAGGY SANDSTONES	FLEXICALYMENE / BRYOZOA ASSEMB.	1	6.3	6 -	0.380
GRIT	MASSIVELY-BEDDED SANDSTONES AND GRITS (with Shale horizons near top)	Tissintia Assemblage	1	7.7	1 -	1.00
		Mixed Brachiopod Assemblage	1	6.0	6 -	0.667
FFAIRFACH					10 m 0	

TABLE 1. Scale representation of the stratigraphical distribution of various sedimentary units (facies) and their entombed faunal assemblages in the type Ffairfach Formation (Fm). The number of samples (ns), mean density ( $\bar{d}$ ), mean Diversity ( $\bar{D}$ ) and range and mean dominance values ( $\bar{C}$ ) for each group of assemblages are also shown. C values in brackets were calculated using only representative, larger samples, as described in the text.

The data derived in this way are presented as a series of charts (Tables and Figs.) and have been further expressed as simple proportions (e.g. Fig. 2) in an attempt to identify associations. Differing associations may reflect different communities which displaced one another within a given succession. They may also become evident during the maturation of a single community from the first phase of colonization of a substrate by an opportunistic stock to a climax in which the full range of species diversity is achieved. The dominance ( $C$ ) of an opportunistic species can be measured as:

$$C = \sum \left( \frac{ni}{N} \right)^2;$$

and the diversity ( $D$ ) of species as:

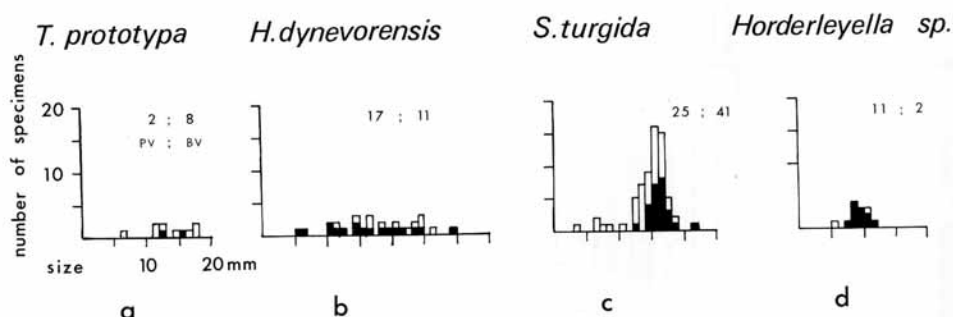
$$D = \frac{S-1}{\log_e N};$$

where  $ni$  = number of individuals in each species;  $N$  = total number of individuals; and  $S$  = number of species. The latter formula is clearly preferable to an index of diversity which is related to sample size and simply records the number of species identified in collections from any one horizon, as in fig. 2. The Index of Affinity (I.A.) may be expressed as:

$$\text{I.A. } kj = \sum_{i=1}^n \min(X_{ki}, X_{ji})$$

where  $i$  =  $i$ th species;  $k, j$  = samples;  $n$  = total number of species (Rodgers 1976, p. 505), and is of particular value in comparing the taxonomic composition of different samples. A plot of I.A. values between stratigraphically adjacent census samples (e.g. Fig. 2) identifies the horizons at which the main faunal changes occur.

The overwhelming predominance of brachiopods in nearly all our collections has prompted us to consider members of that group solely in relationship to one another as well as part of the entire faunal succession. In addition to using the formulae given above to estimate opportunism, diversity and similarity among the assemblages, the commoner brachiopod species have also been expressed as a percentage of the full representation of the phylum at any one horizon. This approach has clarified the taxonomic structure of many associations by identifying the chief elements of their sedentary benthos which in turn has facilitated speculation on their inferred communities.



TEXT-FIG. 3. Size-frequency histograms for complete pedicle (black) and brachial valves of brachiopods in assemblages from the Ffairfach type section showing respective numbers ( $N$ ) of each valve (pv : bv). (a) *T. prototypa* from the Grit; (b) *H. dynevorensis* from Pebbly Sands samples S3 and S4; (c) *S. turgida* from Pebbly Sands samples S5 and S6; (d) *Horderleyella* sp. from samples S6 and F1.

## SEDIMENTARY SUCCESSION AND PALAEOENVIRONMENT AT FFAIRFACH

The Ffairfach Group consists of a variable sedimentary succession which has been subdivided into five mappable units recognizable throughout the Llandeilo district (Williams 1953a, Figs. 1-4). These units have been named as formations (Lockley and Williams 1981) which is consistent with the status of the Group and permits the more distinctive lithostratigraphic units composing the formations to be regarded as members (Table 1 and Fig. 2). We have not, however, formally recognized such finely drawn units although, as will be shown, they are frequently characterized by distinctive fossil assemblages.

The Ffairfach Grit Formation consists almost exclusively of massively bedded clean-washed arkosic grits with beds averaging about 1 m in thickness (range 0.5 to 4 m) and showing predominantly sub-horizontal stratification with rarer cross-stratified sets. Constituent particles are angular to subangular in shape, moderately well-sorted and medium- to coarse-grained with diameters ranging from 0.2 to 1.0 mm. Argillaceous material, biogenic structures, and fossils are uncommon throughout. Thin shales, occurring in the upper part of the Formation, are reminiscent of the middle succession of the Group but the grit facies is confined entirely to this basal stratigraphic unit where it attains a thickness of 26 m in the exposures at the north-east end of the type section (Grid Ref. SN 62972123, Fig. 2).

The succeeding Pebbly Sands Formation consists of two similar facies (Table 1). The transition from the Grits, forming the northern face of the embankment quarry (Williams 1953a, Fig. 4), to the overlying sandstones of the eastern face, is quite abrupt and is marked particularly by increased bioturbation. The sandstones typically consist of flaggy units, 20-25 cm thick, which contain many irregular argillaceous laminae, shale-filled burrows, and occasional ripple marks. The distinction between these flaggy sandstones which attain a thickness of 20 m and the succeeding 15 m of pebbly grits is not strong and the boundary between the two facies is gradational. However, there is a progressive increase in particle size and angularity from the sparsely fossiliferous, slightly micaceous, fine- to medium-grained (0.1-0.5 mm) sandstones of the lower unit to the very coarse (0.5-5.0 mm) pebbly, fossiliferous grits of the upper which is further characterised by the presence of thin volcanic clay horizons (Williams 1953a, Figs. 1 and 4). Neither facies is confined to this Formation.

The Flags and Grits Formation consists of a sequence of seven mainly intergrading lithological units (Table 1), two of which closely resemble the sediments of the underlying Formation. Basal fine calcareous siltstones succeed the underlying pebbly grits in one of the most contrasting sedimentary changes in the Group. This basal unit consists of about 8 m of fine homogeneous siltstones which contain large (20-40 cm) nodules of diagenetic carbonate, thin white bentonites and numerous fossils, and grade imperceptibly into the succeeding 7 m of almost unfossiliferous shales with rarer small (1-2 cm) carbonate nodules. Both of these basal units lack distinctive sedimentary structures although alternations between darker argillaceous and lighter silty bands impart a fine, slightly irregular lamination throughout.

The shales grade upwards into 5 m of flaggy, irregularly-bedded, calcareous, fossiliferous siltstones with bedded units averaging about 7 cm in thickness (range 3 to 12) and displaying some cross-stratification. The siltstones contain considerable fragmentary shell debris which increases in abundance up the succession and leads to the development of the succeeding facies. This calcareous unit is locally developed for a thickness of about 3 m and is composed mainly of the skeletal remains of encrusting bryozoa.

The calcareous unit grades abruptly up into 8 m of impure, medium-grained (0.2-0.5 mm), orange-weathered sandstones which contain irregular impersistent argillaceous laminae. The sandstones are very like those in the lower part of the Pebbly Sands Formation but contain a different fauna. They grade into a sequence of conglomeratic grits, about 2 to 3 m thick, containing well-rounded pebbles (up to 10 mm in diameter) in a poorly sorted, arenaceous, gritty matrix. This pebbly facies is also reminiscent of that encountered in the upper part of the Pebbly Sands Formation.



TABLE 2. The composition of faunal assemblages from the Ffairfach Group type section. The numbers of individual each taxon were estimated by methods outlined in text; *N*: indeterminate number of fragments; *c*: *Hyalostelia* clus

Sample number	Inarticulata Indet.	<i>Pseudolingula granulata</i> (Phillips)	<i>Paterula</i> cf. <i>bohemica</i> Barrande	<i>Schizocrania</i> cf. <i>salopiensis</i> Williams	<i>Schizotreta transversa</i> Ffairfachensis Lockley and Williams	<i>Hesperorthis dynevoensis</i> Williams	<i>Glyptorthis viriosa tumida</i> Lockley and Williams	<i>Corineorthis</i> sp.	<i>Gelidorthis cennensis</i> Lockley and Williams	<i>Skenidoioides</i> sp.	<i>Dalmanella parva</i> Williams	<i>Hordeleyella convexa</i> / ( <i>H.</i> sp.)	<i>Tissintia prototypa</i> / ( <i>immatura</i> ) / [ <i>plana</i> ]	<i>Salopia turgida</i> (McCoy)	<i>Kullervo</i> sp.	<i>Triplesia edgelliana</i> (Davidson)	<i>Oxoplecta</i> cf. <i>nantensis</i> MacGregor	<i>Sowerbyella antiqua</i> Jones	<i>Murinella</i> sp.	<i>Macrocoelia llanidloensis</i> (Davidson)	<i>Rostricellula triangularis</i> Williams
C7	—	—	—	—	—	—	—	—	—	—	4	—	[2]	—	—	—	—	—	—	—	—
C6	—	—	—	—	—	—	1	—	—	—	4	3	—	2	—	—	—	2	—	—	1
C5	1	—	—	—	—	—	—	—	—	—	6	—	—	2	—	—	90	—	—	—	2
C4	—	—	—	—	—	—	—	—	—	—	—	—	[3]	—	—	—	45	—	—	—	—
C3	—	—	—	—	—	—	—	—	—	—	12	4	—	—	—	—	4	51	—	—	5
C2	—	—	—	—	—	—	—	—	—	—	24	2	—	—	—	—	1	97	—	—	6
C1	—	—	—	—	—	—	—	—	—	—	2	1	—	—	—	—	—	—	—	—	2
A7	—	—	—	—	—	—	—	—	—	—	30	—	—	1	—	—	—	—	—	3	1
A6	1	—	—	—	—	—	—	—	—	—	9	—	—	—	—	—	—	—	—	—	—
A5	—	—	—	—	—	—	—	—	—	—	35	1	—	—	—	1	—	—	—	—	—
A4	—	—	—	—	—	—	—	—	—	—	39	—	—	—	—	—	—	—	—	1	—
A3	—	—	—	—	—	—	—	—	—	—	22	—	—	—	—	—	—	—	1	2	—
A2	—	—	—	—	—	—	—	—	—	—	58	—	—	—	—	15	—	—	—	1	—
A1	—	—	—	—	—	—	—	—	—	—	10	—	—	—	—	—	—	—	—	—	—
F56	1	1	—	—	—	—	—	—	—	2	73	—	[8]	2	—	—	—	—	1	2	—
F55	1	—	—	—	—	—	—	—	—	—	23	—	—	—	—	—	—	—	—	1	—
F54	3	—	—	—	—	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—	—
F53	4	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	107	—	—	—	—
F52	4	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—	31	—	—	—	—
F51	2	—	—	—	—	—	—	—	—	—	19	4	—	—	—	—	166	—	—	—	1
F50	1	1	—	—	—	—	—	—	—	—	20	2	—	—	—	—	31	—	—	—	—
F49	4	—	—	—	—	—	—	—	—	—	36	13	—	—	—	—	64	—	—	—	—
F48	1	—	—	—	—	—	—	—	—	—	7	13	—	—	—	—	34	—	—	—	—
F47	2	—	—	—	—	—	—	—	—	—	22	—	—	—	—	2	328	—	—	—	1
F46	1	—	—	—	—	—	—	—	—	—	23	3	—	—	—	1	155	—	—	—	1
F45	11	—	2	—	—	—	—	—	—	—	72	6	—	—	—	8	10	—	11	1	—
F44	11	—	—	—	—	—	—	—	—	—	26	3	(1)	2	—	—	18	—	2	1	—
F43	9	—	2	—	—	—	—	—	—	—	204	7	—	—	—	9	23	—	17	—	—
F42	3	—	—	—	—	—	—	—	—	—	17	3	—	2	—	—	11	—	5	—	—
F41	—	—	—	—	—	—	—	—	—	—	48	5	—	3	—	1	13	—	5	—	—
F40	—	—	—	—	—	—	—	—	—	—	24	3	—	—	—	1	6	—	—	—	—
F39	—	—	—	—	—	—	—	—	—	—	4	29	—	—	—	—	—	—	—	—	—
F38	1	—	—	—	—	—	—	—	—	—	14	58	—	—	—	—	—	—	—	—	—
F37	—	—	—	—	—	—	—	—	—	—	10	48	—	—	—	1	—	—	—	1	—
F36	—	—	—	—	—	—	—	—	—	—	17	56	—	—	—	1	—	—	—	1	—
F35	—	—	—	—	—	—	—	—	—	—	47	71	—	—	—	1	—	—	—	3	1
F34	—	—	—	—	—	—	—	—	—	—	18	31	—	—	—	1	—	—	—	4	1
F33	—	—	—	—	—	—	2	—	—	—	81	60	—	—	—	4	—	—	—	4	4
F32	—	—	—	—	—	—	—	—	—	—	49	5	—	—	—	1	—	—	—	2	5



Sample number	<i>Basilicus tyrannus</i>	<i>Flexicalymene cambriensis</i>	<i>Marrolihus</i> sp.	<i>Atractopyge</i>	<i>Mesotepteraspis</i> sp.	<i>Metopolichus</i>	Trilobita indet	Gastropoda	Dendroid trepostome	Prasoporiid Bryozoa ( <i>Prasopora</i> sp.)	Fenestrate cryptostome	Bryozoa fragments	Boring organism	<i>Hyalostelia fascicula</i> (c = cluster)	Conularida / Machaeridia	<i>Tatinnella</i> sp.	Smooth Ostracod	ossicles / other fragments	Crinoidea	Total (estimated) number of individuals
C7	1	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	11
C6	1	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	1/1	—	18
C5	(2)	—	—	—	—	—	(2)	—	—	—	—	—	—	—	—	—	—	6	—	103
C4	1	—	—	—	—	—	(1)	—	3	—	—	—	—	—	—	—	—	4	—	53
C3	(3)	(2)	—	—	—	—	—	1	5	—	—	(4)	—	N	—	—	—	1	—	87
C2	—	1	—	1	—	—	—	—	3	—	—	(2)	—	N	—	—	—	1	—	137
C1	(6)	1	—	—	—	—	(25)	—	3	1	—	(1)	—	—	—	—	—	1	—	19
A7	—	—	—	—	—	—	—	—	6	—	—	(1)	—	(41)	—	—	—	—	—	43
A6	(9)	—	—	—	—	—	—	—	2	—	—	—	—	(5)	—	—	—	3/5	—	17
A5	(3)	—	—	—	—	1	—	—	3	1	—	(1)	—	(15)	—	1	1	—	—	47
A4	(5)	1	—	—	1	—	(12)	—	—	2	—	(1)	—	1	—	1	1	4/1	—	50
A3	(4)	1	—	—	—	—	(35)	—	—	5	—	(1)	—	1 <sup>c</sup>	—	—	—	1	—	42
A2	(2)	(4)	1	—	—	—	(4)	—	12	—	—	(7)	—	(8)4 <sup>e</sup>	—	—	—	—	—	94
A1	(4)	1	—	—	—	—	(2)	—	1	2	—	(1)	—	(1)1 <sup>c</sup>	—	—	—	1	—	17
F56	(21)	1	(19)	—	—	—	(130)	—	26	—	—	(20)	—	(1)	—	10	—	8	—	168
F55	1	1	(10)	—	—	—	(25)	—	4	—	—	(2)	—	—	—	8	—	—	—	40
F54	(4)	(2)	(8)	—	—	—	(6)	—	4	6	—	(4)	—	—	—	7	—	—	—	39
F53	1	—	(2)	—	—	—	(3)	—	—	—	—	—	—	—	—	—	—	—	—	116
F52	—	—	—	—	—	—	—	—	—	—	—	(1)	—	(1)	—	—	—	—	—	41
F51	(2)	(6)	(6)	—	—	—	—	—	2	—	—	—	—	—	—	2	—	1	—	199
F50	1	1	1	—	—	—	—	—	1	—	—	(1)	—	—	—	—	—	—	—	58
F49	1	—	—	—	—	—	(2)	—	—	—	—	(1)	—	—	—	1	—	—	—	120
F48	1	—	(2)	—	—	—	(2)	—	—	1	—	—	—	1 <sup>c</sup>	—	—	—	—	—	59
F47	(6)	—	1	—	—	—	—	—	—	—	—	—	—	(1)	—	—	—	—	—	358
F46	(3)	—	1	—	—	—	—	—	4	—	—	(3)	—	(1)	—	—	—	—	—	192
F45	(4)	—	(2)	—	—	—	—	—	14	2	—	(5)	—	(8)	—	—	—	—	—	141
F44	(2)	1	1	—	—	—	(1)	—	11	1	—	(4)	—	(8)	—	1	—	—	—	82
F43	(11)	(13)	(6)	—	—	—	(1)	—	80	3	3	(40)	—	(2)	—	1	—	—	—	376
F42	(3)	(16)	—	—	—	—	(6)	—	22	1	—	(6)	—	(1)	1	11	—	1	—	75
F41	(4)	(7)	(4)	—	—	1	(14)	—	22	—	—	(10)	—	(5)2 <sup>c</sup>	1	4	—	1	—	113
F40	—	1	1	—	—	—	—	—	5	—	—	(5)	—	(2)	—	3	—	2	—	46
F39	(13)	—	—	—	—	—	(4)	—	19	—	—	(8)	—	(2)	—	—	—	2/5	—	60
F38	(9)	—	—	—	—	—	—	—	32	—	—	(8)	—	(8)	—	—	—	29/17	—	111
F37	(3)	—	—	—	—	—	(2)	—	50	—	1	(2)	—	(5)	—	—	—	5/2	—	114
F36	—	—	—	—	—	—	(2)	—	25	—	1	(15)	—	(5)	—	—	—	—	—	107
F35	(5)	—	—	—	—	—	(2)	—	128	—	1	(25)	—	(15)	—	—	—	—	2	260
F34	(14)	—	—	—	—	—	—	—	21	—	2	(18)	—	(30)	—	—	—	2/1	—	88
F33	(39)	—	—	—	—	—	(12)	—	63	—	1	(10)	—	(N)1 <sup>c</sup>	—	—	—	2	—	236
F32	(4)	—	—	—	—	—	(15)	—	10	—	—	(7)	—	(20)	—	—	—	1	—	80





The uppermost 15 m of the Flags and Grits Formation consist of calcareous sediments which abruptly succeed the pebbly grits and constitute two related lithofacies. The lower sequence consists of 8 m of shelly, crystalline limestones with beds up to 25 cm thick alternating with thin (1–10 cm) rubbly calcareous shales. The succeeding 7 m of calcareous, irregularly laminated shelly siltstone contain abundant fragmentary shell debris. Massive limestone beds are not developed in this unit, which is characterized more typically by rubbly impure limestones and a number of thin bentonites. A few large (2 cm) rounded pebbles occur sporadically amongst the more finely textured shell debris. These calcareous siltstones are closely comparable with those encountered lower in the Formation.

The Ashes and Lavas Formation attains a thickness of 15 m in the type section but is poorly exposed (Fig. 2). However, where seen, it mainly consists of finely banded, silty, creamy-coloured, crystal ashes which apparently succeed the underlying calcareous shales quite abruptly. The ashes can vary locally from dark grey argillaceous beds to coarser, buff-coloured arenaceous horizons with lithic components (1–2 cm) and pyroclastic ejectamenta. The ashy facies is abruptly succeeded by variable conglomeratic sandstones (the Rhyolitic Conglomerates). The Formation is about 8 m thick and passes up into the Basal Sands of the Llandeilo Series (Williams 1953a, p. 191) although the junction is not exposed in the type section. The conglomerates consist mainly of coarse (0.5–2.0 mm) gritty, locally bioturbated sandstones with bands of sub- to well-rounded rhyolite and quartz pebbles (0.2–2.0 cm). Fine argillaceous partings, up to 1.0 cm thick, and shelly calcareous horizons also occur and the bedded units are quite massive, ranging from 10 to 30 cms in thickness.

*Inferred Palaeoenvironment.* The lithological variation characterizing the Ffairfach Group at the type section reflects significant changes in the local palaeoenvironment during Upper Llanvirn times. The changes were evidently related to repeated influxes of sediment into this part of the Welsh Basin and may be identified as follows.

During late Lower Llanvirn times, the deposition of the Ffairfach Grit in the type area and its vicinity was preceded by a rapid change from blue-black graptolitic shales to arenaceous ashy shales containing a shelly fauna. The Grit thickens towards the north-east whence came the coarser clastic constituents presumably derived by erosion of an emergent volcanic island complex, part of which is exposed today in the Builth area (Williams 1969, p. 121). Goldring (1966, p. 1248) has referred to the Ffairfach Grit as marine 'sandstones of the sublittoral (neritic) facies'. It is reasonable to infer that the transition from the graptolitic shales into the Grit reflects an encroachment of coarser detritus into an anoxic shelf area with restricted circulation initially free of all but the finest clastic sediment. This influx of clean-washed sands was probably accompanied by a regressive shallowing since the depositional characteristics of the Grit suggest strong current action probably associated with longshore drift and wave action (Goldring 1966), producing rapid deposition and sufficient scouring to prevent the accumulation of clay material.

The occurrence of thin beds of shale towards the top of the Ffairfach Grit and of finer-grained, bioturbated sandstones, frequently with wisps and clasts of siltstone and shale, in the succeeding Pebbly Sands Formation indicates a significant change in the palaeoenvironment. The finer texture of sediment could represent a deepening of the basin but the Pebbly Sands accumulated as irregular lenticular beds which are a common feature of subtidal or intertidal sediments (Reineck and Singh 1975, p. 100). The increase in grain size in the upper part of the Formation probably reflects higher current velocities causing transportation of coarse material to predominate over slack-water silt and clay deposition. Both physical and biological reworking were important during deposition of the Pebbly Sands.

A reduced current activity must have brought about the deposition of the basal fine silty and shaly members of the succeeding Flags and Grits. The general lack of sedimentary structures other than parallel-bedding in the lower part of this Formation suggests that deposition took place either in deeper water below wave-base or in a local relatively sediment-starved haven. The occurrence of bentonites in the upper Pebbly Sands and the lower Flags and Grits points to nearby volcanic activity. The sparsely fossiliferous shales of the lower part of the Flags and Grits may have

accumulated under deoxygenated conditions probably during periods of reduced sediment supply and restricted circulation.

The occurrence of lenticular, cross-stratified, calcareous coarse siltstones which are rich in shell debris and succeed the basal argillaceous members of the Flags and Grits, suggests the onset of a second regressive phase. This pause culminated in the deposition of sandstones with conglomeratic intercalations. The progressive increase in grain size represented by an upward passage from shales through siltstones to pebbly sandstones probably reflects a return to the conditions governing the deposition of the Pebbly Sands. The composition of the coarser constituents in this part of the Formation is consistent with their derivation by the reworking of various lavas, pyroclastics and banks and bars of rhyolitic ash. The terminal calcareous siltstones and limestones of the Flags and Grits Formation indicate a sudden reduction in the supply of coarser clastic sediment. Irregular bedding and shell accumulation prevail and there are signs of reworking. However, since the siltstones and limestones are interleaved with bentonite bands which must have accumulated in calm waters, the reworking of the associated sediment was probably biological.

The succeeding Ashes are sporadically banded and contain argillaceous horizons and some volcanic ejectamenta. There are few signs of sedimentary reworking and the accumulation of the Ashes must have been rapid.

The youngest Formation within the Ffairfach group at the type section, the Rhyolitic Conglomerates, contain argillaceous laminae which must have accumulated during periods of slack water between the more turbulent phases responsible for the deposition of the sands and pebbles. The Formation passes up into finer sandstones which constitute the basal member of the overlying Llandeilo Series and is a transgressive sequence initiating a major cycle of submergence represented by the Series (Williams 1953a, p. 188).

This assessment of the sedimentary variation within the Ffairfach Group at the type section, suggests that the entire sequence accumulated in a sub-littoral to intertidal environment in three regressive cycles. The first cycle is represented by the succession from the Lower Llanvirn ashy shales to the upper Pebbly Sands; the second by the lower and middle Flags and Grits up to the top of the pebbly sandstones member; and the third by the remainder of the Group. Apart from being affected by the general subsidence which accommodated the entire sedimentary succession, the basin need not have been subject to the rapid changes in depth usually invoked to account for this kind of cyclic deposition. The occurrence of coarse pebbly sandstones at three horizons within the Group suggests deposition in a high-energy environment within wave-base. Observations by Wilcox (1979) on Lower Llandeilo sandstone and siltstone successions, similar to those of the Ffairfach Group, indicate accumulation in shallow water environments affected by tides. The bentonites which occur at fairly close intervals throughout the succession and the recurring shales and silts did not necessarily accumulate in deep water. These finer sediments could have been deposited in low-energy environments protected from tidal and wave scour by periodically erected ash banks and bars.

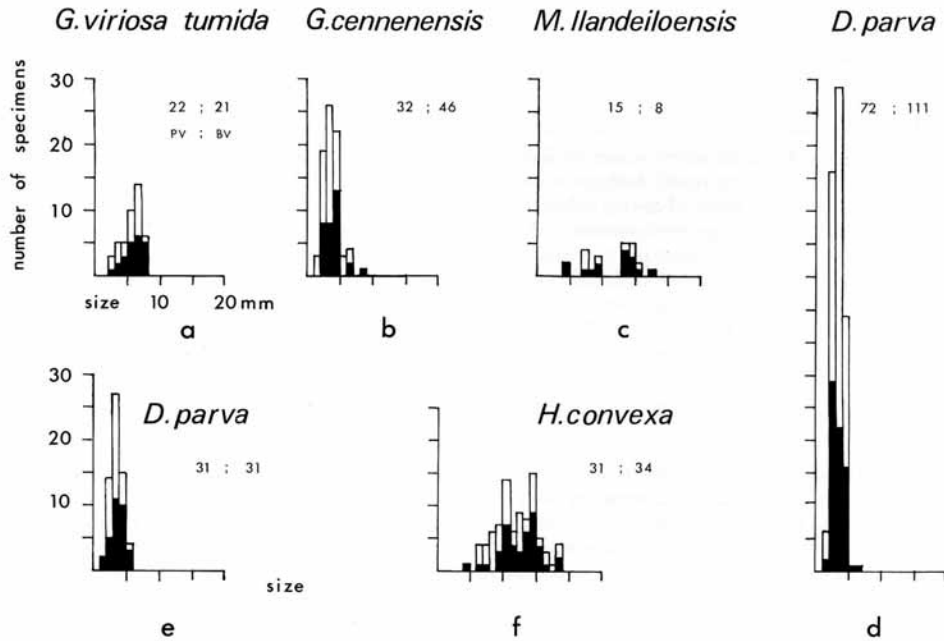
#### FFAIRFACH FOSSIL ASSEMBLAGES, ASSOCIATIONS AND PALAEOCOMMUNITIES

The fossil assemblages recovered from the Ffairfach type section were subjected to the quantitative analyses already outlined to establish the range of those characterized by distinctive suites of species. Fifteen assemblages have been recognized and named after the most commonly occurring taxa (Table 1). They belong to ten associations, one of which recurs four times within the Succession.

The two oldest faunal assemblages were recovered from the upper part of the Ffairfach Grit and are the only ones known from the Formation at the type locality. One was taken from a horizon within the grit, the other from a shaly intercalation. The *Tissintia* assemblage ( $C = 1$ ; Fig. 3a) is represented by a monospecific sample (Fig. 2) of moulds of poorly-sorted disarticulated valves (i.e. with the proportion of articulated valves ( $A$ ) within the sample = 0%). The assemblage is a remnant of an association known from just below the base of the Ffairfach Grit at the type section and from other Lower Llanvirn Successions exposed elsewhere in Wales and Shropshire. The other

penecontemporaneous assemblage from the shale band has yielded small *Glyptorthis*, a small *Dalmanella*, and some Inarticulata, Trilobita, and Bryozoa remains. It is reminiscent of the faunal assemblage known from the younger Flags and Grits of the section (see below) and may be regarded as a precursor of the *Dalmanella-Gelidorthis* association.

Three different assemblages have been recovered from five samples in the intervening Pebbly Sands Formation. These assemblages, dominated, in ascending order, by *Flexicalymene*, *Hesperorthis*, and *Salopia*, are of low to moderate density and diversity (Table 1) and contain numerous, well-preserved bryozoan colonies and disarticulated brachiopod and trilobite remains. The proportion of Bryozoa in all three assemblages (average 49.2% in five samples: range 38.9 to 63.3%) and of *Flexicalymene* (30%), *Hesperorthis* (44.8% and 47.5% in two samples) and *Salopia* (28.1% and 32.4% in two samples) gives dominance values of 0.339, 0.379 to 0.385 and 0.232 to 0.332 respectively. The *Flexicalymene*-dominated assemblage consists of apparently well-sorted remains (e.g. five of six glabellae range from 10.0 to 11.4 mm in length) and contains a few *Tissintia* and *Dalmanella* valves. These are absent from the succeeding *Hesperorthis* assemblages of large, poorly sorted, entirely disarticulated *Hesperorthis* and rarer *Macrocoelia* valves. The *Salopia* assemblages consist of large better-sorted mainly disarticulated valves ( $A = 1.45\%$ ) and contain a more diverse fauna with small rarer *Glyptorthis*, *Gelidorthis*, *Dalmanella*, *Horderleyella*, *Macrocoelia* and *Kullervo* remains. Compositional similarities between the *Hesperorthis* and *Salopia* assemblages are shown by their dominance (C) values and total % Bryozoa. However, the associations differ in the size ranges of *Hesperorthis* and *Salopia* (Figs. 3b and 3c) and in the diversity and taxonomic composition of the Bryozoa (Table 2).



TEXT-FIG. 4. Size frequency histograms for (a) *G. viriosa tumida* from Flags and Grits samples F9 and F10; (b) *G. cennensis* from sample F10; (c) for *M. llanedeiloensis* from sample F10; (d) *D. parva* from sample F10; (e) *D. parva* from Flags and Grits sample F29; (f) *H. convexa* from Flags and Grits samples F38 and F39.

Despite the common occurrence of ramose Bryozoa throughout the Pebbly Sands and the further influx of prasoporiid Bryozoa in the upper part of the Formation, three associations have been recognized. These have been distinguished, like the assemblages, by the sudden appearance of *Flexicalymene*, *Hesperorthis*, and *Salopia* and by their equally abrupt disappearance except for *Hesperorthis* which is represented by a few impressions in the *Salopia* association. Six of the fifteen brachiopod species characteristic of the succeeding *Dalmanella*-*Gelidorthis* association also occur rarely in the *Salopia* association, so that the palaeontological change from the Pebbly Sands to the Flags and Grits is less abrupt than the lithological transition.

The succession of faunal assemblages in the Flags and Grits (Table 1) begins with a diverse, high density series of samples dominated by the small, generally well-sorted and partially-articulated shells of *Glyptorthis*, *Gelidorthis*, and *Dalmanella* with less well-sorted *Macrocoelia* (Fig. 4). The mean proportion of articulated shells ( $\bar{A}$ ) among brachiopods from the eight larger consecutive samples (F4-F11, see Table 2), is 13.9% (range 9.4 to 18.7). The faunal assemblages at those horizons are further characterized by the sporadic occurrence of representatives of the brachiopods *Schizotreta*, *Corineorthis*, *Tissintia immatura*, *Triplesia*, *Sowerbyella*, and *Murinella*, and molluscs tentatively identified as *Modiolopsis* Hall (GSM 22060-61) and *Ophileta* Vanuxem (GSM 30165). These, together with abundant *Hyalostelia*, trilobites like *Metopolichas*, *Atractopyge*, and *Marrolithus*, Conularida, Machaeridia, and Ostracoda, make their first appearance in the section at this level and in many cases represent the earliest known stratigraphical occurrences anywhere (Lockley & Williams 1981). The associated group of fifteen faunal assemblages (samples) and museum specimens known from this horizon (Table 2) embrace at least thirty taxa. The average dominance value ( $\bar{C}$ ) for the eleven consecutive samples F1-F11 (Table 2) is 0.320 (range 0.207 for sample F7 to 0.485 for F3).

Those fifteen assemblages collected from 4.5 m of Flags and Grits constitute a well-knit association dominated by *Dalmanella* and *Gelidorthis* which is almost entirely restricted to this group. Two other stocks, *Glyptorthis* and *Macrocoelia*, are equally persistent but less common. *Orderleyella* survived briefly from the older *Salopia* association but reappears later in contrast to *Kullervo* which is unknown in younger assemblages. In the youngest assemblages from this association the fauna becomes sparser and less diverse. The more fossiliferous samples like F13-F15 exhibit slightly higher  $C$  values (0.389-0.454) than those below and show compositional resemblances to succeeding assemblages.

The shales which succeed the basal calcareous siltstones of the Flags and Grits are poorly fossiliferous with a low density, low diversity fauna (Table 1) in which *Dalmanella* is the only persistent element. *Schizotreta*, *Schizocrania*, *Glyptorthis*, *Triplesia*, *Macrocoelia*, and various trilobite and bryozoan remains occur sporadically in those shales but, in most samples, are insufficiently represented to derive worthwhile estimates of relative abundance, shell articulation ratios and size frequency. Only two samples (F17 and F19 Table 2) which contain more than ten specimens can be effectively compared with samples from other parts of the succession. Their respective  $C$  values of 0.546 and 0.529 are comparable with those noted for succeeding assemblages F25-F32. The relative importance of inarticulate brachiopods, which together are as common as the ubiquitous *Dalmanella*, has prompted us to recognize a *Schizocrania* association extending through 4 m of Flags and Grits.

The calcareous shelly siltstones, from which samples F25-F32 were derived, are dominated by *Dalmanella* ( $\bar{C} = 0.532$ , range 0.410 to 0.648; Fig. 2). *Glyptorthis*, *Triplesia*, *Macrocoelia*, *Basilicus*, and Bryozoa are among the more persistent but poorly represented elements in these high density, moderately diverse assemblages. Brachiopod remains show a normal, well-sorted distribution (Fig. 4e) but consist mainly of disarticulated shells ( $\bar{A} = 4.0\%$ ; range 1.0 to 10.3%). The assemblages from this member resemble those from the older finer calcareous siltstones member in exhibiting high density and diversity values (Table 1) and well-sorted valve assemblages (Figs. 4d and 4e) but differ in their lower articulation ratios and their higher  $C$  values which reflect the greater dominance of *Dalmanella*. The youngest assemblages, F30-F32, from this siltstone member contain the oldest *Rostricellula* recorded from the type section and are further distinguished by a marked increase in the proportion of *in situ*, as distinct from broken and dislodged, bryozoan colonies. These eight assemblages, collected from less than 4 m of Flags and Grits, clearly belong to a recurrent *Dalmanella*



association which mainly differs from its earlier representation in the almost total exclusion of *Gelidorthis*.

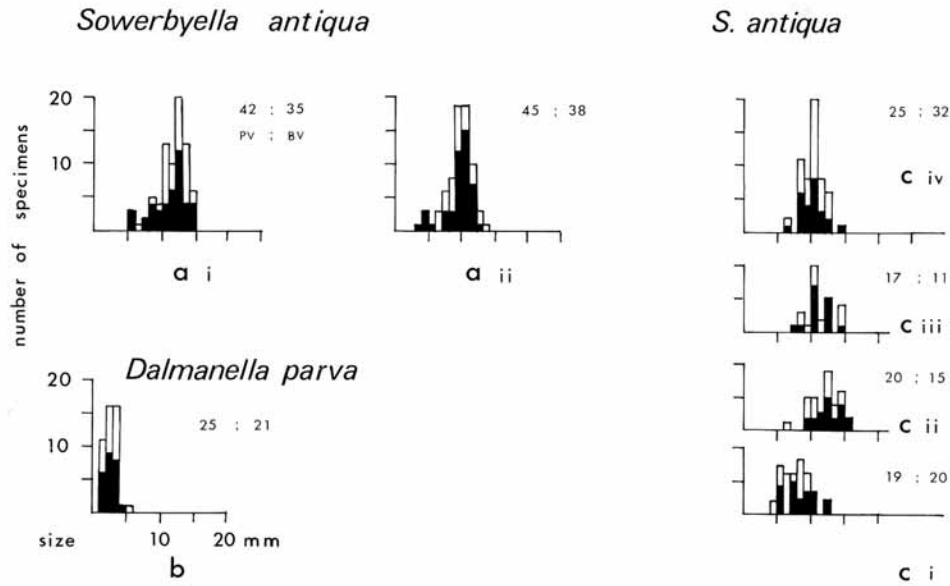
The succeeding sandstones from which samples F33–F39 were derived contain moderately dense and diverse assemblages (Table 1) dominated by *Orderleyella convexa* and Bryozoa in more or less equal proportions ( $\bar{C} = 0.341$ ; range 0.254 to 0.382). *Orderleyella* articulation ratios are low ( $\bar{A} = 0.54\%$ , range 0 to 3.3%) and sorting poor to give a bimodal frequency distribution (Fig. 4f). All other elements of the fauna are poorly represented at these horizons although *Dalmanella* persists and represents an average of 27.7% of the total Brachiopoda compared with as much as 67.8% for *Orderleyella*. The Trilobita are represented only by *Basilicus*. The assemblages found in the sandier member of the Flags and Grits merit recognition as a separate association to emphasise the dominance of *Orderleyella* although the genus occurs sporadically in all but four associations. Yet apart from the sudden profusion of *Orderleyella* and ramose Bryozoa, the association is evidently a variant of that which is normally dominated by *Dalmanella*.

Succeeding samples F40–F42 and F43–F45 from the pebbly sandstones and overlying limestones respectively, contain assemblages which are virtually identical despite the differences in lithology. The samples are dominated primarily by disarticulated valves of *Dalmanella* ( $\bar{A} = 1.56\%$ ; range 0 to 3.13%) which comprise an average of 59.1% of all Brachiopoda; Bryozoa persists as an important element and together with significant occurrences of *Orderleyella*, *Triplesia*, *Macrocoelia*, *Salopia*, *Sowerbyella*, *Flexicalymene*, and *Marrolithus* account for relatively high density and diversity values (Table 1) and correspondingly low dominance values ( $\bar{C} = 0.265$ ; range 0.185 to 0.360). The incoming of the last three forms is noteworthy since they occur only sporadically and rarely in older assemblages. *Paterula* is the only form which is apparently restricted to the limestones (Table 2).

The sudden relegation of *Orderleyella* to less than 5% of the total number of brachiopods identified in the six assemblages just described, marks the re-establishment of the *Dalmanella* association. The most significant change in the association compared with its earlier occurrences is not the absence of *Glyptorthis* but the presence of *Sowerbyella* for the first time within the type section of the Ffairfach Group.

The greater part of the limestones, from which samples F46–F53 were derived (Tables 1 and 2), is dominated almost exclusively by assemblages of moderately well-sorted *Sowerbyella* valves (Fig. 5a;  $\bar{C} = 0.606$  range 0.388 to 0.853) which are mainly disarticulated ( $\bar{A} = 2.61\%$  range 0 to 7.27%) and represent an average of 76.2% of the total Brachiopoda as compared with 15.1% for *Dalmanella* the only other persistent taxon. This low diversity contrasts with the moderately high density values (Table 1). The eight assemblages described above constitute a typical fully developed *Sowerbyella* association which recurs towards the top of the Ffairfach Group and also prevails at certain horizons within the Lower Llandeilo successions.

The calcareous shelly siltstones, which succeed the *Sowerbyella*-dominated limestones at the top of the Flags and Grits, and the tuffaceous siltstones and shales of the overlying Formation contain faunal assemblages dominated by *Dalmanella* showing variable articulation ratios ( $\bar{A} = 5.14$ ; range 0 to 21.62). The highest articulation ratios values are characteristic of well-sorted assemblages (Fig. 5b) occurring at the more argillaceous horizons. *Dalmanella* averages 85% of the total Brachiopoda in samples F54–C1 ( $\bar{C} = 0.437$  for eight larger samples) and *Macrocoelia*, *Basilicus* and *Flexicalymene* persist at most horizons; but the fauna is too sparse at certain horizons to permit more than a generalized estimate of relative abundance. Furthermore, sporadic but noteworthy variation in the composition of some assemblages (Table 2) warrants comment. Sample F56, for example, contains a relatively diverse assemblage dominated by disarticulated *Basilicus* remains and small *Dalmanella* valves together with rarer *Tissintia plana*, *Pseudolingula*, *Skenidioides*, *Salopia*, and *Murinella*. Similarly, sample A2 contains an exceptionally high proportion of *Triplesia* (20.3% of Brachiopoda) and sample A4 yields a single specimen of the oldest known *Mesotephraspis* from the Ordovician of the Anglo-Welsh and Baltic provinces. Despite the wide proportional variation in the eleven assemblages collected from the Ashes and Lavas and the bounding sandstones and siltstones, they can all be assigned to a recurring *Dalmanella* association which, in the absence of *Sowerbyella*, is more like the occurrence in the lower than the upper part of the Flags and Grits.



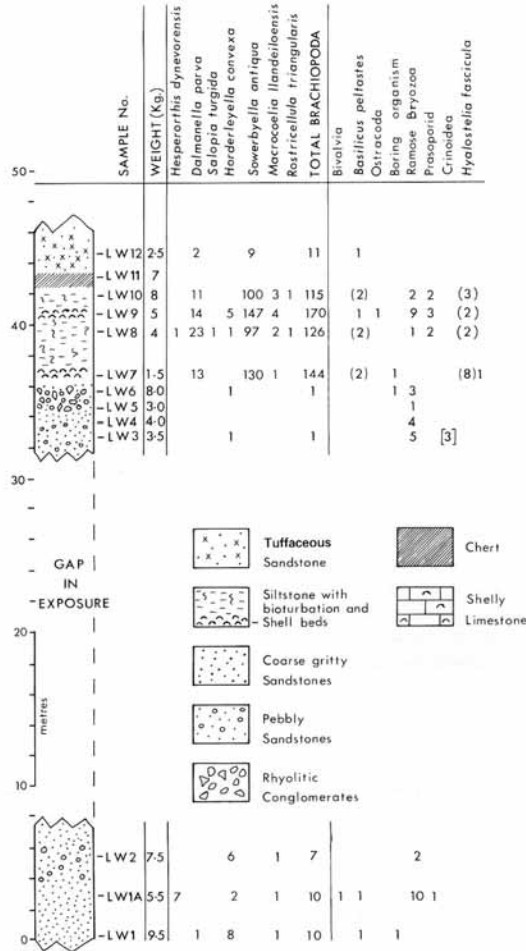
TEXT-FIG. 5. Size frequency histograms for (a) i and ii, *S. antiqua* from Flags and Grits samples F46 and F47; (b) *D. parva* from Ashes and Lavas samples A1; (c) i-iv, *S. antiqua* from samples C2-C5.

The Rhyolitic Conglomerates Formation is characterized by variably sorted *Sowerbyella*-dominated assemblages consisting mainly of disarticulated valves ( $\bar{C} = 0.603$ ;  $\bar{A} = 4.66$ , range 0.77 to 14.58 for samples C2-C5 Fig. 5c). *Sowerbyella* make up an average 81.2% of the brachiopods in these four samples, with *Dalmanella* (10.0%), *Horderleyella*, *T. plana*, *Salopia*, *Rostricellula* and *Oxoplecia* also occurring. *Oxoplecia* is unknown in underlying formations at the type section but has been collected from the Flags and Grits at Coed Duon (Fig. 7). These assemblages represent the re-establishment of the *Sowerbyella* association chiefly through the return of *S. antiqua*, which is even more abundant than *Dalmanella parva*.

#### FOSSIL ASSOCIATIONS AND INFERRED PALAEOCOMMUNITIES

A comparative study of the fossil assemblages outlined above (Table 1) permits various associations to be defined. Some, like those which are virtually monospecific, are readily identifiable on taxonomic consideration alone, but other criteria include: size-frequency distribution as an index of age; the ratios of conjoined valves (*A*); and estimates of density of occurrence, dominance (*C*), and diversity (*D*) and affinities (I.A.) of the various taxa composing the associations. As can be seen in Figs. 2 to 5, these parameters were subject to great fluctuations, which may have been coincident not only with one another but with changes in the composition of assemblages and in the entombing sediments. These fluctuations have an important bearing on the extent to which an association may reflect a palaeocommunity. What is left to speculation is whether an association represents the skeletal residues of a community which accumulated *in situ* or the transported remains of one or more communities unconnected in life with the sediments in which they are now found.

Conflicting views have been expressed on how best to interpret size-frequency data of the skeletons of fossil marine benthos which grew indefinitely and are therefore a measure of age. Boucot (1953) considered that the skeleton remains of life assemblages accumulating *in situ* conform to a positively skewed size-frequency distribution and that normally distributed data reflect post-mortem winnowing of shells by sea currents. Many investigators, on the other hand, agree with Craig and Hallam (1963) that normally distributed size-frequency samples of shells need not indicate transported assemblages of skeletal remains, only the absence of juvenile forms, which may be seasonally controlled. The problem has been exhaustively explored by Craig and Oertel (1966) in their computer



TEXT-FIG. 6. The lithological and faunal succession in exposures south of the Longwood road (LW1-2 from SN 69252570 and LW3-12 from 69352580).

simulation of variation in recruitment after breeding and in the growth of the skeleton. They demonstrated that size-frequency distribution of dead shells accumulating *in situ* can, in fact, vary from being positively to negatively skewed dependent on the interplay between the growth and mortality rates of individuals making up a population. More recently, Curry has shown (1979, Text figs. 6–8) that size-frequency counts of large life assemblages of living brachiopods tend to be positively skewed because of the preponderance of juvenile shells. The common occurrence of normally distributed shell sizes of fossil brachiopod assemblages even in sediment which accumulated in current velocities that must have been too low for the transport of any skeletal remains, accords with Curry's observations when the limited fossilization potential of very small shells is considered. We have, therefore, viewed our size-frequency distributions with less regard for the absence of young shells than for the absolute size of shells in relation to the texture of the entombing sediment and the range of size of skeletal remains within a sample.

The extent to which skeletal remains of organisms occur in their entirety in the rock is normally taken as an indication of the dynamics of the environment in which they lived. The strength of articulation of the valves or pieces making up a complete skeleton does, however, vary greatly even within phyla. Among brachiopods, for example, the post-mortem articulation of shells depends not only on the nature of the teeth and accommodating sockets but also on the rate of autolysis of soft tissues.

As was first shown by Jaanusson (1971, p. 34), articulate brachiopods are basically equipped with two kinds of teeth, prismatic structures described as deltidodont and knoblike undercut processes (cyrtomatodont). The latter grow by resorption as well as secretion and interlock laterally with the walls of their sockets so that the valves tend to remain together after autolysis even in moderately turbulent environments. In contrast, the more primitive deltidodont teeth which are characteristic of nearly all the brachiopods identified in this paper did not undergo differential resorption during growth and were not an impediment to a drifting apart of valves once the binding tissue had disappeared. Moreover, muscle systems and other tissues connecting both valves, are very quickly removed by reaction with sea-water and by saprophages. Indeed the only organic material which is likely to persist for any length of time is the periostracal band secreted by the fused mantle lobes across the cardinal areas of both valves (Williams and Hewitt 1977, p. 107). But even this seemingly solid cover actually consists of two pieces bonded by a metastable mucopolysaccharide film coincident with the hinge-line and is, therefore, likely to become separated into its ventral and dorsal parts within a short period of death. In general, we have interpreted high proportions of conjoined brachiopod shells in any given samples as indicating relatively rapid burial. The proportion of brachial to pedicle valves, dependent on their relative thicknesses and shapes and the degree of completeness of the more fragile parts of the shells seem to us to be more reliable guides to the amount of winnowing and transport assemblages have undergone.

The functional interpretation of the morphology of extinct species also imposes some constraints on our views on the structure of palaeocommunities. Only a small number of morphological features of the brachiopod shell can assist in speculation on those habits of a fossil species which ensured it a niche in the palaeocommunity to which it belonged. Shell shape can throw some 'light on the way individuals were packed in relation to their preferred substrate and on the disposition of the feeding current systems created by the lophophore (Rudwick 1970). Ornamentation can reflect the arrangement of setae (Williams in Williams *et al.* 1965, p. H80); while the clarity of the pedicle callist and the spread of the muscle scars may respectively reflect the strength of the pedicle and the mobility of species lacking a pedicle.

The Trilobita constitute the other important group of fossils calling for comment. The proportion of various skeletal pieces of the trilobites can indicate the extent of post-mortem and post-ecdysis sorting, and the morphology of complete individuals permits life habits to be inferred (cf. Clarkson 1966). Clarkson's comments on the life habits of trilobites (1979, p. 283) confirm the general opinion that many trilobites, particularly flat forms like *Basilicus* and *Flexicalymene*, and those with well-developed genal spines (cf. *Marrolithus*), were adapted for resting on soft substrates whilst deposit-feeding. Indeed Bergström (1972, p. 89) refers to trinucleids which 'ploughed the superficial mud' and discusses the resultant cruzianiform traces produced by these and other species.

### 1. The *Tissintia prototypa* palaeocommunity.

The widespread and abundant distribution of *Tissintia prototypa*, in both the Llandeilo (at Llwyn Bedw SN 653211) and Built Wells (SO 088576) districts, in assemblages of late Lower Llanvirn age (Williams 1953a, p. 180; 1969, p. 121), has a bearing on the sporadic occurrence of the species in the basal part of the Ffairfach Group. Its appearance in large, often monospecific assemblages ( $C \leq 1.0$ ) in Lower Llanvirn silty mudstones indicates its opportunistic character and its importance as a recurrently successful colonist of newly deposited, silty, oxygenated substrates derived from volcanic piles erected within the Welsh Basin (Williams 1969, p. 121). In these exposures *Pseudolingula granulata* (Phillips) is the only other brachiopod found with *T. prototypa*, although trilobites, graptolites and bivalves may also occur. Both species again appear together in the penecontemporaneous Weston Beds of Salop (Williams 1974, Table 4) where *P. granulata* gives its name to a characteristic association (the 'set' of Williams 1976, p. 39).

The profusion of large specimens of *Tissintia* in fine-grained clastic successions and their occurrence in more or less equal numbers of pedicle and brachial valves, suggest that such fossil bands are *in situ* remains of a wide-ranging pioneer palaeocommunity. It is noteworthy that the posterolateral costellae ornamenting the shell of *Tissintia* are retroflexed so that the setae, which they accommodated in life, projected backwards around the cardinal angles (Williams 1974, p. 108). Such splayed fringes of setae are also characteristic of inarticulates and assist living lingulids in burrowing and maintaining individuals at the interface between seawater and substrate during periods of heavy sedimentation. Moreover, since *Tissintia* probably possessed a strong pedicle ventrally attached by cuticle to a well-defined callist, both *T. prototypa* and *P. granulata* could have burrowed quickly into silty substrates and subsisted as low-level suspension feeders.

The *Tissintia* palaeocommunity is represented in the silty mudstones immediately underlying the Ffairfach Grit at the type section but not within that Formation, despite the presence there of a horizon containing moulds of the dominant species. The sample collected by us consists exclusively of the moulds of disarticulated shells with considerably more brachial than pedicle valves despite their subequal convexity (Fig. 3a). The moulds occur at the base of a sandstone bed immediately succeeding a shale horizon (Fig. 2) and are associated with irregular black phosphatic clasts, up to 2 cm long and containing 23.08%  $P_2O_5$ . The fossils are evidently the transported remnants of a *Tissintia* palaeocommunity which had become established elsewhere in finer sediment presumably to the west of the type section.

The only other fossil remains found in the type section of the Ffairfach Grit consist of *Skolithus*-like burrows and some impressions of a sparse fauna of four species of Brachiopoda together with some trilobite and bryozoan moulds (the mixed brachiopod assemblage) in siltstones within a shaly intercalation towards the top of the Formation (Table 1). Rare transported assemblages as well as trace fossils are found in the Ffairfach Grit exposed elsewhere in the district. The mixed brachiopod assemblage, however, is a precursor of the *Dalmanella*-*Gelidorthis* association and will be reviewed in that context.

### 2. *Hesperorthis*/*Salopia*-Bryozoa palaeocommunity

Three associations are found in the Pebbly Sands and robust ramose trepostomate Bryozoa are common in all three and have been found in positions of growth. There would have been sufficiently coarse clastic material available throughout the succession to support the first-formed zooids before the massive spread of mature colonies provided their own substrates for further growth. In contrast the discoidal prasoporidae, which first appeared towards the top of the Formation, could have existed as free-living benthos like Recent lunulitiform Bryozoa (Ryland 1970, p. 68). Both types of Bryozoa are, therefore, regarded as relicts of the community which inhabited the Pebbly sands.

The bioturbated nature of the sediments also indicates that burrowing organisms were an important constituent of the community. Most of the cylindroid tunnels have well-defined boundaries suggesting that the walls were coated with mucus and therefore probably formed by polychaetes (Schäfer 1972, p. 271). These detritus feeders may have derived their food from the same

source as trilobites when the lithofacies was first established. *Flexicalymene cambrensis* commonly occurred and probably accounted for the cruzianiform markings which can be found in the lower part of the succession. This species and the rarer *Basilicus tyrannus* probably worked the substrate for its organic content by ploughing the superficial layers. Traces of trilobite exoskeletons, however, virtually disappear from the upper part of the Pebbly Sands and we have assumed that their occurrence in the basal succession of the Formation represents a transient phase in the development of a wider-ranging community. The two succeeding associations within the Pebbly Sands are characterized by a number of distinctive brachiopod species in addition to ramose and lunulitiform Bryozoa.

*Hesperorthis dynevorensis* is overwhelmingly dominant in the older association but also occurs rarely in the younger. The species had a robust costate shell with elevated follicular embayments acting as particle sieves when the valves gaped (see Fig. 83 in Williams *et al.* 1965, p. H82), and a powerful pedicle and diductor muscles as adducted from the well-developed pedicle callist and notothyrial platform respectively. With these aids for suspension feeding in turbulent water, and for attachment and keeping the mantle cavity free of sediments, individuals could have lived in a pebbly sand environment either attached to bryozoan colonies or cobbles or with their long apsacline ventral interareas and pedicles buried in a soft substrate. The species is admittedly represented by the moulds of disarticulated shells; but these accumulated in a very wide range of size and include a significant proportion of brachial as well as pedicle valves despite their strikingly different shapes (Fig. 3b). On such evidence it seems safe to conclude that *Hesperorthis* was an important epifaunal constituent of a palaeocommunity which lived *in situ*.

In the top 2 m or so of the Pebbly Sands, *Salopia turgida* displaces *H. dynevorensis* as the key epifaunal member of the palaeocommunity. The morphology of the species suggests that it had similar habits to *H. dynevorensis*. *Salopia* also had a powerful muscle system and pedicle and a long apsacline ventral interarea. The shell differs in being strongly biconvex and in possessing weak follicular embayments; but it is multicostellate and, in life, was almost certainly equipped with a denser fringe of setae which could have acted as an efficient particle sieve. Moreover, although the species is represented in the collections almost exclusively by impressions of disarticulated valves, their frequencies are not significantly different from equal representation (Fig. 3c); while both the considerable size range and the invariably good preservation of impressions of such internal features as the long delicate brachiophores confirm that *Salopia* had lived more or less *in situ*.

As already stated, only seven other brachiopod species occur rarely in the Pebbly Sands. Hence the three associations identified in the Formation appear to be remnants of a single restricted palaeocommunity. In view of the possibility that *Hesperorthis* and *Salopia* were mainly alternative tenants of the same microhabitat, the unit has been named the *Hesperorthis/Salopia*-Bryozoa community.

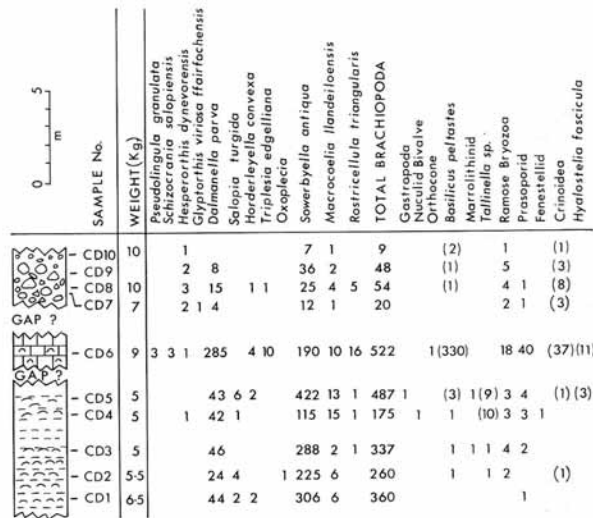
### 3. *Dalmanella-Gelidorthis* palaeocommunity

The change from the *Salopia* to the *Dalmanella-Gelidorthis* associations may not be taxonomically profound but is heralded by the sudden profusion of *Dalmanella parva*, *Gelidorthis cennenensis*, and *Glyptorthis viriosa tumida* following an equally abrupt disappearance of *Salopia*. The change is closely enough phased with a rapid passage from sandstones to calcareous siltstones to be ascribed to an incursion of finer sediment brought about by a significant drop in current flow. Why this should have favoured certain species already represented within the benthos inhabiting the changing substrate has now to be considered.

The three dominant species of the *Dalmanella-Gelidorthis* association are alike in many respects and, indeed, conform closely to the modal morphology of strophic articulate brachiopods. Thus all are subquadrate in outline and biconvex in profile and essentially small even as adults with mean dorsal lengths varying from 2.24 mm to 3.75 mm in three large samples (Lockley and Williams 1981). The finely costellate ornamentation of their shells suggests that individuals were equipped with dense fringes of setae, and the sulcate or uniplicate folding of the anterior commissures would have given rise to differentially wider gapes in the median section of shells and, therefore, a more efficient



exhalant and inhalant current system for filter feeding. The relative delicacy of such small shells (*Glyptorthis*, for example, is ornamented by concentric lamellae scarcely more than 100 μm thick distally) and the presence of mucus-coated setae in a sufficiently close mesh to have filtered fine sediment out of the inhalant feeding current suggests that the three species were better adapted to a silty substrate than, say, *Salopia* or *Hesperorthis*. In all three stocks, pedicle callists were well developed and delthyria large so that individuals were probably anchored to the substrate by strong pedicles throughout their lives. There was no lack of solid substrate for attachment by these small benthos, especially with crinoids and *Hyalostelia* becoming plentiful in this part of the succession in addition to stony Bryozoa and large Brachiopoda like *Macrocoelia*. However, the striking reduction in the frequency of occurrence of the widespread *D. parva* in the *Sowerbyella antiqua* palaeocommunities (Fig. 2) suggest that the former species could have been a low-level suspension feeder like the latter; and individuals may well have been capable of living attached to one another in free-lying clusters like those of Recent *Terebratulina septentrionalis* (Couthouy), see Curry (1979, p. 246).



TEXT-FIG. 7. The lithological and faunal succession in exposures on the northern side of Coed Duon (SN 709256).

Despite the common occurrence of *Gelidorthis* and *Glyptorthis* in the lower part of the Flags and Grits Formation, where they constitute 24% and 10% respectively of the brachiopod fauna, the dominance of *Dalmanella* cannot be masked. This species accounts for 55% of all brachiopods assigned to the *Dalmanella-Gelidorthis* association. It is, moreover, remarkably euryoecious for it has been found in all but seven of the seventy-eight fossil assemblages recovered from the type section of the Ffairfach Group and is present in every Member irrespective of lithology. There were possibly a number of features of living *Dalmanella* which rendered the stock more adaptable to such a comprehensive palaeoecosystem than seemingly unspecialized stocks like *Gelidorthis*. The most obvious difference, however, is that the dalmanellid shell is densely punctate; and, since the punctae accommodated mantle papillae (caeca) almost certainly filled with nutrients as in living brachiopods (Owen and Williams 1969), the species would have been less affected by fluctuations in external food supply than those which were impunctate.

The only other brachiopods to occur as widely as *Dalmanella* are certain lingulids, *Macrocoelia* and *Tissintia* which are also found in the association under discussion. The lingulids are comparatively rare constituents of any assemblage although fragments are fairly common at some horizons within the succession. This suggests that lingulids were not members of the *Dalmanella-Gelidorthis* palaeocommunity, or at best constituted a thinly distributed infauna vulnerable to continual changes in substrate composition.



*Tissintia* has already been identified as an opportunistic genus. Its presence in the *Dalmanella-Gelidorthis* association, as a widely dispersed sedentary benthos, is consistent with the minor role that such forms play in diverse communities. *Macrocoelia*, on the other hand, which is equally euryoecious, is a plano-convex, slightly geniculate strophomenacean. The genus lacked a pedicle in adult stages of growth but had strong widely splayed muscles which, by sudden contraction or relaxation, could almost certainly have caused the shell to jerk around on the sea-bed (Williams 1953b, p. 34). Without this snapping movement of the shell and in the absence of a pedicle on which to rotate, *Macrocoelia* could not have survived any appreciable sedimentation. But such mobility, no matter how cumbersome, does imply that adult *Macrocoelia*, which may have been 20 mm or more in length, would have filter-fed over relatively large areas and would have been widely scattered in life. Indeed, if it is assumed that a *Macrocoelia* 20 mm long could have done no more than jerk its shell through 180° about its hinge axis, it would have occupied about the same area of substrate as six adult *Dalmanella*. In the light of this comparison, the fact that *M. llandeiloensis* represents only 5% of the brachiopods composing the *Dalmanella-Gelidorthis* association understates its importance within the palaeocommunity.

Four other species are mainly restricted to this association. All are rare stocks which were attached to the substrate by cementation (*Schizotreta*) or by a strong pedicle (*Kullervo* and *Pseudolingula*) which may have been squat enough to induce malformation in shell growth (*Murinella*). Except for *Pseudolingula*, which probably burrowed like other lingulids, the pyramidal-shelled *Kullervo* and the large suberect *Murinella* with their well-developed pedicle foramina and the cemented *Schizotreta* would have subsisted as relatively high-level suspension feeders.

Two other species are also noteworthy. *Triplesia edgelliana* first appeared in the lower Flags and Grits and, although it persisted thereafter throughout the Group, it was always a minor constituent of any association (e.g. only 1.2% of the brachiopods composing the *Dalmanella-Gelidorthis* association). *Triplesia* is strongly dorsibiconvex and, although the pedicle must have been thread-like (Wright 1963), individuals probably remained anchored throughout life, rocking on the postero-median area of the brachial valve with the ventral umbo normally pulled close to the substrate so that the uniplicate commissure and strongly trilobate mantle cavity would have been well-elevated for filter-feeding.

The fascicostellate brachiopod, *Horderleyella convexa*, probably adopted the same suberect attitude when feeding, although it differed from *Triplesia* in the style of folding of its commissure. The pedicle valve of *Horderleyella* is sharply carinate medianly and the brachial valve correspondingly sulcate. Thus, when the shell was slightly opened, a narrow aperture would have been created medianly and would have been encircled by strong setae clustered in fascicostellate patterns. Assuming that inhalant and exhalant current systems are reversible, this 'funnel' arrangement of the *Horderleyella* commissure with its capacity to eject relatively large indigestible particles is likely to have been especially effective in high energy environments where coarse sediment was in transit. *Horderleyella* appeared briefly when the *Salopia* association gave way to that dominated by *Dalmanella* and *Gelidorthis*, but it did become a dominant member of a later palaeocommunity occupying a sandy substrate.

The association is characterized by as wide a range of other phyla as are found anywhere within the Ffairfach Group. *Hyalostelia* clusters, crinoids, and ramose and fenestellid Bryozoa were common and probably provided elevated substrates for brachiopod settlement. Ostracods also occurred but the trilobite *Basilicus* and, to a lesser extent, *Flexicalymene* and *Marrolithus*, are noteworthy. All three genera would have been responsible for disturbing the superficial layers of the sea-bed because *Marrolithus* is also likely to have worked the substrate with its comb-like exites (Bergström 1972, p. 85).

The *Dalmanella-Gelidorthis* association evidently represents a mature palaeocommunity as can be seen by the size/frequency distributions of the remains of the principal brachiopod species involved and the more or less equal representation of their brachial and pedicle valves in the samples studied. Only lingulids and a few articulate like *Sowerbyella* and *Salopia* appear to have been transient colonists from contemporary palaeocommunities. The epifauna was dominated by brachiopods,

particularly *Macrocoelia* and *Triplesia*, representing the low- and high-level filter feeders respectively. The three commonest species, *Dalmanella*, *Gelidorthis* and *Glyptorthis*, probably thrived at both levels dependent upon the nature of the substrate to which they were attached in life.

#### 4. *Schizocrania* palaeocommunity

A rapid reduction in the occurrence of *Dalmanella parva* throughout about 7 m of shale until the species is no more frequently represented than rare inarticulates was probably effected by a change in substrate. It seems likely that the redox discontinuity vacillated at the interface between the mud substrate and overlying water, which would account for the sporadic, rare occurrence of infaunal lingulid and epifaunal articulate skeletal remains and the almost complete absence of traces of other phyla. The listing of a brachial valve of the cemented inarticulate *Schizocrania* in addition to similarly-attached *Schizotreta* recalls the restricted fauna of the Betton and Rorrington Beds of Shropshire (Williams 1974, p. 20). In that area, *Schizocrania* has been recorded in all major Ordovician lithofacies (Williams 1976, p. 41) but is especially noteworthy in what are inferred to have been anoxic sediments, where it may be associated solely with graptolites and trilobites. For these reasons, *Schizocrania* may have been an epiplanktonic form attached to floating organic debris (cf. Lockley and Antia 1980) as well as a sedentary benthic stock dependent on the availability of a solid substrate. The entire facies in which the genus is found certainly represents a significant palaeontological and lithological variant within the Ffairfach Group and has prompted a provisional recognition of a distinct palaeocommunity.

#### 5. *Dalmanella* palaeocommunities (phases 1 to 3)

The renewed deposition of calcareous silts, presumably in an oxygenated environment, in succession to poorly fossiliferous and normally anoxic muds, permitted the rapid re-establishment of a benthic fauna dominated by *Dalmanella*, and the remnants of three such faunas occur within the Flags and Grits and overlying Ashes and Lavas. The brachiopod species recorded in the succession were mainly disarticulated, but are usually represented by more or less equal numbers of valves (Figs. 4 and 5). It, therefore, seems reasonable to assume that the associations are residues of three *Dalmanella*-dominated palaeocommunities.

The taxonomic composition of the palaeocommunities is basically the same and very much like that of the *Dalmanella-Gelidorthis* palaeocommunity except in two respects. The first is the disappearance of *Glyptorthis* and *Gelidorthis* within the time range of the oldest palaeocommunity (phase 1) where the former genus is rarely recorded in successive samples and the latter at only one horizon. The second change in taxonomic composition is the appearance of *Rostricellula triangularis* in the first part of the palaeocommunity, and thereafter its persistence as a minor constituent throughout the succession. This species, with a plicate zig-zag gape (Rudwick 1970) and a rostrate beak which bore a functional pedicle, may well have competed with *Triplesia* for the same ecological niche among the relatively high-level suspension feeders. A few impressions of the micromorphic pyramidal *Skenidioides* were also found in phase 3 of the palaeocommunity. This stock, with what was probably a short stout pedicle supported by a spondylium, must have lived as a high-level suspension feeder attached to ramose Bryozoa or a similarly elevated substrate. Within the Ffairfach Group, however, it occurred too rarely to be considered further.

Notwithstanding the striking taxonomic similarities between the *Dalmanella* palaeocommunity in all its phases and the older *Dalmanella-Gelidorthis* palaeocommunity, each is distinguishable by changes in the frequency of occurrence of its chief constituents. This suggests that all the important ecological niches, normally occupied by brachiopods in the palaeoenvironments represented by the Flags and Grits and Lavas and Ashes Formations, had been filled when the *Dalmanella-Gelidorthis* palaeocommunity had achieved its full expression, and that further changes were effected mainly by replacements. Thus *D. parva* may only account for 55% of the total number of brachiopods recorded in the *Dalmanella-Gelidorthis* palaeocommunity compared with 90% in the first phase of the *Dalmanella* palaeocommunity. But if we compare the proportion of small, subquadrate biconvex brachiopods with costellate ornamentation (i.e. *Dalmanella*, *Gelidorthis* and *Glyptorthis*) the

proportions are 89% : 91.3% respectively. This concordance suggests that the overwhelming dominance of *Dalmanella* in the younger palaeocommunity was achieved at the expense of *Gelidorthis* and *Glyptorthis* which are likely to have occupied the same niches. Indeed the distributions of brachiopods within these palaeocommunities expressed in terms of shapes and inferred life-habits are noteworthy:

Palaeocommunity	(a) Costellate shells (%)	(b) Trilobate shells (%)	(c) Carinate shells (%)	Concavo-convex shells		(f) Inarticulate shells (%)
				(d) Large (%)	(e) Small (%)	
<i>Dalmanella</i> (phase 3)	86	5.1	0.5	2.7	—	1.9
<i>Dalmanella</i> (phase 2)	65	3.3	4.5	6.6	13	5.7
<i>Dalmanella</i> (phase 1)	91.3	3.5	1.0	3.0	—	1.0
<i>Dalmanella</i> - <i>Gelidorthis</i>	89	1.2	0.3	5.0	—	1.5

where (a) represents *D. parva*, *G. cennenensis* and *G. viriosa tumida*; (b) *T. edgelliana* and *R. triangularis*; (c) *H. convexa*; (d) *M. llanedeiloensis*; (e) *S. antiqua* and (f) mainly lingulids and *S. transversa ffairfachensis*.

The most striking departure from the pattern of species distribution characteristic of the *Dalmanella-Gelidorthis* palaeocommunity is that of the *Dalmanella* palaeocommunity (phase 2) where a significant decrease in the dominance of *D. parva* is balanced by an increase in inarticulates, *Sowerbyella* and *Horderleyella*. The increase in inarticulate brachiopods may not be directly related to the distribution of *Dalmanella* but *Sowerbyella* and *Horderleyella* almost certainly were. The *Sowerbyella* were without pedicles and must have lived like small *Macrocoelia* as mobile low-level suspension feeders. They appeared abruptly and quickly established dominance over the *Dalmanella* palaeocommunity. The *Horderleyella* shells, on the other hand, are the relicts of a species which briefly attained dominance within a palaeocommunity intervening between phases 1 and 2.

Phase 2 is further characterized by the reappearance of *Flexicalymene* and *Marrolithus* in addition to the persistent *Basilicus*, and in that respect echoes the relationship within the *Dalmanella-Gelidorthis* palaeocommunity. Other phyla are also widely represented although less richly so in Bryozoa than the preceding *Horderleyella* palaeocommunity or the later stages of the *Dalmanella* palaeocommunity (phase 1) when brachiopod shells were commonly encrusted.

The *Dalmanella* (phase 2) palaeocommunity evidently had hybrid characteristics. It was dominantly a *Dalmanella* palaeocommunity but significantly enlarged by the presence of the principal constituents of two other palaeocommunities, *Sowerbyella* and *Horderleyella*. *Salopia* is also present although its appearance is not surprising in view of the fact that the substrate is very much like that of the Pebbly Sands Formation in which the genus commonly occurs.

Assuming that this association is made up mainly of the remains of species which lived and died more or less *in situ*, it is best interpreted as transitional between the more restricted *Dalmanella* and *Sowerbyella* palaeocommunities. The reduction in the proportion of *Dalmanella* within the residues accords with an invasion of this habitat by a low-level mobile feeder like *Sowerbyella* and a concomitant increase in the representation of both *Macrocoelia* and *Horderleyella*.

Remnants of the third *Dalmanella* association occurs throughout 16 m of sporadically exposed reworked banded ashes with siltstones. Despite its intercalation within a faunal succession dominated by *Sowerbyella antiqua*, no trace of that species has been found. This is the final Llanvirn expression of the *Dalmanella* palaeocommunity, and much more like phase 1 than phase 2. The noteworthy differences are, of course, the absence of *Gelidorthis* and *Glyptorthis* and the reappearance of the 'infaunal' *Tissintia* in the same minor role it played in the *Dalmanella-Gelidorthis*

palaeocommunity. In view of the differences distinguishing phase 3 from the two older, it probably represents the climax of a succession of palaeocommunities in which *Dalmanella parva* was the dominant taxon.

#### 6. *Orderleyella* palaeocommunity

The main point of interest in the sudden commonness of occurrence of *Orderleyella convexa* throughout about 3 m of the sandstones within the Flags and Grits Formation, is the relationship between that species and *Dalmanella*. Changes in the occurrence of other taxa were much less significant. *Rostricellula*, for example, first appears towards the end of phase 1 of the *Dalmanella* palaeocommunity in sufficient numbers to characterize a distinctive assemblage but presumably not to displace *Dalmanella* from more than a few of the several habitats it normally occupied. Impressions of *Orderleyella*, on the other hand, constitute 62% of the brachiopod remains recovered from this horizon and were almost twice as common as those of *Dalmanella* and *Glyptorthis* put together. Other brachiopods, like *Macrocoelia*, *Rostricellula* and *Triplesia* persisted, albeit in a very minor role, and the proliferation of *Orderleyella* could only have come about at the expense of *Dalmanella*. As already indicated, the morphology of *Orderleyella* suggests that the genus was well adapted to a high energy environment with coarser sedimentary particles in transit. In circumstances where the sedimentary substrate was subject to movement, *Dalmanella* might well have survived to the extent it did only because the relatively large *Orderleyella* shells, even more than ramose bryozoans, afforded stable substrates for attachment, and this would explain why *Dalmanella* once more became dominant in the succeeding pebbly sands. A close scatter of pebbles bearing densely distributed *Dalmanella* might well have militated against the continuing proliferation of *Orderleyella*.

#### 7. *Sowerbyella* palaeocommunity

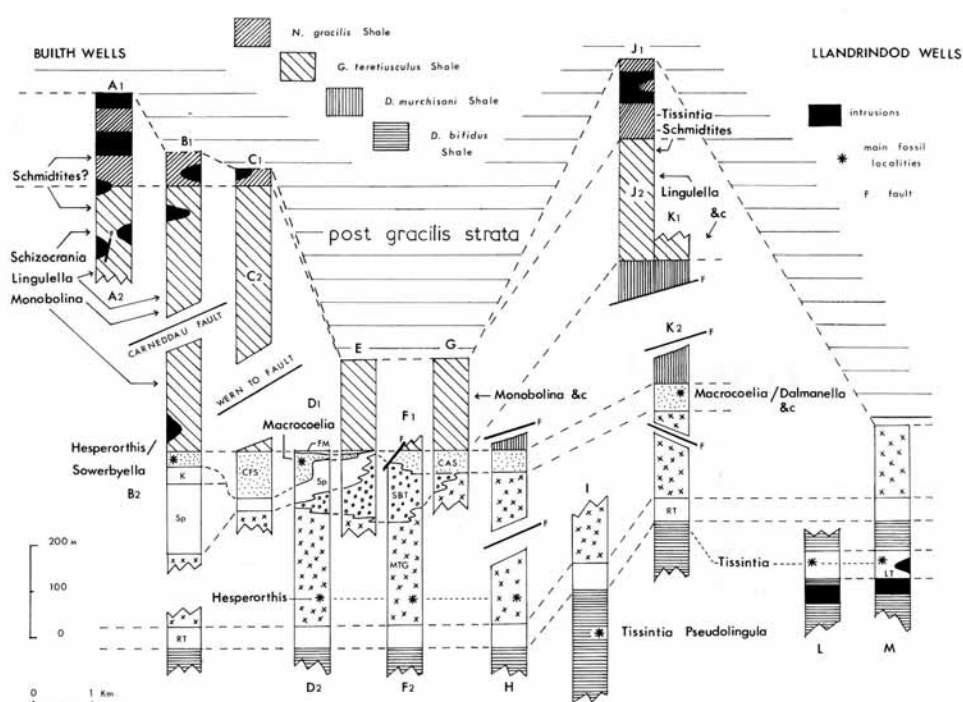
The appearance of *Sowerbyella* within the Ffairfach succession is as significant a faunal change as that which led to the introduction of *Dalmanella*. The inferred life-habits of *Sowerbyella*, as a mobile, low-level suspension feeder, have already been alluded to in discussing phase 2 of the *Dalmanella* palaeocommunity where it first appeared. Thereafter it became overwhelmingly dominant, constituting respectively four-fifths and three-quarters of all the brachiopods occurring in the topmost Flags and Grits and the Rhyolitic Conglomerates. The size ranges and valve frequencies of the taxon (Fig. 5) suggests that both manifestations of the association are the remains of the same palaeocommunity, despite the fact that the older lived on silty and calcareous substrates and was seemingly unaffected by volcanic dust falls (bentonite bands) and the younger on calcareous silts or even coarser beds within pebbly sands. The taxonomic structure of both phases is, however, similar. All stocks other than *Sowerbyella*, are also characteristic of the *Dalmanella* palaeocommunity and *Dalmanella* itself is the second most common genus. This relationship suggests that, provided the substrate was suitable, *Sowerbyella* was capable of colonizing even a well-established *Dalmanella* palaeocommunity to form a mobile pavement. The absence of the other low-level suspension feeder, *Macrocoelia*, at least from these two phases of the *Sowerbyella* palaeocommunity, confirms the blanket-like cover of the substrate by established *Sowerbyella*. Yet, notwithstanding its mobility, *Sowerbyella* was actually less completely dominant than *Dalmanella* in their respective palaeocommunities. *Dalmanella*, *Orderleyella*, *Rostricellula* and, to a lesser extent, *Triplesia* and even *Glyptorthis* survived in fair numbers; presumably by subsisting at varying levels above the substrate and its pavement of *Sowerbyella*.

### COEVAL FOSSIL ASSEMBLAGES, ASSOCIATIONS AND INFERRED PALAEOCOMMUNITIES

Contemporaneous fossil assemblages have been collected from two other successions of the Ffairfach Group and from sediments and bedded pyroclastics associated with the Builth-Llandrindod volcanic complex of Llanvirn age. They confirm the inferences that can be drawn when assemblages of the Ffairfach type succession are regarded as remnants of several distinctive benthic communities. They

also provide further information on the relationship between, and the maturation of, the palaeocommunities previously identified.

*Longwood palaeocommunities.* The sedimentary succession of the Ffairfach Group exposed at Longwood is similar to that at the type section except that the conglomeratic beds in the middle of the Flags and Grits are coarser and thicker, while the rest of the Formation is less calcareous and is separated from the succeeding coarse lithic Ashes by a thin unfossiliferous chert horizon. The lateral equivalent of the Pebbly Sand contain traces of the *Hesperorthis*/*Salopia*-Bryozoa palaeocommunity but with *Hordeleyella* becoming a significant constituent. This association adds weight to the evidence at Ffairfach that the *Hordeleyella* and *Hesperorthis*/*Salopia*-Bryozoa palaeocommunities are closely related with the former a likely climatic development of the latter. The Flags and Grits, irrespective of their coarser textures in Longwood, contain the remnant of a *Sowerbyella* palaeocommunity, which is virtually indistinguishable from the contemporaneous phase 1 found at Ffairfach. The principal difference is the presence of *Macrocoelia*, which also occurs in the coeval *Sowerbyella* palaeocommunity represented on the Coed Duon successions. *Sowerbyella* is also more



TEXT-FIG. 8. Dominant brachiopod faunas in the Builth-Llandrindod inlier, Sections A-M: A1, Gwern y fed fach SO 030526, A2, Penddol rocks 032521; B1, Harpers Quarry 037534, B2, Tan y Graig 047528; C1, Pen Cerrig (lake section) 043540, C2, Stream section 048537; D1, Tan lan (Newmead) 057547, D2, Carn 065539; E, Trecoed 054552; F, Camp 072548; G, Dulas Brook 059556; H, Upper House 071569; I, Upper Camnant Brook 088575; J1, Llanfawr Quarry 066617, J2, Bach y Graig 072610; K1, Shaky Bridge 079609, K2, Howey Brook 092592; L, Bwlch y Cefn 120609; M, Llandegley Rocks 128614.

densely distributed relative to other articulate brachiopods in these northerly sections, which suggests that conditions were especially favourable for both of these mobile low-level suspension feeders.

*Coed Duon palaeocommunities.* Collecting in the Coed Duon successions, where outcrops and faunas are sporadic in occurrence, was concentrated on either side of the unconformable junction between the Ashes and Lavas and the underlying Flags and Grits. The unconformity, which is locally quite spectacular, is represented in Long Wood by the chert horizon. In both Coed Duon and Ffairfach, trilobite fragments increase greatly towards the junction and may be death assemblages accumulating along strand lines. Such complications, however, do not disguise the existence within the calcareous siltstones of the Upper Flags and Grits of Coed Duon of a full expression of a *Sowerbyella* palaeocommunity terminated by an association in which *Dalmanella* becomes the dominant brachiopod but not entirely at the expense of *Sowerbyella*, which still exceeds one-third of all the brachiopods recorded. Such proportions may reflect some degree of *post-mortem* transport but they are more likely to represent a transition between the first and third phases respectively of the *Sowerbyella* and *Dalmanella* palaeocommunities which were so sharply distinguishable in the Ffairfach successions. The faunal succession of Coed Duon demonstrates how euryoecious *Sowerbyella* really was because it occurs even with *Hesperorthis*.

TABLE 3. The composition of various assemblages from the Builth-Llandrindod area; BW 11 from Llandegley Tuffs (SO 128614); BW 7-11 from the Pebbly Feldspar Ash 1 km ESE of Newmead Farm (065539); BW 4-6 and BW 1-3 respectively from the same unit at Camp (072548) and Upper House (071569); NMW.68.376 G. 151-161 from Grey Feldspar Sands exposed in Tan y Craig Quarry (047528); NMW.176 and 177 from contemporary beds exposed at Tan Lan (057547); BW 12a from a sandstone bed in the Upper *D. murchisoni* Shales, Howey Brook (SO 091591).

Locality no.	Inarticulata indet	<i>Schizocrania salopiensis</i> Williams	<i>Hesperorthis dynevoensis</i> Williams	<i>Glyptorthis cf. viriosa</i> Williams	<i>Dalmanella parva</i> Williams	<i>Tissintia prototypa</i> Williams	<i>Sowerbyella antiqua</i> Jones	<i>Macrocoelia llandeloi-</i> <i>ensis</i> (Davidson)	Total Brachiopoda	<i>Flexicalymene</i> sp.	Trilobita indet.	Ostracoda	Bryozoa	Mollusca <i>Hyalostelia lasicala</i> (M'Coy)	Crinoidea	
BW 11	—	—	3	1	—	9	—	1	14	1	1	(2)	12	1	—	1
„ 10	—	—	128	—	—	—	—	—	128	—	—	—	2	—	—	—
„ 9	—	1	300	—	—	—	—	—	301	—	1	—	1	—	—	—
„ 8	—	2	211	—	—	13	—	—	226	—	—	—	1	—	(15)	—
„ 7	—	—	84	—	—	—	—	—	84	1	—	—	—	—	—	—
„ 6	—	—	330	—	—	—	—	—	330	—	—	—	—	—	—	—
„ 5	—	—	279	—	—	3	—	—	282	—	—	—	—	—	—	—
„ 4	—	—	430	—	—	—	—	1	431	—	—	—	—	—	2 <sup>e</sup>	—
„ 3	—	—	588	1	1	—	—	1	591	—	—	—	—	—	—	—
„ 2	1	—	937	—	15	—	—	1	954	—	—	—	1	—	—	—
„ 1	2	—	742	—	8	—	—	—	752	—	—	(3)	2	1	12 <sup>e</sup>	—
NMW.68.376 G																
150-161	—	—	78	—	(6)	—	134	2	220	—	—	—	2	—	(40)	—
176	—	—	—	1	—	—	—	—	1	—	—	—	—	—	<i>N</i>	—
177	—	—	1	—	3	—	—	19	23	(1)	—	—	5	—	<i>N</i>	—
BW 12a	—	1	3	1	1	—	—	9	15	—	—	—	3	—	1	1



*Builth-Llandrindod palaeocommunities.* The Builth-Llandrindod fossil assemblages containing articulate brachiopods came almost exclusively from the coarse clastic facies associated with an assortment of lavas, agglomerates and ashes. Their provenance contrasts sharply with that of the inarticulates, which are mainly found in the shaly graptolitic facies. The relationships between these two facies and among the several palaeocommunities which seem to be represented in the coarser sediments and bedded pyroclastics are shown in Fig. 8. The first Ordovician articulate brachiopod to establish itself in the Builth-Llandrindod area was the opportunistic *Tissintia prototypa*. Traces of the eponymous palaeocommunity, which also included *Pseudolingula* and various *Bivalvia* as minor constituents and is inferred to have been infaunal, are found in the siltier horizons of the *Didymograptus bifidus* shales. *T. prototypa* also occurs in a subordinate role with *Hesperorthis* in the Bwlch y Cefn and Llandegley Tuffs (Table 3). This association is a prelude to the colonization of the early deposits of the Main Tuff Group by the *Hesperorthis/Salopia*-Bryozoa palaeocommunity. This palaeocommunity is chiefly characterized by the extraordinary dominance of *Hesperorthis*; *Salopia* is so far unrecorded at this level. Indeed *Hesperorthis* persisted into the Coarse Feldspathic Sandstones and, although subordinate to *Sowerbyella* in the proportion of 1 : 3, evidently survived the pavement-like spread of the latter as a relatively high-level suspension feeder elevated above the substrate by its powerful pedicle. This ability to survive is further seen in the persistence of *Hesperorthis* as a minor constituent even in the presence of that other contemporaneous mobile low-level suspension feeder, *Macrocoelia*, which dominates a collection from the more northerly outcrop of the Feldspathic Sandstones.

The most interesting assemblage, however, is the diverse one recovered from fine sandstones within the 'Cwm Amlw Series' of Howey Brook (Table 4). The association represented by this assemblage is reminiscent of the *Dalmanella/Glyptorthis* fauna of the basal Flags and Grits at Ffairfach. The two orthoid species constituted 40% of all brachiopods recorded and presumably occupied various feeding levels within the benthic environment, in view of the commonness of occurrence of organic substrates like that afforded by ramose bryozoans. But the *Hesperorthis/Salopia*-Bryozoa palaeocommunity is well represented as 16% of the total brachiopod content while low-level suspension feeders (*Macrocoelia* and *Christiania*) are extraordinarily abundant (37% of all brachiopods). Other brachiopods were minor and either infaunal (*Tissintia*) or high level epifaunal suspension feeders by virtue of their strong to globose biconvexity (*Mcewanella*, *Porambonites*, *Parastrophinella*). The hybrid nature of the assemblage may reflect a post mortem admixture of transported death assemblages of several palaeocommunities. It is, however, noteworthy that the two smallest constituents, *D. parva* and *G. cf. viriosa* (Fig. 9), are represented by more or less equal proportions of disarticulated valves. These assemblages may therefore be interpreted as an ecotone between the *Hesperorthis/Salopia*-Bryozoa and *Dalmanella* palaeocommunities in which *Macrocoelia* proliferated as a low-level epifaunal taxon and *Christiania* appeared as an 'edge' species (Ricklefs 1973, p. 596).

#### CONCLUSIONS

Our analysis of faunal assemblages from the Ffairfach Group of the Llandeilo area and the contemporaneous successions of the Builth-Llandrindod area suggests that the benthos living on or in the varied sediments of that part of the Anglo-Welsh Province during Llanvirn times belonged to five palaeocommunities. One of these, the *Schizocrania* palaeocommunity, appeared briefly with a temporary incursion of anoxic muds and silts. The brachiopods found were exclusively inarticulate and probably epiplanktonic or infaunal in habit. This palaeocommunity is also known to have been prevalent in Llandeilo times (Williams 1976, p. 39; Wilcox 1979, p. 125) and will not be considered further. Another palaeocommunity, dominated by *Tissintia prototypa*, is equally simple in structure, and was composed essentially of opportunistic species which exploited a transient substrate built up of variable inflows of oxygenated silts and anoxic clay sedimentation. Both *Tissintia* and the parallel-sided *Pseudolingula* as infaunal stocks would have been well adapted to surviving these contrasting conditions. The palaeocommunity may therefore be regarded as representing an early phase in the

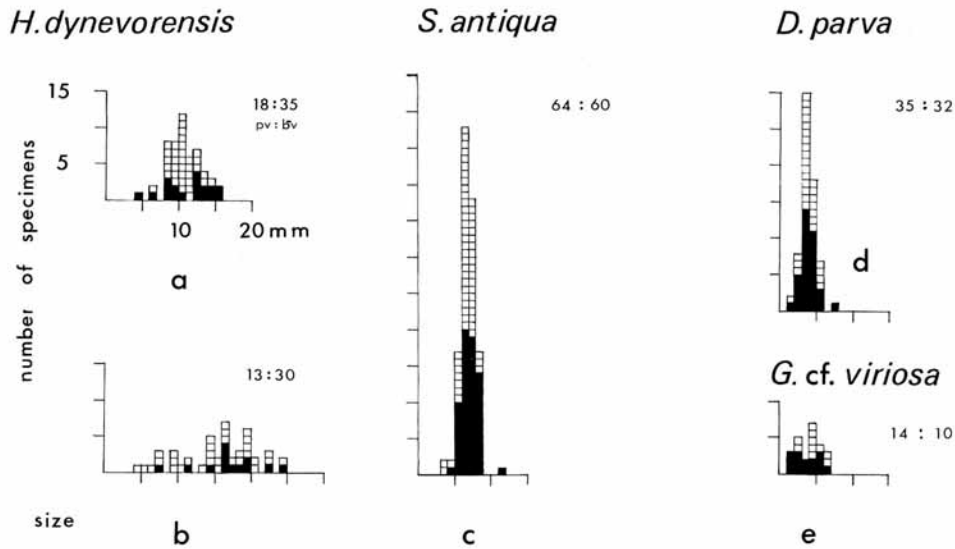


TABLE 4. The composition of the faunal assemblage from sample BW 13 from Upper Llanvirn sandstones exposed near Howey Brook (SO 092591).

		%	% B
<i>Hesperorthis dynevorensis</i> Williams	25	(7.6)	11.7
<i>Glyptorthis</i> cf. <i>viriosa</i> Williams	20	(6.1)	9.3
<i>Mcewanella berwynensis</i> MacGregor	6	(1.8)	2.8
<i>Dalmanella parva</i> Williams	67	(20.4)	31.3
<i>Tissintia prototypa</i> (Williams)	2	(0.6)	0.9
<i>Salopia turgida</i> (M'Coy)	10	(3.0)	4.7
<i>Macrocoelia llandeiloensis elongata</i> —Lockley and Williams	67	(20.4)	31.3
<i>Christiania elusa</i> Lockley and Williams	14	(4.3)	6.5
<i>Porombonites</i> sp.	2	(0.6)	0.9
<i>Parastrophinella parva</i> MacGregor	1	(0.3)	0.5
Total Brachiopoda	214	(66.9)	—
Asaphid	1	(0.3)	
Calymenid	1	"	
<i>Bettonia chamberlaini</i> (Elles)	1	"	
Odontopleurid	1		
<i>Lyrodesma</i> sp.	6	(1.8)	
<i>Similodonta</i> sp.	3	(0.9)	
'Pterineid' bivalve	1	(0.3)	
<i>Matherella</i> cf. <i>acuticostata</i> Bates	1		
<i>Sinuites</i> sp.	1		
Ornamented bellerophontid	1		
Orthocerida	3	(0.9)	
<i>Orthoceras vagens</i> Salter/ <i>Cyrtoceras macrum</i> Blake	2/1		
Fenestellid Bryozoa	1	(0.3)	
Ramose Bryozoa (etc.)	83	(25.2)	
Boring organism	1	(0.3)	
Conularid	1		
<i>Hyalostelia fascicula</i> (M'Coy)	<i>N</i> = 1		
Crinoidea	<i>N</i> = 1		
Cystoidea?	<i>N</i> = 1		
Sponge spicule?	1		
<i>Didymograptus</i> sp.	5	(1.5)	
Estimated number of individuals	329		
Diversity	31		

benthic colonization of any sector of the Anglo-Welsh basin which was beginning to undergo a change in substrate from the typical anoxic muds of the graptolitic facies to the more varied oxygenated sediments of the shelly facies. In this respect it is significant that *T. prototypa*, or its Llandeilo descendant *T. immatura*, are widely and repeatedly distributed as the sole articulate brachiopod occurring with graptolitic and trilobitic remains in the Lower Ordovician successions of South Wales and Shropshire.

The three remaining palaeocommunities are restricted to those sediments which are normally described as shelly facies. There is inevitably some overlap among them in taxonomic content, possibly through recruitment of the more euryoecious constituents. This can be shown by plotting the proportions of those brachiopod species which are either dominant in any one of the climactic stages of the three palaeocommunities or occur in significant numbers in two or more (Fig. 10). The general pattern is of one species achieving overwhelming dominance with the remainder playing a variable



TEXT-FIG. 9. Size-frequency histograms for complete pedicle (black) and brachial valves from the Builth-Llandrindod district showing respective numbers ( $N$ ) of each valve (pv : bv): (a) and (b) respectively *H. dynevorenensis* from samples BW 8 and NMW. 150-61; (c) *S. antiqua* from sample NMW. 150-61; (d) and (e) respectively *D. parva* and *G. cf. viriosa* from sample BW 13. Locality details given in text and in explanations of Tables 3 and 4.

but minor role. Such a pattern accords with the conclusion that they all existed independently of one another and that each best flourished on a particular type of substrate.

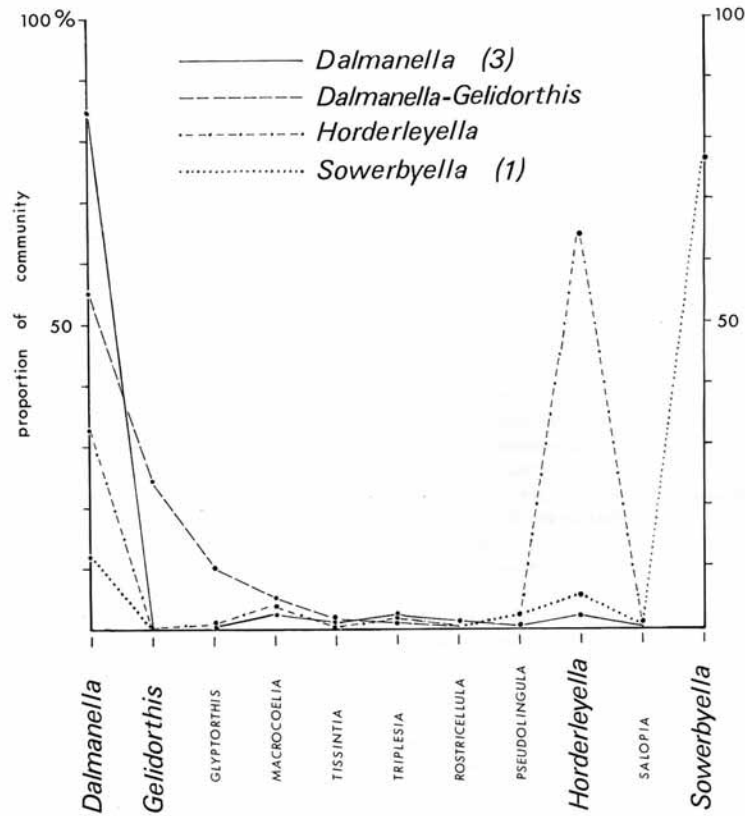
The first of the three palaeocommunities to appear was that involving *Hesperorthis*, *Salopia*, and *Hordeleyella* as dominant elements at one time or another. The palaeocommunity, as understood by us, was well adapted to coping with coarse well-washed sediments and its earliest manifestation was the colonization of a substrate by *Hesperorthis*. Thereafter other brachiopod taxa, especially *Salopia* and *Macrocoelia*, appeared and together with Bryozoa formed a noteworthy variant of the palaeocommunity. We have, however, interpreted the diverse benthic fauna dominated by *Hordeleyella* as the climax of the palaeocommunity. The maturation of this almost exclusively epifaunal palaeocommunity involved an increase in diversity of its constituents although all were subordinate to one dominant species. In the early stages of its development, the dominant role was assumed by *Hesperorthis*, *Salopia* or even *Macrocoelia* but in the climactic stages *Hordeleyella* was the most abundant form.

The most persistent palaeocommunity in the Ffairfach section was that dominated by *Dalmanella parva*. The species is the most commonly occurring taxon at Ffairfach, accounting for 51% of all the 7,500 or so brachiopods recovered during our investigation, and the taxa with which it formed a well-integrated benthic unit are unmistakable. The palaeocommunity occurs in some form or other at four distinct intervals throughout more than 25 m of pre-Llandeilo sediments but especially those which had constituted silty substrates. We attributed its success to the possibility that its principal components were attached to high-standing organisms like Bryozoa as well as to the sedimentary substrate and were therefore capable of filter-feeding at several different levels above the sea bed. This range in altitude of microhabitats may explain why the palaeocommunity was the most diverse of all

those inferred to have existed during Llanvirn times; and why the entire fauna rather than certain species within it seems to have been affected by colonizing waves of *Sowerbyella*.

The four phases of the *Dalmanella* palaeocommunity (s.l.) represented within the Ffairfach succession may be interpreted as showing a progressive maturation involving significant changes in its taxonomic structure. *Dalmanella*, *Gelidorthis* and *Glyptorthis* first appeared more or less together, as minor constituents of the *Hesperorthis/Salopia*-Bryozoa palaeocommunity but did not become dominant until an influx of silt instead of sand seems to have favoured their proliferation into the *Dalmanella-Gelidorthis* palaeocommunity. This unit together with the first and second phases of the *Dalmanella* palaeocommunity *sensu stricto* may be regarded as precursory to a climax which is represented by phase 3 when the diversity of the fauna was actually reduced.

The remaining palaeocommunity is characterized by a proliferation of *Sowerbyella*. There are two aspects to the spread of the genus which suggest that its long-ranging success as a benthic organism



TEXT-FIG. 10 Graphic representation of the varying proportions within the three identified climax palaeocommunities of those genera which constitute more than 5% of any one palaeocommunity or more than 1% in any two. Proportions for the diverse *Dalmanella-Gelidorthis* association are also shown.

was related to its novel ability to occupy a habitat as a mobile rather than a sedentary bivalve. The first is that *Sowerbyella* asserted itself rapidly rather than abruptly within the second phase of the *Dalmanella* palaeocommunity and, in becoming the dominant constituent, did not even completely displace the other low-level suspension feeder *Macrocoelia* except locally at Ffairfach. The same relationship is evident between *Sowerbyella* and the *Hesperorthis*-Bryozoa palaeocommunity in the Coarse Feldspathic Sandstones of the Builth-Llandrindod area. In effect, mobility enables *Sowerbyella* to become established in different communities without greatly changing their taxonomic structure except for those species which lived at the interface between sea and sediment.

The second noteworthy aspect of the spread of *Sowerbyella antiqua* was its tolerance of variation in the sedimentary substrate. The species thrived best on carbonates and calcareous silts but was capable of colonizing sands and even coarser sediments. This tolerance, which may have been due in part to the mobility of adult shells, must have given impetus to the successful incursion of the genus into other palaeocommunities. Mobility and tolerance of substrate variation may have been the main factors in the extraordinary persistence of *Sowerbyella* as a cosmopolitan stock throughout much of the Ordovician.

The associations which are the basis for inferring the palaeocommunities described above are known from younger and contemporaneous rocks in Wales and Shropshire. The *Tissintia*, *Schizocrania*, *Dalmanella*, *Sowerbyella*, and a variant of the *Hordeleyella* palaeocommunities have been identified in the Llandeilo Series of the type area. A similar succession exists in west Shropshire and, although a different nomenclature has been used to describe brachiopod associations found there, striking resemblances are evident (Williams 1974, pp. 16-23; 1976, pp. 38-44). *Tissintia* palaeocommunities, for example, are well represented in the Weston, Betton and Meadowtown Beds. The last Formation also contains good examples of the *Dalmanella* and *Sowerbyella* climax communities. In the older Caradoc, however, a palaeocommunity dominated by *Dalmanella* which occurred in the Spy Wood Grit was eventually replaced by another dominated by triplesiaceans *Bicuspina* and *Caeroplecia* and the orthaceans *Orthambonites* and *Nicolella*. These stocks, and other genera like *Reuschella*, *Platystrophia* and *Leptaena* occurring in the Whittery Shales, are characteristic of some of the palaeocommunities found in the younger Caradoc sediments of the Bala (Lockley 1980) and east Shropshire areas.

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