CARADOC MARINE BENTHIC COMMUNITIES OF THE SOUTH BERWYN HILLS, NORTH WALES

by R. K. PICKERILL *and* P. J. BRENCHLEY

ABSTRACT. The Upper Ordovician (mid Caradoc: Soudleyan–Longvillian) clastic rocks of the south Berwyn Hills, North Wales, contain an abundant and diverse macrobenthic fauna dominated by epifaunal brachiopods. Based on studies in the south Berwyns, Shropshire, and Snowdonia, four communities are recognized and examined in terms of composition and related palaeoenvironmental parameters. It is concluded that the communities are intergrading and exhibit a close correlation with substrate and a broad correlation with depth, distance from shore, turbulence, and rates of sedimentation. The low diversity *Howellites* community was best developed on muddy silt and silty mud substrates in low energy turbid conditions and in water depths of less than 25 m. The *Dinorthis* community exhibits a low to moderate diversity and based on the balance of constituent genera and relationship to substrate is divisible into two sub-communities: the *Dinorthis* sub-community was best developed on shifting coarse sand substrates in high energy, non-turbid, well-oxygenated environments of water depths of less than approximately 10 m. The *Macrocoelia* sub-community was developed on finer sand substrates deposited in lower energy conditions and slightly more off-shore in deeper water (25 m). The *Dalmanella* community developed on non-turbid, well-oxygenated, mobile fine sand substrates in water depths of 25 m or less and in areas of reduced sedimentation. The *Nicolella* community inhabited a variety of substrates but developed best on calcareous silt and fine sands. Energy conditions were variable at any one time but in general low-energy conditions prevailed, sedimentation rates were low and water depth was in the order of approximately 30 m. The communities are examined in terms of their stratigraphical distribution within the Berwyn succession and are discussed in relation to previously described Lower Palaeozoic communities. It is suggested that benthic faunas progressively migrated into deeper waters throughout the Lower Palaeozoic.

SINCE the pioneering work of Petersen (1911, 1913) marine benthic communities have generally been considered to be real phenomena and only on occasion has this reality been contested (e.g. Lindroth 1935; MacGinitie 1939; Muller 1958). One of the major goals of marine palaeoecology is the description of community structure and evolution over long periods of geological time and the ultimate development of general models relating them to controlling environmental parameters. Attempts have already been made to trace the evolution of certain communities, for example, Bretsky (1969*a*), Anderson (1971), Watkins and Boucot (1975), and Boucot (1975), though as Thayer (1974) points out, such efforts must be regarded with some caution until a sufficient number of detailed palaeoecological investigations have been completed. Unfortunately, relatively few detailed studies of Ordovician community palaeoecology have been undertaken, notable exceptions being those of Walker and Laporte (1970) and Walker and Alberstadt (1975) in carbonate sequences, and Bretsky (1969*b*, 1970*a*, *b*) and Bretsky and Bretsky (1975) in clastic sequences. This paper is therefore intended to document just such an investigation which was undertaken in the Caradoc rocks (Ordovician) of the south Berwyn Hills, North Wales.

Brachiopoda were the numerically dominant taxonomic group of sedentary marine macrobenthos during Ordovician times (Williams 1976) and predominate in the communities described here. Additional taxa comprising these communities,

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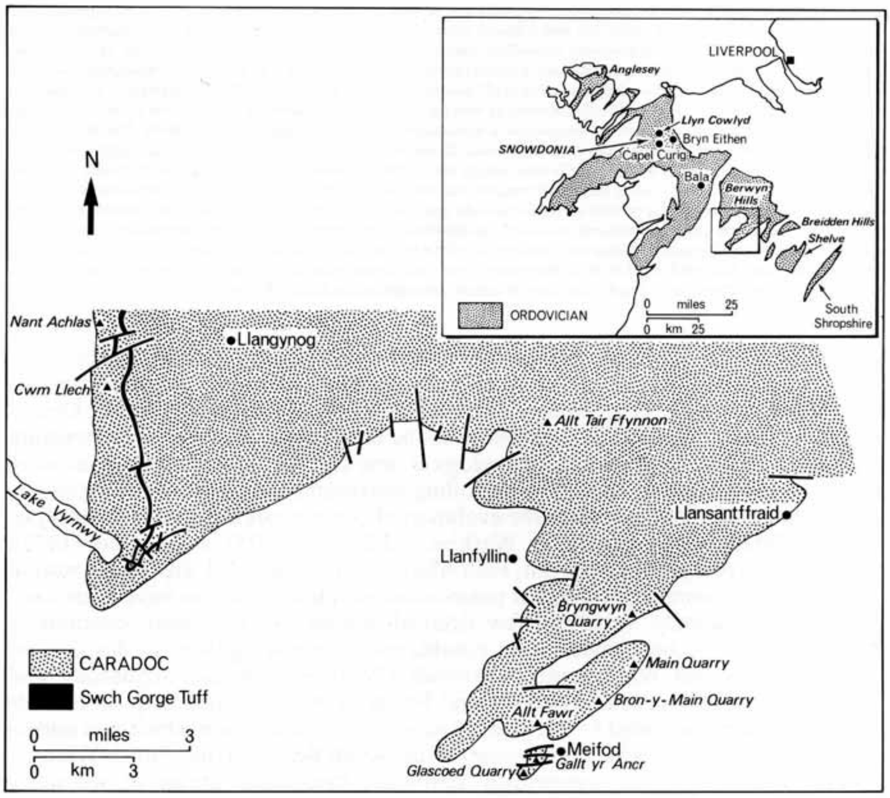
though of lesser abundance, include bivalves, gastropods, ostracodes, trilobites, and crinoids, and these elements are also included. The work arose from the observations of Williams (1963, 1973), who in his treatment of Caradoc brachiopods of the Bala district, North Wales, noted briefly that the faunas occurred in four 'associations', the *Nicolella*, *Dinorthis*, *Onniella*, and *Howellites* associations, which were subsequently adopted by Pickerill (1975, 1976, 1977). Williams (1963), however, stated 'whether these associations represent remains of biotic communities that existed in a north Welsh province during Caradocian times is a matter for further exploration'. Research was therefore undertaken in the Berwyn Hills to investigate this statement in some detail. In addition to detailed sampling and data collection in the Berwyn Hills, further material was obtained from south Shropshire (now south Salop) and east Snowdonia, where lower Caradoc lithofacies are more clearly differentiated.

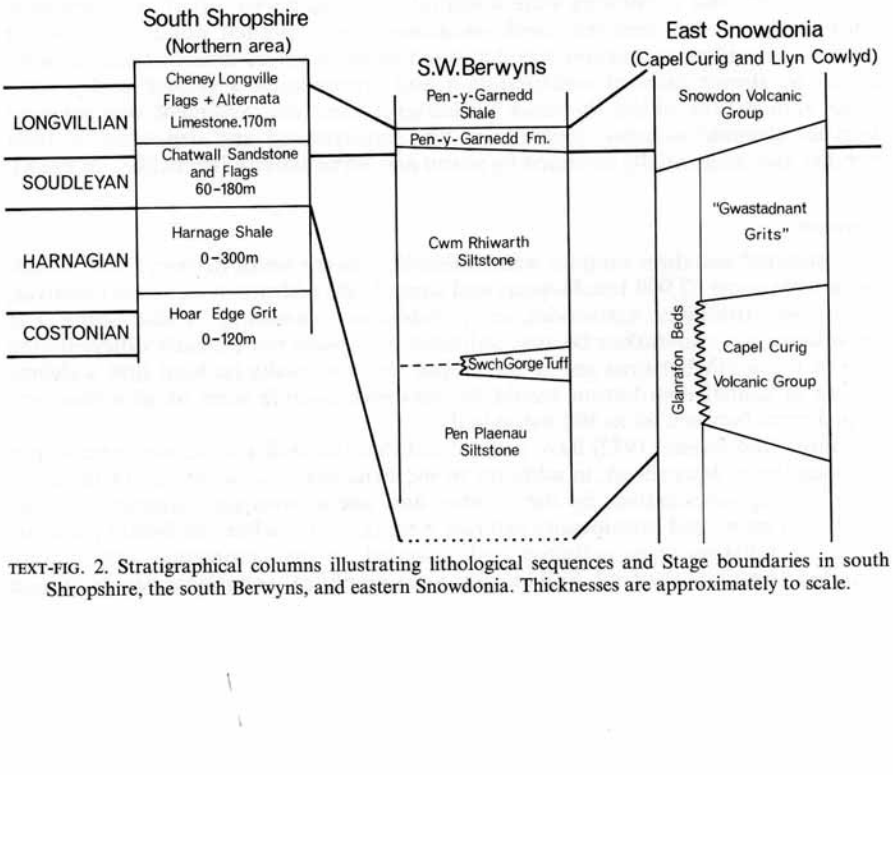


TEXT-FIG. 1. Generalized map of outcrop of Ordovician rocks in North Wales, and more detailed map of the south Berwyn Hills indicating localities referred to in the text.

Stratigraphical setting

The Berwyn Hills (text-fig. 1) are formed by a dome-like upfold of Ordovician rocks flanked on three sides by Silurian strata, and on the eastern edge by sediments of Permo-Carboniferous age. Stratigraphically the oldest material exposed is Llandeilo in age (MacGregor 1961) and this is overlain by several hundred metres of unfossiliferous sediments with thin tuffs and lavas which have not been precisely dated but are probably of lower Caradoc age. These are followed by a succession of fossiliferous sediments and volcanics of proved Caradoc (Soudleyan and Longvillian) age (King 1923; Brenchley 1969; Pickerill 1977). These fossiliferous sediments, with which this study is concerned, are composed of a thick sequence (*c*. 900 m) of thinly interbedded muds and silts and/or sands. The stratigraphical sequence in the south Berwyns is illustrated in text-fig. 2. The present study does not include in detail the graptolitic Pen-y-Garnedd Shales (=Nod Glas) as these are generally poorly exposed and have a limited shelly fauna.

Samples collected in Snowdonia were obtained from the Glanrafon Beds and Snowdon Volcanic Group (Soudleyan and Longvillian), which are composed essentially of interbedded mudstones and siltstones with thick intercalations of volcaniclastic sandstones. In south Shropshire samples were taken mainly from coarse sandstone facies within the Hoar Edge Grit (Costonian), which lies unconformably on rocks of Precambrian age and represents a transgressive fining-upward sequence, but some collections were made for comparative purposes from rocks of Harnagian and Soudleyan age (text-fig. 2).



TEXT-FIG. 2. Stratigraphical columns illustrating lithological sequences and Stage boundaries in south Shropshire, the south Berwyns, and eastern Snowdonia. Thicknesses are approximately to scale.

Environmental setting

The environmental setting briefly outlined here is based on a combination of knowledge of the general position of the Berwyn Hills in relation to the well-established regional environmental framework of the Welsh Basin (Brenchley 1969) and on more detailed examination of lithofacies, associated bedforms, and ichnofacies within the region itself. Faunal information is used only in a very general sense in environmental reconstruction as the objective is to interpret the fauna in terms of its environmental distribution (cf. Thayer 1974).

Geographically the Berwyn Hills now lie in what was formerly part of the central region of the NE–SW trending Welsh Basin during Caradoc times. The Welsh Basin itself was a fault bounded tectonically active graben during the Ordovician, approximately 120 km in width and bounded to the north-west by the Anglesey–Rosslare Horst and to the south-west by the Church Stretton or Pontesford–Linley Fault. A land area composed of Borrowdale Volcanics lay to the north until at least Longvillian times (Brenchley 1969). Within the graben a series of volcanic islands extended east–west across Wales and erosion of many of these islands provided a major source of intrabasinal sediment (Bassett 1963). It has long been recognized that sedimentation in the northern part of the Welsh Basin was shallow-water in origin (Brenchley 1969) though accurate delineation of specific sub-environments has not really been attempted.

For the purposes of this paper we present the pertinent observations and conclusions on the sedimentary environments of the Caradocian rocks in the south Berwyns in Table 1. Basically, the whole succession was deposited in a generally quiet subtidal to shallow marine shelf environment (inner infralittoral, 0–30 m). In the Soudleyan the environmental conditions were essentially homogeneous, apart from episodic volcanicity, and the relatively thick succession was deposited rapidly. The much thinner Longvillian succession was deposited in more varied environments characterized by slower rates of sedimentation and representing a greater bathymetric range, though still within the inner infralittoral spectrum. Sediment was supplied from intrabasinal volcanic sources and was redistributed and deposited by tidal currents and occasionally modified by storm and wave activity (Brenchley, in press).

Material

Four hundred and three samples were obtained from the south Berwyn Hills, including in total some 72,000 brachiopods and some 6,000 additional elements (bivalves, gastropods, trilobites, ostracodes, etc.). Additional sampling in Shropshire and Snowdonia was undertaken because sediment types were more clearly differentiated than in the south Berwyns and it was hoped and eventually realized that a clearer picture of faunal distribution would be obtained. Sample sizes of all collections ranged from between 60 to 500 individuals.

Stanton and Evans (1972) have pointed out that the ability to define or recognize communities is determined, in addition to the structural characteristics of the community being investigated, by the number and size of available samples. A large number of inter- and intralocality samples were taken to define the faunal patterns. Some assemblages were collected and recorded in the laboratory, others were recorded directly in the field. Full locality, stratigraphical, and faunal details of each

TABLE 1. Summary of environmental analysis of the Caradoc succession in the south Berwyn Hills.

	Description	Interpretation
VOLCANICS	Volcanics, including welded tuffs occur associated with the mudstone sequence in the north and west Berwyns. The tuffs form widespread sheets of relatively constant thickness.	The normally marine area was subject to periodic emergence. Deposition of subaerial tuffs occurred on a relatively flat, undissected surface (Brenchley 1969).
FACIES	A vertically and laterally variable association of mudstones with thin, parallel bedded, lenticular bedded, and bioturbated siltstones and fine sandstones.	A facies association commonly found in shallow subtidal environments (depths 10–30 m).
SEDIMENTARY STRUCTURES	Very common small scale cross lamination and common ripple marks, both asymmetric and symmetric. Interference ripple patterns frequent. Small (<30 cm deep) sharply incised scour and fill structures, and some broader channels, mud clasts in sandstones.	Evidence of both current and wave ripples. Locally, stream-like current channelled muds.
ICHNOLOGY	A variable ichnofaunal suite including *Cruziana* spp., *Rusophycus* spp., *Trichophycus*, *Skolithos*, *Planolites*, ? *Gyrochorte*, *Diplocraterion*, *Arenicolites*, ? *Palaeophycus*, *Vermiforichnus*, *Teichichnus*, and ? *Imponoglyphus*.	Coexistence of the *Skolithos* and *Cruziana* ichnofacies in a shallow subtidal inner infralittoral shelf environment (Pickerill 1976, 1977).
BODY FOSSILS	Normal 'shallow water' marine benthic assemblages.	Marine shelf.

sample are given in Pickerill (1974). A locality list, maps, and sample details have been deposited with the British Library, Boston Spa, Wetherby, Yorkshire LS23 7BQ U.K. as Supplementary Publication No. SUP 14011 (175 pages). A selection of the fauna has been deposited in the British Museum (Natural History).

Most of the fauna in the south Berwyns is well known taxonomically through the comprehensive description of the brachiopods of the near-by Bala area by Williams (1963) and through the monographs of the trilobites of the Bala area by Whittington (1962, 1965, 1966, 1968) and of the south Shropshire area by Dean (1960*b*, 1961, 1963*a*, *b*). The crinoids have been monographed by Ramsbottom (1961) but the remainder of the fauna is still imperfectly described. Quantification of faunal data was facilitated by the good preservation of most taxa and each sample was counted with a view to assessing its composition in terms of relative abundance of individual genera. For brachiopods and bivalves, unless the specimen was articulated, the number of individuals was taken as the number of the most abundant valve. For trilobites the number of the most abundant part (cephalon or pygidium) was divided by a factor of ten to allow for ecdysis (see Harrington 1959, p. O111). Crinoids, bryozoans, and ostracodes proved more difficult to handle quantitatively. These elements usually occurred as only a very minor part of the collections and were for ease of data handling referred to as single individuals.

ASSEMBLAGES AS LIFE ASSEMBLAGES

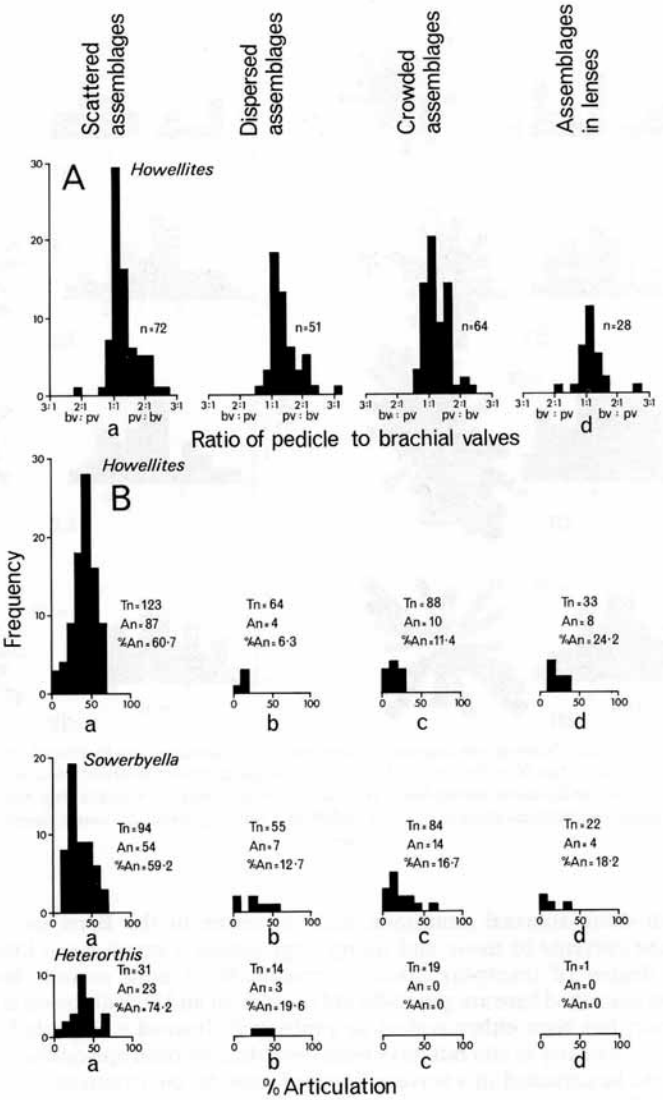
Johnson (1960) and Lawrence (1968) have discussed the problem of deriving from fossil assemblages an understanding of the original community. Unfortunately many of these problems, such as non-preservation as a result of chemical dissolution and diagenetic activity and selective winnowing of extremely small forms, etc., must remain obscure as there is no positive evidence by which to assess them. However, in spite of such problems we consider that the assemblages are representative of the original communities based on our following observations:

1. Life clusters of completely articulated shells have been observed in most sediment types, and these assemblages are of similar composition to assemblages in which some degree of disturbance is clearly demonstrable. Such life clusters are most common in muds and silty muds which have not been subjected to higher energy current regimes or intense biogenic reworking.

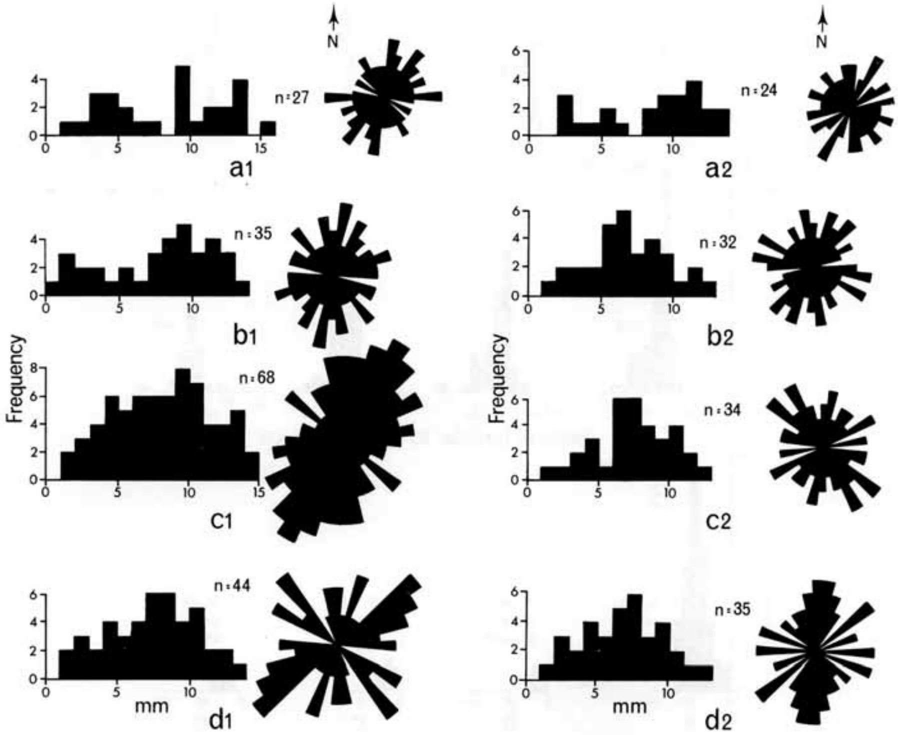
Commonly observed are monospecific clusters of three to seven individuals of the dalmanellid *Howellites*, which lived with the umbo pointing down and the commissure vertical or nearly vertical (Richards 1972). Monospecific clusters of the plectambonitid *Sowerbyella* are also common and this genus appears to have lived on the substratum supported by the gently convex ventral valve. Less frequently observed are life clusters of associated *Sowerbyella* and *Howellites* and monospecific clusters of the craniopsid *Paracraniops*, which appear to have been free-living craniids like *Pseudocrania* (Williams 1963). Rare examples of the orthid *Platystrophia sublimis* and the triplesid *Bicuspina spiriferoides* were also observed and these appear to have lived umbo down with the plane of the commissure nearly vertical. Finally the lingulid *Lingulasma tenuigranulatum* was also observed in vertical burrowing position, details of which are given by Pickerill (1973).

2. Detailed analysis of the various taxa has indicated that post-mortem reworking, transportation, and hydraulic mixing of the assemblages was limited. This is particularly true for those assemblages scattered within mudstones and muddy siltstones, which accumulated under low-energy conditions. Of these assemblages 60·7% contain some articulated valves and these articulated valves commonly form a high percentage of all valves present (median 40–50%, text-fig. 3), but the remaining 39·3% of the assemblages contain no articulated valves. Therefore there are apparently two types of assemblages present; those which have a percentage of articulation and which have suffered little or no hydraulic disturbance, and those assemblages which have been sufficiently disturbed to cause complete disarticulation.

Assemblages occurring on bedding planes or in calcareous lenses less commonly have articulated valves (text-fig. 3), and amongst the assemblages which have articulated valves the percentage articulation is generally low (text-fig. 3). This indicates that nearly all these assemblages have been disturbed but that the degree of disturbance in some cases is limited. The wide size distribution and lack of strongly preferred orientation of the valves (text-fig. 4) and a ratio of pedicle to brachial valves approaching unity (text-fig. 3) in all these disturbed assemblages indicates that they have not been subjected to prolonged winnowing and sorting by currents. Poorly sorted, poorly oriented assemblages could have been moved and dumped by violent wave and current activity during storms, particularly in near-shore and littoral environments.



TEXT-FIG. 3. (A) Histograms showing ratio of pedicle to brachial valves in n collections of *Howellites*. (B) Histograms showing percentage of valves which are articulated in collections containing *Howellites*, *Sowerbyella*, or *Heterorthis*. Tn = total number of collections. An = collections with articulated specimens. $\% \text{ An} = \frac{\text{An}}{\text{Tn}} \times 100$. a = scattered assemblages; b = assemblages dispersed on bedding planes; c = assemblages crowded on bedding planes; d = assemblages in calcareous lenses.



TEXT-FIG. 4. Histograms showing size-frequency distribution of brachial valves in assemblages containing *Dalmanella* (a_1 b_1 c_1 d_1 b_2) or *Howellites* (a_2 c_2 d_2). The rose diagram shows the orientation of the hinge lines of the brachial valves in the same assemblages. n = number of specimens. a = assemblage widely dispersed on a bedding plane; b = medium dispersed; c = crowded on a bedding plane; d = assemblages in calcareous lenses.

In more off-shore subtidal situations, such as occur in the Berwyns, the ability of waves and currents to move and dump large grains is much more limited and a significant degree of transport takes a considerably longer period. Because the assemblages described here are generally unfragmented and lack abrasion it is unlikely that transport has been either violent or prolonged. Instead it is probable that the assemblages are nearly *in situ* but have been disturbed by brief episodes of turbulence such as might be expected in a wave-influenced subtidal environment.

3. The similarity of taxonomic composition between those assemblages which are in life position, those scattered assemblages which have a high percentage of articulated valves, and those clearly transported assemblages which occur on bedding planes, in lenses, or in cross-stratified beds, suggests that in all cases there has been little mixing of faunal elements.

Thus, we agree with Johnson (1965) and Walker and Bambach (1971), who point out that most benthic assemblages on clastic substrates represent the remains of organisms that lived nearly in place, even though the resultant assemblages may be 'time averaged'.

In summary, though it is clear that some transport and winnowing of many of the assemblages has occurred, we conclude that this was not sufficiently extensive to modify the original associations and therefore regard the assemblages as representative of the original communities.

TERMINOLOGY

The classification of ecological and palaeoecological units is still beset by numerous differences of approach and terminology (Kauffman and Scott 1976). Therefore to avoid confusion we have defined below certain terms used in this account.

(i) An assemblage refers to a single collected sample.

(ii) An association refers to the recurrent association of taxa in a group of assemblages.

(iii) A community refers to a spatially repeated and temporally recurring group of organisms usually related to specific environmental parameters. Palaeontologically a community is usually inferred from the occurrence of one or more associations. We have used sub-community to distinguish associations within a community which have a different abundance of the constituent genera. Generally, communities have been named either after their environment of occurrence or, as in the case here, after a genus which, in the sense of Johnson (1972), is dominant or characteristic and hence is one of the most abundant. More recently Hurst (1975) proposed that communities should be named after one of the most abundant and ecologically restricted invertebrate species. This avoids confusion as far as extra-regional applicability of localized community types are concerned, and, in addition, it attempts to avoid the problem that different species of the same genus can possibly have different ecological preferences (e.g. Hurst 1975). However, this procedure can lead to a proliferation of community names and we have preferred a generic designation.

Johnson (1972) has pointed out that a community is composed of three kinds of species: (a) *characteristic species*, which occur more frequently in the community than in any other and are therefore characteristic of the particular community. It is not necessary for a species to be abundant for it to be characteristic and in this account we have referred to genera as being characteristic even if they are uncommon; (b) *intergrading species*, which are characteristic of another usually adjacent community; and (c) *ubiquitous species*, which occur in several communities but are not characteristic of any one. In the description below we adopt this general scheme and therefore describe what we regard as the elements characteristic of a particular community and also indicate those elements of adjacent co-existing communities which may sometimes form part of the particular association.

(iv) Diversity refers to the number of genera in an assemblage. We have calculated mean diversity for each community by totalling the number of genera and dividing this total by the number of assemblages in the community.

THE CARADOC COMMUNITIES

The nature of shallow-water benthic communities on clastic substrates has been succinctly summarized by Johnson (1972, p. 152), who states that such communities '. . . exhibit low diversity, recur in variable combinations of species and are often revised by fluctuations in the physical environment. The environmental gradients tend to be low. As a consequence benthic communities on clastic substrates tend to be continuous and intergrading.' Thus, the actual delineation of distinct communities is often quite arbitrary and, indeed, this has been our experience in examining the Caradoc rocks of the Berwyn Hills where the mudstone and siltstone lithofacies are poorly differentiated and the communities exhibit nearly continuous intergradation.

TABLE 2. Faunal list and stratigraphical distribution of taxa from the south Berwyn Hills.

BRACHIOPODA

Bicuspina spiriferoides (M'Coy)	1, 2, 3, 5	*Lingulella* cf. *ovata* (M'Coy)	1, 2, 5
Cremnorthis parva (Williams)	5	*Lingulella* sp.	3
Dalmanella horderleyensis (Whittington)	3	Linguloid gen. et sp. indet.	1, 2, 3, 4, 5
Dalmanella indica (Whittington)	3	*Macrocoelia expansa* (Sowerby)	3
Dalmanella cf. *modica* (Williams)	4, 5	*Macrocoelia prolata* (Williams)	2, 3
Dalmanella sp.	1, 2	*Nicolella actoniae* (Sowerby)	4, 5
Dinorthis berwynensis (Whittington)	1, 2	*Obolus* sp.	5
Dinorthis berwynensis angusta (Williams)	2, 3	*Onniella* cf. *soudleyensis* (Bancroft)	2
Dinorthis cf. *flabellulum* (M'Coy)	3	*Orbiculoidea* sp.	3
Dinorthis sp.	5	*Oxoplecia* sp.	1, 2, 3, 5
Dolerorthis duftonensis prolixa (Williams)	3, 4, 5	*Paracraniops* sp.	1, 2
Eoplectodonta rhombica (M'Coy)	4, 5	*Platystrophia sublimis* (Opik)	3, 5
Eoplectodonta sp.	2	*Reuschella horderleyensis* (Bancroft)	1, 2
Howellites antiquior (M'Coy)	3, 4	*Reuschella horderleyensis undulata* (Williams)	3, 4
Howellites spp.	1, 2, 5	*Reuschella oblonga* (Whittington)	1
Kiaeromena kjerulfi (Holtedahl)	2, 3, 4, 5	*Rhactorthis* cf. *crassa* (Williams)	4, 5
Kiaeromena sp.	5	*Rhynchotrema* sp.	4
Kjaerina hedstroemi (Bancroft)	3	*Rostricellula sparsa* (Williams)	1, 2, 4
Kjaerina jonesi (Bancroft)	3, 4	*Sericoidea* sp.	2
Kjaerina sp.	3	*Skenidioides costatus* (Cooper)	3, 4, 5
Kjerulfina sp.	4	*Sowerbyella* spp.	1, 2, 3, 4
Leptaena ventricosa (Williams)	2, 3	*Strophomena* sp.	4
Leptaena sp.	3, 5	*Trematis* sp.	2
Leptestiina oepiki (Whittington)	2, 3	*Vellamo* sp.	5
Lingulasma tenuigranulatum (M'Coy)	5	Strophomenid gen. et sp. indet.	5
Lingulasma sp.	5	Plectambonitid gen. et sp. indet.	5
		Clitambonitid gen. et sp. indet.	5

TRILOBITA

Deacybele pauca (Whittington)	3, 4, 5	*Flexicalymene caractaci* (Salter)	3, 4
Broeggerolithus broeggeri (Bancroft)	1, 2, 3	*Flexicalymene* (*Reacalymene*) *limba* (Shirley)	1
Broeggerolithus nicholsoni (Reed)	3	*Flexicalymene planimarginata* (Reed)	3, 4
Broeggerolithus soudleyensis (Bancroft)	2, 3	*Flexicalymene* sp.	2
Broeggerolithus sp.	4, 5	*Illaenus* sp.	2
Brongniartella cf. *ascripta* (Reed)	2, 3	*Kloucekia apiculata* (M'Coy)	3, 4, 5
Brongniartella minor (Salter)	1, 2, 3	*Otarion* sp.	3
Brongniartella sp.	3, 4, 5	*Parabasilicus powisi* (Salter)	1, 2, 3
Calyptaulax sp.	4	*Pharostoma* sp.	5
Chasmops cambrensis (Whittington)	3, 4, 5	*Proetidella* sp.	2, 3
Conolichas sp.	3, 4		
Estoniops alifrons (M'Coy)	5		

GASTROPODA

Bellerophontid gen. et sp. indet.	2, 3	*Kokenospira* sp.	1, 2
Bucania sp.	3	*Lophospira* spp.	1, 2, 3, 4, 5
Bucaniopsia sp.	1, 2	*Murchisonia* sp.	2
Clathrospira sp.	1, 2, 3	? *Seelya* sp.	2
Cyclonema crebristria (M'Coy)	1, 2	*Sinuites soudleyensis* (Reed)	1, 2
Cyrtolites sp.	1, 2, 3	*Sinuites* spp.	1, 2, 3, 4, 5

TABLE 2 (*cont.*):

BIVALVIA

Ambonychia sp.	2	*Modiolopsis modiolaris* (Conrad)	1, 2
? *Arca* sp.	3	Modiomorphid gen. et sp. indet.	1, 2
Colpomya sp.	2	? *Psilonychia* sp.	2
Ctenodonta sp.	3	Pterineid gen. et sp. indet.	2
Cyrtodontid gen. et sp. indet.	1, 2	*Vlasta* sp.	2
Goniophorina sp.	2		

OTHERS

Cystoid plates	1, 2	*Pyritonema* sp.	3
Crinoid ossicles	1, 2, 3, 4, 5	*Stenopora* sp.	1, 2, 3, 4, 5
Favosites sp.	3	Stick bryozoa indet.	1, 2, 3, 4, 5
Monticulipora sp.	1, 2, 3, 4, 5	*Tallinnella scripta* (Harper)	1, 2, 3
Orthoceras sp.	1, 2, 3	*Tentaculites* sp.	3, 4, 5

1 = Lower Soudleyan
2 = Middle and upper Soudleyan
3 = Lower Longvillian Cwm Rhiwarth Siltstones
4 = Lower Longvillian Pen-y-Garnedd Limestone
5 = Upper Longvillian Pen-y-Garnedd Limestone

Our experience from a study of the 403 samples from the south Berwyns was that certain genera commonly occurred together forming recurrent associations and also that particular genera numerically dominated certain associations. Consequently our definition of the communities has attempted to take account of both the association of taxa and their abundance. Q-mode and R-mode cluster analysis could have produced results which were reproducible but could not handle taxa association and abundance at the same time (MacDonald 1975) and we are not convinced that the statistically defined clusters would have been more meaningful than our intuitively clustered groups. We were influenced in our decisions as to which taxa should be included in a particular community in the south Berwyns by our parallel studies in Shropshire and Snowdonia, where coarse sandstone lithofacies are better differentiated and contain more discrete brachiopod associations.

We have defined each community by the presence of certain characteristic genera which must form a greater percentage of an assemblage than elements from any single other community. Most assemblages in the south Berwyns could be assigned to a community on this basis though there are a small number of assemblages composed of ubiquitous genera which cannot be rigorously assigned.

Wherever possible the material was identified to species level and a faunal list is given in Table 2. We failed to recognize any species of the same genus which showed different ecological preferences and therefore believe that there is little loss of information in describing the communities at generic rather than specific level. This procedure has avoided the cumbersome formulation of many communities which have essentially the same structure and composition.

The communities which we recognize commonly show a moderately good correlation with a particular substrate. This is hardly surprising as the majority of taxa in this study are benthic and therefore the substrate is a variable with potentially powerful ecological effects. Not only is substrate readily observable, but it also reflects

TABLE 3. Composition of the *Howellites* community in the south Berwyn Hills

Included here are all assemblages in which *Howellites*, *Sowerbyella*, and *Paracraniops* form a greater percentage of the assemblage than elements from any single other community. The column headed 'characteristic community' adopts the general model proposed by Johnson (1972) to indicate the types of genera present in the particular community. Thus C = a characteristic genus, I = an intergrading genus, and U = an ubiquitous genus. For the intergrading genera we have also indicated their characteristic community or sub-community where H = *Howellites* community, Da = *Dalmanella* community, N = *Nicolella* community, O = *Onniella* community, DD = *Dinorthis* community, *Dinorthis* sub-community, and DM = *Dinorthis* community, *Macrocoelia* sub-community. Thus, for example, IDa and IN we regard as intergrading genera from the *Dalmanella* and *Nicolella* communities respectively. Column A represents a presence percentage where the number of collections in which a genus occurs is divided by the total number of collections of a particular community (× 100) and is therefore a measure of how widespread a particular genus is. Thus, for example, *Howellites* occurs in 95·8% of all collections assigned to this community (229 out of 239). Column B represents the average percentage abundance of an individual genus in those collections of a community where the particular genus is present, thus indicating its average percentage of occurrence. Therefore, employing the same example, *Howellites* occurs in 95·8% of all collections and in these collections occurs with an average abundance of 47·2%. Column C represents the average percentage occurrence of each genus within all the collections allocated to the community. Thus, out of a total of 239 samples, *Howellites* has an average abundance of 45·2%.

Genera	Group (Superfamily or order)	Characteristic Community	A Presence %	B % Abundance	C Average %
Brachiopods					
1. *Howellites*	Enteletacea	C	95·8	47·19	45·21
2. *Sowerbyella*	Plectambonitacea	C–U	74·9	43·18	32·34
3. *Paracraniops*	Lingulacea	C	42·3	11·95	5·05
4. *Macrocoelia*	Strophomenacea	IDM	38·9	9·10	3·54
5. *Dinorthis*	Orthacea	IDD	36·4	9·86	3·59
6. *Reuschella*	Enteletacea	IDD	28·0	6·37	1·79
7. *Bicuspina*	Triplesiacea	IDa	8·8	3·68	0·32
8. *Onniella*	Enteletacea	IO	5·0	6·59	0·33
9. *Leptaena*	Strophomenacea	IDa	4·6	1·21	0·06
10. *Rostricellula*	Rhynchonellacea	IDM	3·8	3·44	0·13
11. *Dalmanella*	Enteletacea	IDa	2·9	13·35	0·39
12. *Heterorthis*	Enteletacea	IDD	2·5	13·98	0·35
13. *Lingula*	Lingulacea	U	2·1	1·55	0·01
14. *Kjaerina*	Strophomenacea	IDa	1·7	3·77	0·01
15. *Kiaeromena*	Strophomenacea	IDa	1·3	2·73	0·03
16. *Eoplectodonta*	Plectambonitacea	IN	0·8	1·77	0·02
17. *Dolerorthis*	Orthacea	IN	0·8	7·34	0·06
18. *Oxoplecia*	Triplesiacea	IDa	0·4	1·21	0·01
19. *Sericoidea*	Plectambonitacea	IO	0·4	0·72	0·01
Trilobites					
20. *Broeggerolithus*	Trinucleina	U	64·7	1·02	0·66
21. *Brongniartella*	Calymenina	C	38·9	0·65	0·25
22. *Parabasilicus*	Asaphacea	C	23·0	0·70	0·16
23. *Flexicalymene*	Calymenina	IDa	6·3	0·31	0·02
24. *Illaenus*	Illaenina	?	0·4	0·21	0·01

Genera	Group (Superfamily or order)	Characteristic Community	A Presence %	B % Abundance	C Average %
Gastropods					
25. *Cyclonema*	Platyceratacea	C	13·0	4·26	0·58
26. *Cyrtolites*	Bellerophontacea	IDa	2·1	3·04	0·24
27. ? *Seelya*	Murchisoniacea	C	2·1	1·65	0·08
28. *Sinuites*	Bellerophontacea	C?	0·4	0·24	0·04
29. *Bucaniopsis*	Bellerophontacea	C?	0·4	0·22	0·04
Bivalves					
30. *Modiolopsis*	Modiomorphacea	C	13·8	2·56	0·45
31. *Goniophorina*	Modiomorphacea	C	2·9	0·21	0·14
32. *Arca*	Arcacea	C	2·1	0·23	0·14
33. *Psilonychia*	Ambonychacea	C	2·1	0·18	0·10
34. *Vlasta*	Praecardiacea	C?	0·8	0·14	0·09
Others					
35. *Tallinnella*	Ostracode	U	30·5	7·46	2·28
36. Crinoids	—	U	45·6	4·02	1·83
37. Bryozoa	—	U	13·4	4·60	0·62
38. *Tentaculites*	Cricoconarid	IDa	1·7	2·15	0·04
39. *Orthoceras*	Nautiloid	U	1·7	2·57	0·04

Ichnofauna includes *Skolithos*, *Planolites*, *Teichichnus*, ? *Gyrochorte*, ? *Palaeophycus*, *Monomorphichnus*, *Dimorphichnus*, and *Cruziana*.

Number of collections—239 (Cwm Rhiwarth Siltstones, locality details in SUP 14011).
Relationship to substrate—mudstone 21, silty mudstone 27, muddy siltstone 69, siltstone 72, fine sandstone 40.
Brachiopod diversity—3·6.
Total diversity—6·1.

other factors such as aeration, stability, degree of consolidation, and organic matter (Fürsich 1976). Indeed, the importance of substrate in influencing the distribution of organisms or communities has been demonstrated by workers in both Recent (e.g. Petersen 1911, 1913; Craig and Jones 1966; Driscoll 1967; Johnson 1971) and ancient (e.g. Wobber 1968; Fürsich 1976) examples. However, substrate does not appear to have been the only factor in the community distribution and we therefore discuss other likely limiting environmental parameters for each community.

The Howellites *community*

The *Howellites* community is characterized by the brachiopod genera *Howellites*, *Sowerbyella*, and *Paracraniops*, which all appear to have been ecologically tolerant genera as they also occur within all the other communities described here but with a lower abundance. Commonly occurring trilobites include the ubiquitous *Broeggerolithus*, *Brongniartella*, and *Parabasilicus*. Other characteristic taxa include the gastropods *Cyclonema*, *Sinuites*, *Bucaniopsis*, and ?*Seelya*, and the bivalves *Modiolopsis*, *Goniophorina*, *Vlasta*, ?*Arca*, and *Psilonychia*. Apart from *Cyclonema* and *Modiolopsis*, however, these taxa always occur in a low number of collections and with low abundance. The community must also have possessed an important polychaete and oligochaete annelid element as ichnofaunas produced by these taxa, particularly *Skolithos*, *Planolites*, and *Teichichnus*, are also characteristic and occur with moderate to high frequency of abundance (Pickerill 1977). Other elements found in associations referred to the *Howellites* community are considered to be taxa from adjacent coexisting communities. Thus, *Macrocoelia*, *Reuschella*, *Dinorthis*, *Bicuspina*, *Dalmanella*, *Leptaena*, *Rostricellula*, *Heterorthis*, *Kjaerina*, *Kiaeromena*, and *Flexicalymene* intergrade from the more sandy substrates associated with the *Dinorthis* and *Dalmanella* communities, *Eoplectodonta* and *Nicolella* intergrade from the more silty substrates associated with the *Nicolella* community, and *Onniella* and *Sericoidea* intergrade from more muddy substrates. Such intergrading taxa, apart from *Macrocoelia*, *Reuschella*, and *Dinorthis*, are found in only occasional assemblages and usually with a low abundance (Table 3).

The community was widespread on silty mud and muddy silt substrates in the Soudleyan throughout both the north and south Berwyn Hills, and was also common in the lower Longvillian when similar substrates and environmental conditions prevailed. The community was also present in the Bala district and east Snowdonia in rocks of similar age and facies, and appears to have been the most widespread community in the Anglo-Welsh area (Williams 1963). In Snowdonia, for example, it can be observed in muddy siltstones and similarly in the Arenig-Bala district, at Dolwyddelan and Betwys-y-Coed (e.g. Bryn Eithen SH 810518). In the south Berwyns good localities exist throughout the region and the community can be particularly well observed in rocks of Soudleyan age in Cwm Llech (SJ 016248) and lower Longvillian age in the Main Quarry on the southern slopes of Allt y Main (SJ 178157).

The *Howellites* community has a notably low diversity of characteristic shelly benthos and, in fact, most assemblages contain only three or four brachiopod genera and occasional additional taxa such as bivalves, gastropods, and trilobites. Apart from *Howellites*, *Sowerbyella*, and *Paracraniops* only the soft-bodied infaunal benthos appears to have been reasonably common, as both ichnofauna and general bioturbation are frequent. The sediments in which the *Howellites* community is most frequently found are bioturbated silty mudstones and muddy siltstones with thin, interbedded, parallel, cross-laminated, or rippled siltstones. The generally muddy silt or silty mud substrate appears to have been relatively soft with moderate cohesion which enabled the preservation of a varied ichnofauna and widespread bioturbation. Muddy substrates with moderate cohesion are usually related to relatively high sedimentation rates and such conditions are indicated for the Soudleyan which is represented by a large thickness (300–400 m) of muddy sediments. The facies association, sedimentary structures, and ichnofaunas all suggest a generally low energy, shallow subtidal environment of less than 25 m water depth (Pickerill 1977; Brenchley, in press). A rather quiet environment is also suggested by the presence of numerous articulated brachiopod shells and the preservation of many life clusters of *Howellites*, in particular, *Sowerbyella* and *Paracraniops*.

The Dinorthis *community*

The characteristic brachiopods of the *Dinorthis* community in the south Berwyns are *Dinorthis*, *Heterorthis*, *Reuschella*, *Macrocoelia*, and *Rostricellula*. Intergrading brachiopod genera include *Howellites*, *Sowerbyella*, and *Paracraniops* from the muddy silt related *Howellites* community, and *Bicuspina*, *Kiaeromena*, *Leptaena*, and *Dalmanella* from the *Dalmanella* community (Table 4). The associated non-brachiopod fauna is typically quite sparse but does include occasional gastropods, such as *Cyrtolites*, *Lophospira*, and *Sinuites*; occasional bivalves, such as *Byssodesma* and *Psilonychia* and low numbers of trilobites which include the ubiquitous *Broeggerolithus*, in particular, and *Brongniartella*, *Parabasilicus*, and *Flexicalymene*. The associated ichnofauna is also quite rare apart from *Vermiforichnus*, which occurs in association with both *Macrocoelia* and *Heterorthis* (Pickerill 1976), and occasional intergrading *Skolithos* and *Planolites*.

Within the *Dinorthis* community we recognize two sub-communities ('populations' in the sense of Bretsky (1970*b*)), which are characterized by a different balance in the abundance of the constituent genera and a different distribution in relation to substrate (Table 4). The *Dinorthis* sub-community is characterized particularly by *Dinorthis* together with variable proportions of *Heterorthis* and the common intergrading elements *Reuschella* and *Macrocoelia* and is particularly associated with coarse silt and fine to coarse sand substrates. The *Macrocoelia* sub-community is dominated by *Macrocoelia*, which often forms monospecific assemblages, but also typically contains *Reuschella* and *Rostricellula* and intergrading *Dinorthis* and *Heterorthis*. This latter sub-community is particularly associated with laminated fine sandstones. The following discussion will therefore be directed towards each of the sub-communities in turn.

1. Dinorthis *sub-community*. In the south Berwyns the *Dinorthis* sub-community is clearly defined only in the coarse volcaniclastic sandstones of the Swch Gorge Tuff. Elsewhere, on finer substrates, *Dinorthis* and *Heterorthis* are commonly associated, but often with intergrading elements from other communities, such as *Howellites*, *Reuschella*, and *Sowerbyella* (Table 4). Because of the limited development of a coarse sandstone facies in the south Berwyns it was not clear whether this was generally the preferred facies of the *Dinorthis* sub-community. We therefore examined comparable lithofacies in Snowdonia and south Shropshire. In Snowdonia at Llyn Cowlyd (SH 719615), for example, the sub-community contains abundant *Dinorthis* and subordinate *Macrocoelia* and occurs in coarse sandstones (the Soudleyan *Multiplicata* Sandstone of Diggens and Romano 1968). At Capel Curig (SH 709578) a similar association occurs in massively bedded tuffaceous sandstones. In the Costonian of Shropshire, *Dinorthis*-rich assemblages also containing *Heterorthis*, harknesselids, and *Salopia* as major elements occur in fine conglomerates and coarse sandstone facies of the Hoar Edge Grit (Table 5). The presence of a *Dinorthis* association in coarse lithofacies at all the above localities suggests to us a preference for a coarse substrate, but the presence of *Dinorthis* and *Heterorthis*, in particular, on finer substrates in the south Berwyns suggests that these genera were sufficiently eurytopic to colonize other environments.

In all those localities where coarse sandstones are present the assemblages occur as disarticulated valve on bedding planes or as dispersed and sometimes fragmented valves within massive coarse sandstones, which indicates that the assemblages were reworked. However, the similarity of taxonomic composition of the assemblages

TABLE 4. Composition of the *Dinorthis* community in the south Berwyn Hills. Included here are all assemblages in which *Dinorthis*, *Macrocoelia*, *Reuschella*, *Heterorthis*, and *Rostricellula* form a greater percentage of the assemblage than elements from any single other community. Legend as in Table 3.

Genera	Group (Superfamily or order)	Characteristic Community	A Presence %	B % Abundance	C Average %
A. DINORTHIS SUB-COMMUNITY					
Brachiopods					
1. *Heterorthis*	Enteletacea	C	80·9	65·47	52·96
2. *Howellites*	Enteletacea	IH	69·7	16·16	11·26
3. *Reuschella*	Enteletacea	IDM	56·1	7·99	4·40
4. *Dinorthis*	Orthacea	C	51·7	15·02	7·76
5. *Sowerbyella*	Plectambonitacea	IH–U	49·4	26·26	12·98
6. *Paracraniops*	Lingulacea	IH	34·8	11·60	4·04
7. *Macrocoelia*	Strophomenacea	IDM	10·1	10·73	1·08
8. *Lingula*	Lingulacea	U	5·6	0·89	0·05
9. *Bicuspina*	Triplesiacea	IDa	4·5	1·77	0·08
10. *Kiaeromena*	Strophomenacea	IDa	2·3	6·71	0·16
11. *Leptaena*	Strophomenacea	IDa	2·3	2·22	0·05
12. *Onniella*	Enteletacea	IO	2·3	2·04	0·06
13. *Dalmanella*	Enteletacea	IDa	1·1	9·00	0·10
14. *Oxoplecia*	Triplesiacea	IDa	1·1	1·96	0·02
Trilobites					
15. *Broeggerolithus*	Trinucleina	U	49·4	1·37	0·68
16. *Brongniartella*	Calymenina	IH	38·1	1·33	0·49
17. *Parabasilicus*	Asaphacea	IH	11·2	0·99	0·11
18. *Flexicalymene*	Calymenina	IDa	4·5	3·86	0·18
19. *Proetus*	Proetacea	?	1·1	0·66	0·01
Gastropods					
20. *Cyrtolites*	Bellerophontacea	IDa	3·4	4·06	0·14
21. *Lophospira*	Pleurotomaracea	IDa	3·4	4·06	0·14
Bivalves					
22. *Byssodesma*	Modiomorphacea	IDa	1·1	1·04	0·04
23. Pteriaceid indet.		?	1·1	0·90	0·01
Others					
24. Crinoids	—	U	66·3	1·46	0·97
25. *Tallinella*	Ostracode	U	27·0	7·15	1·93
26. *Bryozoa*	—	U	10·1	2·82	0·29
27. *Orthoceras*	Orthocone nautiloid	U	3·4	1·01	0·03

Ichnofauna includes *Vermiforichnus* and occasional intergrading *Skolithos* and *Planolites*.

Number of collections—89 (Cwm Rhiwarth Siltstones, locality details in SUP 14011).
Relationship to substrate—muddy siltstone 10, coarse siltstone 52, fine sandstone 27.
Brachiopod diversity—3·0.
Total diversity—5·0.

Genera	Group (Superfamily or order)	Characteristic Community	A Presence %	B % Abundance	C Average %
B. MACROCOELIA SUB-COMMUNITY					
Brachiopods					
1. *Macrocoelia*	Strophomenacea	C	100·0	39·52	39·52
2. *Howellites*	Enteletacea	IH	63·2	26·62	16·85
3. *Reuschella*	Enteletacea	C	57·9	7·52	4·35
4. *Bicuspina*	Triplesiacea	IDa	57·9	5·49	3·18
5. *Paracraniops*	Lingulacea	IH	47·4	11·75	5·57
6. *Sowerbyella*	Plectambonitacea	IH–U	26·3	36·73	9·67
7. *Strophomena*	Strophomenacea	C?	26·3	2·48	0·66
8. *Leptaena*	Strophomenacea	IDa	15·8	4·83	0·76
9. *Dalmanella*	Enteletacea	IDa	10·5	29·32	3·09
10. *Rostricellula*	Rhynchonellacea	C	10·5	10·85	1·14
11. *Onniella*	Enteletacea	IO	10·5	3·70	0·39
12. *Dinorthis*	Orthacea	IDD	10·5	3·45	0·36
13. *Kiaeromena*	Strophomenacea	IDa	10·5	2·02	0·21
14. *Eoplectodonta*	Plectambonitacea	IN	5·3	9·69	0·51
15. *Kjerulfina*	Strophomenacea	IDa	5·3	1·32	0·07
Trilobites					
16. *Broeggerolithus*	Trinucleina	U	68·4	1·55	1·06
17. *Brongniartella*	Calymenina	IH	42·1	0·76	0·35
18. *Parabasilicus*	Asaphacea	IH	26·3	0·47	0·12
19. *Flexicalymene*	Calymenina	IDa	5·3	0·35	0·02
Gastropods					
20. *Cyrtolites*	Bellerophontacea	IDa	10·5	6·25	0·66
21. *Lophospira*	Pleurotomaracea	IDa	10·5	6·25	0·66
22. *Sinuites*	Bellerophontacea	IDa	5·3	5·39	0·29
Bivalves					
23. *Psilonychia*	Ambonychacea	IH	15·8	13·78	2·18
24. Pteraceid indet.		?	5·3	10·00	0·53
Others					
25. Crinoids	—	U	89·5	12·01	10·75
26. Bryozoa	—	U	21·1	4·16	0·88
27. *Tallinnella*	Ostracode	U	15·8	5·26	0·83
28. *Orthoceras*	Orthocone nautiloid	U	5·3	1·48	0·08

Ichnofauna includes *Vermiforichnus* and occasional intergrading *Planolites*.

Number of collections—19 (Cwm Rhiwarth Siltstones, locality details in SUP 14011).
Relationship to substrate—mudstone 0, coarse siltstone 10, laminated fine sandstone 9.
Brachiopod diversity—3·9.
Total diversity—7·5.

TABLE 5. Composition of the *Dinorthis* association in south Shropshire. Included here are all assemblages in which *Dinorthis*, *Harknessella*, *Heterorthis*, and *Salopia* form a greater percentage of the assemblage than elements from any single other community. Legend as in Table 3.

Genera	Group (Superfamily or order)	Characteristic Community	A Presence %	B % Abundance	C Average %
Brachiopods					
1. *Dinorthis flabellulum*	Orthacea	C	100·0	28·8	28·8
2. *Heterorthis patera*	Enteletacea	C	100·0	25·3	25·3
3. *Harknessella vespertilio*	Enteletacea	?C	100·0	19·0	19·0
4. *Salopia salteri*	Enteletacea	C	50·0	8·7	4·5
5. *Dolerorthis* sp.	Orthacea	IN	33·3	8·8	2·9
6. *Leptaena* sp.	Strophomenacea	IDa	33·3	3·3	1·6
7. *Dalmanella* sp.	Enteletacea	IDa	16·7	27·0	4·5
8. *Rafinesquina* cf. *complanata*	Strophomenacea	IDM	16·7	18·0	3·3
9. *Oxoplecia* sp.	Triplesiacea	IDa	16·7	4·0	0·7
10. *Platystrophia* sp.	Orthacea	IN	16·7	2·5	0·4
11. *Howellites* sp.	Enteletacea	IN	16·7	1·3	0·2
Trilobites					
12. *Flexicalymene* cf. *acantha*	Calymenina	IDa	16·7	2·5	0·4
13. *Costonia ultima*	Trinucleina	U	16·7	1·2	0·2
Others					
14. Bryozoa	—	U	50·0	10·7	5·8
15. *Solenopora*	Solenoporaceae	?	16·7	15·0	2·5
16. Crinoids	—	U		indet.	

Ichnofauna includes rare intergrading *Skolithos* and occasional *Planolites*.

Number of collections—6 (Hoar Edge Grit).
Relationship to substrate—coarse sandstone 6.
Brachiopod diversity—4·7.
Total diversity—5·8.

suggests that in spite of some transport the assemblages reflect original benthic associations.

The epiclastic volcaniclastic sandstones of the Swch Gorge Tuff were deposited in extremely shallow-water, sublittoral, well-oxygenated conditions, as laterally they pass rapidly northwards into a subaerially deposited ignimbritic facies. In the Costonian of Shropshire the coarse sediments are commonly massive or have large-scale cross-stratification and lie immediately above the unconformity between the basal Costonian and the Precambrian (see Greig *et al.* 1968). They are frequently poorly sorted and appear to represent sand sheets deposited rather rapidly during the basal Caradoc transgression across the irregular Precambrian surface. We regard these sediments as an extremely shallow sublittoral facies and probably formed in less than approximately 10 m water depth.

The nature of the coarse substrates indicates that there must have been high-energy conditions. Sedimentation rates must have been high for any single unit, as indicated by the internal bedforms and the general absence of bioturbation and ichnofauna. Turbidity must have been negligible, as indicated by the 'clean' nature of individual sandstone units and we therefore infer that the *Dinorthis* sub-community was best developed on shifting, coarse sand substrates in high-energy, non-turbid, well-oxygenated environments of water depths of less than approximately 10 m.

2. Macrocoelia *sub-community*: In the south Berwyns the *Macrocoelia* sub-community is best developed in rocks of Lower Longvillian age, particularly on the slopes of Gallt yr Ancr (SJ 143125) and in Bryngwyn Quarry (SJ 182175), where it also includes several intergrading elements from adjacent communities. At these localities the coarse siltstones and laminated fine sandstones containing the *Macrocoelia* sub-community are interbedded with muddy siltstones and silty mudstones containing an associated *Howellites* community and with massively bedded fine sandstones containing an associated *Dalmanella* community. Typically, the sub-community has abundant *Macrocoelia*, common *Reuschella*, and relatively rare *Rostricellula* as characteristic elements but also contains a variable proportion of intergrading elements (Table 4).

In the south Berwyns the preferred substrate for the *Macrocoelia* sub-community was coarse silt and laminated fine sand. This is also the case where the sub-community is found in Snowdonia, Shropshire, and the Breidden Hills. For example, in Snowdonia at Capel Curig (SH 709578) *Macrocoelia*-dominated assemblages with occasional intergrading elements from the *Dalmanella* community are present in parallel laminated sandstones of lower Longvillian age. In the Breidden Hills virtually monospecific *Macrocoelia* assemblages are present in rocks of questionable age (? upper Costonian–lower Soudleyan) but of similar lithology, and in Shropshire the sub-community is also present in similar lithologies of Costonian age.

The preferred environment of the *Macrocoelia* sub-community is difficult to assess from sedimentary evidence, but its intimate association with the *Howellites* community suggests that it occupied a similar range of 25 m or less. Furthermore, the presence of the fossil-boring *Vermiforichnus* in association with *Macrocoelia* has been taken by Pickerill (1976) to indicate water depths of 25 m or less. Sedimentation rates for any single unit must have been at least moderately high, as indicated by the parallel laminated nature of the sandstones, the absence of ichnofaunas and general bioturbation, and the presence of the sub-community in reworked coquinite assemblages. As with the *Dinorthis* sub-community and for similar reasons turbidity must have been low. We therefore interpret the preferred environment of the *Macrocoelia* sub-community as having been reasonably similar to that of the *Dinorthis* sub-community, but regard it as having been slightly more off-shore, in deeper waters, and in slightly lower energy situations perhaps associated with more stable substrates.

The Dalmanella *community*

The characteristic elements of the *Dalmanella* community are the brachiopod genera *Dalmanella*, *Kjaerina*, *Bicuspina*, *Leptaena*, and to a lesser extent *Kiaeromena*; the trilobites *Flexicalymene*, *Kloucekia*, and possibly *Otarion*; the gastropods *Lophospira*, *Sinuites*, and *Murchisonia*, and the bivalves *Byssodesma* and *Colpomya*.

Though the majority of these genera occur in many of the collections assigned to the community they usually occur with a low or moderate frequency of abundance, and of the characteristic genera only *Dalmanella* appears to have been abundant. Ichnofaunas are also relatively common, though the majority appear to have been produced by trilobites, for example, *Rusophycus*, *Cruziana*, and *Trichophycus*, or bivalves, for example, *Lockeia*, and ichnofaunas produced by soft-bodied organisms are infrequent though they do include *Arenicolites* and intergrading *Skolithos* and *Planolites*. Other elements found in associations assigned to the *Dalmanella* community are considered to be intergrading elements from adjacent coexisting communities. Of these intergrading elements the brachiopod genera *Howellites* and *Sowerbyella* from the *Howellites* community are major components, occurring in the majority of associations and with a moderate frequency of abundance (Table 6). Similarly the ubiquitous

TABLE 6. Composition of the *Dalmanella* community in the south Berwyn Hills. Included here are all assemblages in which *Dalmanella, Bicuspina, Kjaerina, Kiaeromena, Kjerulfina*, or *Leptaena* form a greater percentage of the assemblage than elements from any single other community. Legend as in Table 3.

Genera	Group (Superfamily or order)	Characteristic Community	A Presence %	B % Abundance	C Average %
Brachiopods					
1. *Dalmanella*	Enteletacea	C	90·9	34·36	31·23
2. *Howellites*	Enteletacea	IH	88·6	30·06	26·64
3. *Sowerbyella*	Plectambonitacea	IH–U	79·6	20·27	16·13
4. *Kjaerina*	Strophomenacea	C	50·0	5·21	2·60
5. *Bicuspina*	Triplesiacea	C	45·5	7·04	3·20
6. *Leptaena*	Strophomenacea	C	40·9	1·71	0·70
7. *Kiaeromena*	Strophomenacea	C	36·4	2·42	0·88
8. *Macrocoelia*	Strophomenacea	IDM	29·6	8·99	2·65
9. *Dinorthis*	Orthacea	IDD	11·4	7·41	0·84
10. *Nicolella*	Orthacea	IN	11·4	6·90	0·78
11. *Dolerorthis*	Orthacea	IN	9·1	2·93	0·27
12. *Paracraniops*	Lingulacea	IH	6·8	1·69	0·11
13. *Strophomena*	Strophomenacea	C	6·8	0·43	0·03
14. *Oxoplecia*	Triplesiacea	C	4·6	2·12	0·10
15. *Skenidioides*	Orthacea	IN	4·6	2·30	0·09
16. *Kjerulfina*	Strophomenacea	C	4·6	1·89	0·09
17. *Lingula*	Lingulacea	U	4·6	0·61	0·01
18. *Rostricellula*	Rhynchonellacea	IDM	2·3	2·95	0·07
19. Strophomenid indet.		?	2·3	0·37	0·01
Trilobites					
20. *Broeggerolithus*	Trinucleina	E	93·2	0·85	0·79
21. *Flexicalymene*	Calymenina	C	70·5	0·56	0·40
22. *Kloucekia*	Dalmanitacea	C	50·0	0·46	0·23
23. *Parabasilicus*	Asaphacea	IH	50·0	0·33	0·16
24. *Brongniartella*	Calymenina	IH	29·6	0·15	0·05
25. *Conolichas*	Lichidacea	IN	2·3	0·05	0·01
26. *Chasmops*	Dalmanitacea	IN	2·3	0·05	0·01
27. *Otarion*	Proetacea	C?	2·3	0·05	0·01

Genera	Group (Superfamily or order)	Characteristic Community	A Presence %	B % Abundance	C Average %
Gastropods					
28. *Lophospira*	Pleurotomaracea	C	40·9	5·48	2·24
29. *Sinuites*	Bellerophontacea	C	36·4	4·03	1·46
30. *Murchisonia*	Murchisoniacea	C	29·6	2·66	0·78
31. *Cyrtolites*	Bellerophontacea	C	29·6	1·85	0·55
32. *Cyclonema*	Platyceratacea	IH	2·3	6·85	0·16
33. Bellerophontacean indet.		?	2·3	3·0	0·07
Bivalves					
34. *Byssodesma*	Modiomorphacea	C	9·1	1·89	0·17
35. *Colpomya*	Modiomorphacea	C	2·3	3·42	0·08
36. Pteriacean indet.		?	2·3	2·10	0·05
37. Modiomorphacean indet.		?	2·3	1·30	0·02
Others					
38. Bryozoa	—	U	56·8	10·03	5·70
39. *Tallinnella*	Ostracode	U	47·7	2·59	1·24
40. Crinoids	—	U	36·4	0·63	0·23
41. *Tentaculites*	Cricoconarid	C	22·8	1·40	0·32
42. *Orthoceras*	Orthocone nautiloid	U	15·9	0·60	0·10
43. *Favosites*	Tabulate coral	?	2·3	0·43	0·01

Trace fossils include *Arenicolites, Lockeia, Trichophycus, Rusophycus, Cruziana* and intergrading *Skolithos* and *Planolites*.

Number of collections—44 (Cwm Rhiwarth Siltstones, locality details in SUP 14011).
Relationship to substrate—mudstone 0, coarse siltstone 5, fine sandstone 39.
Brachiopod diversity—5·1.
Total diversity—10·7.

trilobite *Broeggerolithus* occurs in most assemblages but usually with a low frequency of abundance. Other intergrading elements characteristically occur in only a few collections and with a low frequency of abundance. These include the brachiopods *Macrocoelia*, *Dinorthis*, *Strophomena*, and *Rostricellula* from the *Dinorthis* community, and *Nicolella* and *Dolerorthis* from the *Nicolella* community, and the trilobite genera *Parabasilicus* and *Brongniartella* from the *Howellites* community and *Deacybele*, *Platylichas*, and *Chasmops* from the *Nicolella* community. Finally, the *Dalmanella* community frequently contains bryozoa which appear to have been moderately abundant, ostracodes and crinoids (Table 6).

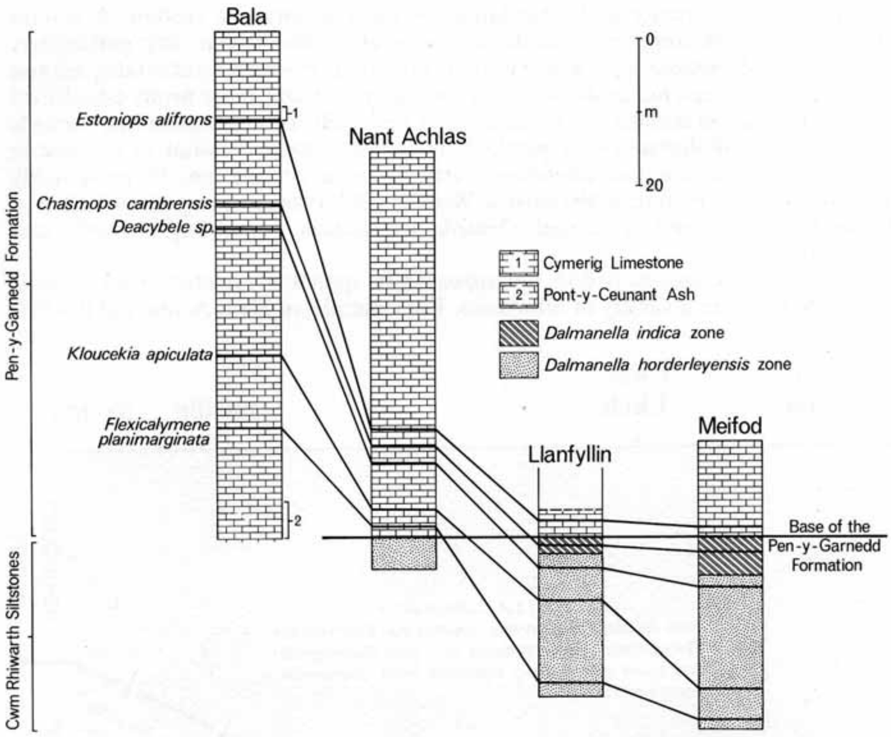
In the south Berwyns the preferred substrate for the *Dalmanella* community was fine sandstones or sometimes coarse siltstones (Table 6). A similar substrate preference can be observed in other areas. For example, in Snowdonia at Capel Curig (SH 709578) and Betwys-y-Coed (SH 810518), it can be observed in similar lithologies of lower Longvillian age. In the south Berwyns the fine sandstones may be massive, cross-stratified, or more occasionally exhibit small scale cross-lamination. The community here is developed particularly in rocks of lower Longvillian age and good localities exist in the south-east Berwyns where such sandstones have been extensively quarried. Thus, on the south-eastern facing slopes of Allt y Main quarries such as the Main Quarry (SJ 178157), Glascoed Quarry (SJ 142122), and the Bron-y-main Quarries (SJ 167145) all illustrate the typical *Dalmanella* community. At these localities, as elsewhere in the south Berwyns and Snowdonia, the sandstone facies are invariably interbedded with muddy siltstones and silty mudstones, which characteristically contain an associated *Howellites* community and also are commonly associated with thick laminated fine sandstones containing the *Macrocoelia* sub-community of the *Dinorthis* community.

Unfortunately there are no diagnostic environmental indicators of the precise environmental position of the *Dalmanella* community. However, as it is frequently associated with both the *Howellites* and *Dinorthis* (*Macrocoelia* sub-community) communities it would be imprudent to infer a substantial difference in depth. Consequently, we believe that the community lived in water depths of 25 m or less. Where the community is best developed in the south Berwyns the lower Longvillian sediments are at maximum just over 20 m in thickness, and we therefore infer that accumulation rates were relatively slow, probably being related to reduced rates of intrabasinal subsidence (Brenchley 1969). However, the presence of cross-stratification and parallel lamination indicates that sedimentation rates for individual sandstone units must have been relatively high and we therefore infer that sedimentation rate and substrate mobility may have been significantly related to this community.

The Nicolella *community*

The characteristic brachiopod genera of the *Nicolella* community are *Nicolella*, *Dolerorthis*, *Eoplectodonta*, *Platystrophia*, *Skenidioides*, and *Leptestiina*. These genera are present in the majority of collections and commonly occur with moderate to high frequency of abundance (Table 7). Additional characteristic brachiopod genera forming part of the community but only occurring in a few assemblages and usually with a low or moderate abundance are *Cremnorthis*, *Rhactorthis*, *Vellamo*, *Obolus*, and *Lingulasma*. It is notable that these latter genera are entirely restricted to the *Nicolella* community. Characteristic trilobites include *Conolichas*, *Deacybele*, *Calyptaulax*, *Chasmops*, and *Estoniops*, which though present in several assemblages are not necessarily abundant. Other taxa found in assemblages designated to the *Nicolella* community are considered to be intergrading elements from adjacent coexisting communities. These elements include the brachiopod genera *Sowerbyella*, *Bicuspina*, *Dalmanella*, *Kiaeromena*, *Reuschella*, *Rostricellula*, *Howellites*, *Paracraniops*, *Lingulella*, *Kjaerina*, *Strophomena*, and *Onniella*; the trilobites *Flexicalymene*, *Broeggerolithus*, *Brongniartella*, *Parabasilicus*, and *Kloucekia*; the gastropods *Sinuites* and *Lophospira*, and the ichnofauna *Skolithos* and *Planolites* (Table 7). These intergrading taxa are normally found in only a few assemblages and characteristically exhibit a low frequency of abundance. Finally, the community frequently contains indeterminate bryozoan and crinoidal debris.

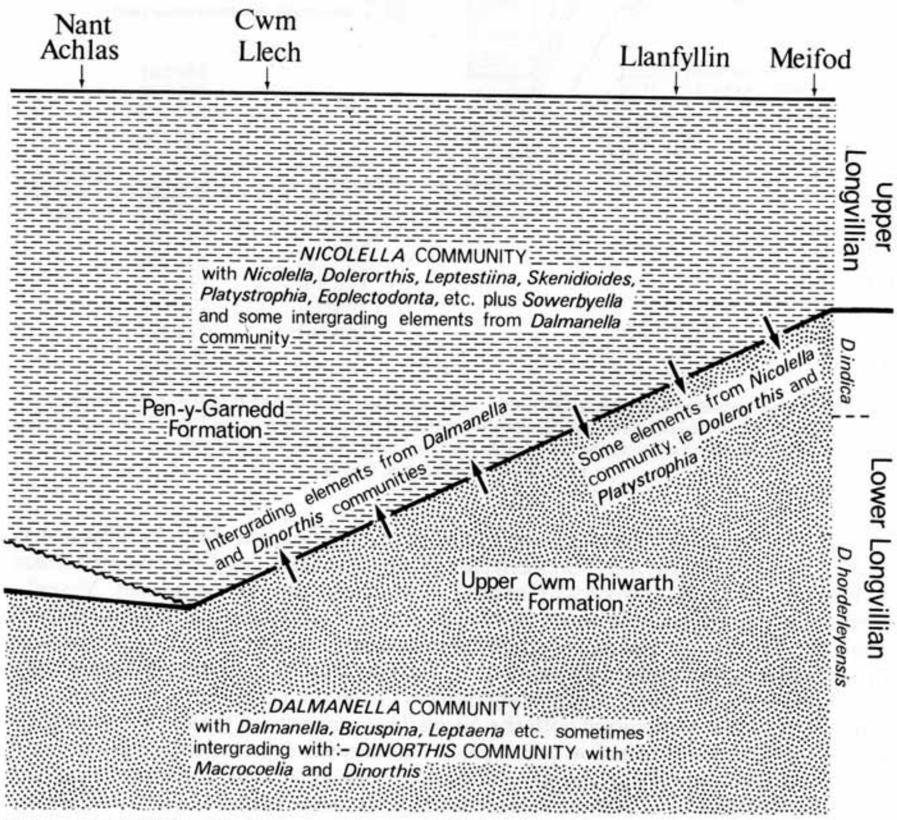
Williams (1963) noted that the *Nicolella* 'association' was of lower Longvillian age in the Bala district and Marshbrookian–Actonian in Shropshire. In the south Berwyns there is evidence to suggest that the Pen-y-Garnedd Formation and its associated



TEXT-FIG. 5. Diachronism of the Pen-y-Garnedd Formation from the north-west to the south-east Berwyns based on the first recorded occurrence of listed trilobite species. Rocks similar to the Pen-y-Garnedd Formation in the Bala area are known as the Gelli Grin Calcareous Ashes, and the distribution of the trilobites is recorded in Bassett *et al.* (1966).

Nicolella community is diachronous within the Longvillian (text-fig. 5). Thus, early in the Longvillian in the north-western part of the south Berwyns, for example at Nant Achlas (SJ 014267), the Pen-y-Garnedd Formation and its associated *Nicolella* community passes laterally south-eastwards into fine sandstones of the Upper Cwm Rhiwarth Formation and its associated *Dalmanella* community, with the result that the *Nicolella* community was 'diluted' by intergrading taxa of this adjacent community (text-fig. 6). Thus, intergrading elements from the *Dalmanella* community are typically found in association with the *Nicolella* community in the lower horizons of the Pen-y-Garnedd Formation and include *Dalmanella*, *Leptaena*, *Kjaerina*, *Kiaeromena*, and *Bicuspina*. Progressively during the Longvillian, calcareous sediments of the Pen-y-Garnedd Formation became more widespread and the *Dalmanella* community was excluded from the area, with the result that the *Nicolella* community *sensu stricto* became firmly established and intergrading elements decreased in both frequency of occurrence and abundance vertically in any one section. A similar pattern exists with components of the coexisting *Howellites* community, particularly *Howellites* and *Paracraniops*, which initially intergrade from adjacent muddy silt and silty mud substrates, but as the *Nicolella* community became more firmly established this intergradation became less pronounced. Conversely, components of the *Onniella* association of Williams (1973), particularly *Onniella* itself, is found to increase in frequency of occurrence and abundance vertically in any one section, this presumably reflecting or 'anticipating' in the sense of Worsley (1971) the incoming of muds (Pen-y-Garnedd Shale) with a related *Onniella* association containing *Onniella* and *Sericoidea*.

The *Nicolella* community does not appear to be specifically related to substrate as it may be found in a variety of lithofacies. For example, in Nant Achlas (SJ 014267)



TEXT-FIG. 6. Vertical and lateral community and facies relationships at the top of the Cwm Rhiwarth Siltstones and base of the Pen-y-Garnedd Formation.

it is associated both with sandy wackite conglomerates and bedded calcareous siltstones; in the south-eastern Berwyns, on the southern slopes of Allt Fawr (SJ 147138), it is associated with metre-thick massively bedded siltstones, and in the Main Quarry (SJ 178157) it is associated with bedded muddy siltstones and fine sandstones. With the exception of the latter locality the sediments are generally calcareous owing to a variable bioclastic component.

The general absence of sedimentary structures, the virtually complete bioturbation of the sediment, and the increased accumulation of fine bioclastic debris suggests that sedimentation rates were relatively slow. Energy conditions were likely to have been variable from time to time, as reflected by the variation in lithology. However, though high-energy conditions briefly moved coarse sediment, the rocks usually consist of coarse silt mixed with poorly sorted bioclastic debris and a low-energy situation must generally have prevailed. The most common substrates associated with the *Nicolella* community appear to have been silt and fine sand (Table 7) and this suggests that the community colonized an environment similar to the *Dalmanella* community. However, the lower rates of sedimentation and lower-energy conditions suggest that the community occupied a slightly more off-shore position. The depth parameter cannot be accurately assessed but it is unlikely to have greatly exceeded the 25 m suggested previously for the *Dalmanella* community.

Diversity of the *Nicolella* community is moderate to high, which presumably reflects low environmental stress typically associated with more off-shore environments (Bretsky and Lorenz 1970) and the increasing stability and predictability of the environment (Slobodkin and Sanders 1969).

Summary of communities. Though the four communities which we recognize in the Caradoc of the south Berwyn Hills all show some correlation with substrate (Tables 3–7) we do not consider this to have been the only limiting environmental factor. Despite the fact that it is difficult to assign an absolute depth of habitation to any of the defined communities, all four probably existed within a relatively narrow depth range (0–?30 m) and we do not recognize, for example, the distinctive depth zonation commonly described in the Silurian (Ziegler 1965; Ziegler *et al.* 1968; Calef and Hancock 1974). There does, however, appear to be a broad correlation with depth and, perhaps more importantly, distance from shore. Thus, with increasing distance from shore we find the *Dinorthis* community, the *Howellites* and *Dalmanella* communities, and the *Nicolella* community. The more in-shore communities were affected by a relatively higher sedimentation rate which is reflected in their lower diversities. The two most off-shore communities, the *Dalmanella* and *Nicolella* communities, occupied more stable environments and exhibit slightly higher diversities (cf. Bretsky and Lorenz 1970).

There is an approximate correlation between distance from shore and turbulence and we find the *Dinorthis* community related to higher-energy environments, and the *Howellites* and *Nicolella* communities to quieter regimes, with the *Dalmanella* community in an intermediate situation. It should be noted, however, that both the higher diversity *Nicolella* community and the lower diversity *Howellites* community occupied environments of similar low energy so that at least in these cases turbulence does not appear to have been a limiting factor in community distribution.

TABLE 7. Composition of the *Nicolella* community in the south Berwyn Hills. Included here are all assemblages in which *Nicolella*, *Eoplectodonta*, *Platystrophia*, *Skenidioides*, *Leptestiina*, and *Dolerorthis* form a greater percentage of the assemblage than elements from any other community. Legend as in Table 3.

Genera	Group (Superfamily or order)	Characteristic Community	A Presence %	B % Abundance	C Average %
Brachiopods					
1. *Nicolella*	Orthacea	C	95·0	36·05	34·25
2. *Dolerorthis*	Orthacea	C	85·0	24·24	20·60
3. *Platystrophia*	Orthacea	C	80·0	19·43	15·54
4. *Skenidioides*	Orthacea	C	60·0	15·06	9·04
5. *Leptestiina*	Plectambonitacea	C	55·0	10·39	5·71
6. *Eoplectodonta*	Plectambonitacea	C	50·0	8·82	4·41
7. *Howellites*	Enteletacea	IH	45·0	6·43	2·89
8. *Sowerbyella*	Plectambonitacea	IH–U	40·0	8·46	3·38
9. *Cremnorthis*	Orthacea	C	25·0	2·65	0·66
10. *Vellamo*	Clitambonitacea	C	20·0	1·67	0·33
11. *Leptaena*	Strophomenacea	IDa	20·0	2·20	0·44
12. *Bicuspina*	Triplesiacea	IDa	20·0	2·86	0·57
13. *Rhactorthis*	Orthacea	C	15·0	2·49	0·37
14. *Kiaeromena*	Strophomenacea	IDa	15·0	1·87	0·28
15. *Strophomena*	Strophomenacea	IDM	15·0	1·24	0·19
16. *Lingulasma*	Lingulacea	C	15·0	4·33	0·65
17. *Dinorthis*	Orthacea	IDD	10·0	2·01	0·20
18. *Reuschella*	Enteletacea	IDM	10·0	0·94	0·09
19. *Rostricellula*	Rhynchonellacea	IDM	10·0	1·13	0·11
20. *Obolus*	Lingulacea	C?	10·0	1·07	0·10
21. *Kjaerina*	Strophomenacea	IDa	10·0	1·64	0·17
22. *Onniella*	Enteletacea	IO	10·0	3·43	0·34
23. *Paracraniops*	Lingulacea	IH	5·0	2·62	0·13
24. *Lingulella*	Lingulacea	U	5·0	1·83	0·09
25. Strophomenid indet.			5·0	0·89	0·04
26. Plectambonitid indet.			5·0	0·86	0·04
27. Clitambonitid indet.			5·0	0·88	0·04
Trilobites					
28. *Chasmops*	Dalmanitacea	C	55·0	1·82	1·00
29. *Estoniops*	Dalmanitacea	C	50·0	1·01	0·50
30. *Conolichas*	Lichidacea	C	45·0	1·05	0·47
31. *Deacybele*	Cheirurina	C	35·0	0·48	0·19
32. *Flexicalymene*	Calymenina	IDa	35·0	1·26	0·50
33. *Broeggerolithus*	Trinucleina	U	25·0	0·69	0·17
34. *Kloucekia*	Dalmanitacea	IDa	15·0	0·38	0·06
35. *Calyptaulax*	Dalmanitacea	C	10·0	0·16	0·02
36. *Brongniartella*	Calymenina	IH	10·0	0·25	0·03
37. *Parabasilicus*	Asaphacea	IH	5·0	0·23	0·01
Gastropods					
38. *Sinuites*	Bellerophontacea	IDa	15·0	1·62	0·24
39. *Lophospira*	Pleurotomaracea	IDa	15·0	1·68	0·25
Others					
40. Bryozoa	—	U	60·0	5·49	3·29
41. Crinoids	—	U	50·0	3·46	1·73
42. *Pyritonema*	Sponge spicules	?	5·0	0·20	0·01

Ichnofauna includes rare intergrading *Skolithos* and *Planolites*.

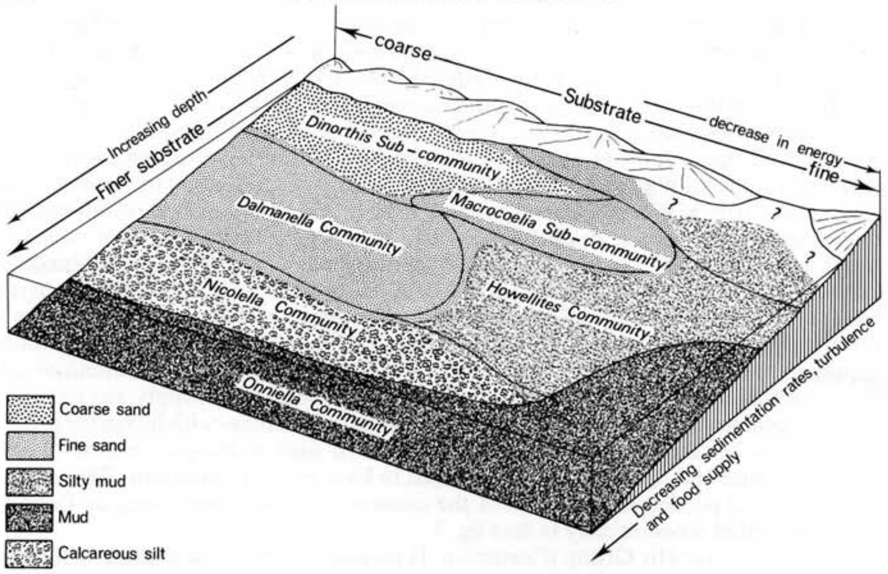
Number of collections—20 (Pen y Garnedd Formation, locality details in SUP 14011).
Relationship to substrate—wackite conglomerates 2, sandstone 1, fine sandstone 8, coarse siltstones 8, mudstones 1.
Brachiopod diversity—14·0.
Total diversity—19·0.

Other environmental factors which are commonly related to the distribution of marine organisms or communities, such as salinity and water temperature (Jones 1950; Berry and Boucot 1967) are considered to have been unimportant in determining the distribution of the Caradoc communities described here. There is no evidence of a near-by major land area, which implies that the marine region was not subject to fluviatile influences and was not one of restricted near-shore marine circulation, thus removing the possibility of local brackish or hypersaline conditions. In addition, the area is of such a restricted geographical extent that geographical variations in temperature are unlikely. Availability of food as a controlling environmental parameter in the distribution of benthic communities has been stressed by Marshall (1954), Calef and Hancock (1974), and Fürsich and Hurst (1974). Generally, increase in depth is accompanied by a decrease in organism density which reflects a decreased food supply. Unfortunately there is no positive evidence by which to assess food supply in the rocks described here, but we feel that because the communities all existed within a relatively narrow depth range, variation in food supply was unlikely to have been pronounced, though we assume that it did decrease with increased depth and distance off-shore. Other depth-related factors, such as oxygen content of the water, pressure and light, etc., are considered to have been unimportant. The salient environmental parameters for each of the communities are summarized in Table 8 and represented schematically in text-fig. 7.

Within the Nant Hir Group (Costonian–Harnagian) of the Bala district, Williams (1973) recognized, but unfortunately without giving details, a further community, the *Onniella* community, which he correlated with a mud substrate. In the Berwyn Hills there is a possibility that this community is present within the lower horizons of the Pen-y-Garnedd Shales (text-fig. 2), where *Onniella* is associated with *Sericoidea*, *Paterula*, and graptolites, but outcrop is limited and therefore sample numbers for this horizon are small and the significance of this association is therefore difficult to assess.

TABLE 8. Relationship between the Caradoc communities and interpreted environmental parameters.

Community	Diversity	Substrate	Sedimentation Rate	Energy	Distance from Shore	Depth
DINORTHIS (*Dinorthis* sub-community)	low 3·0 brachiopods 5·0 total	medium to coarse sand	high	high	nearshore	?0–10 m
DINORTHIS (*Macrocoelia* sub-community)	low–medium 3·9 brachiopods 7·5 total	fine sand	high	medium	nearshore moderate	25 m
DALMANELLA	medium 5·1 brachiopods 10·7 total	fine sand to coarse silt	low but variable	low but variable	moderate	25 m
HOWELLITES	low 3·6 brachiopods 6·1 total	muddy silt	high	low	moderate	25 m
NICOLELLA	high 14·0 brachiopods 19·0 total	variable calcareous silt or sand	low	low	offshore	?30 m



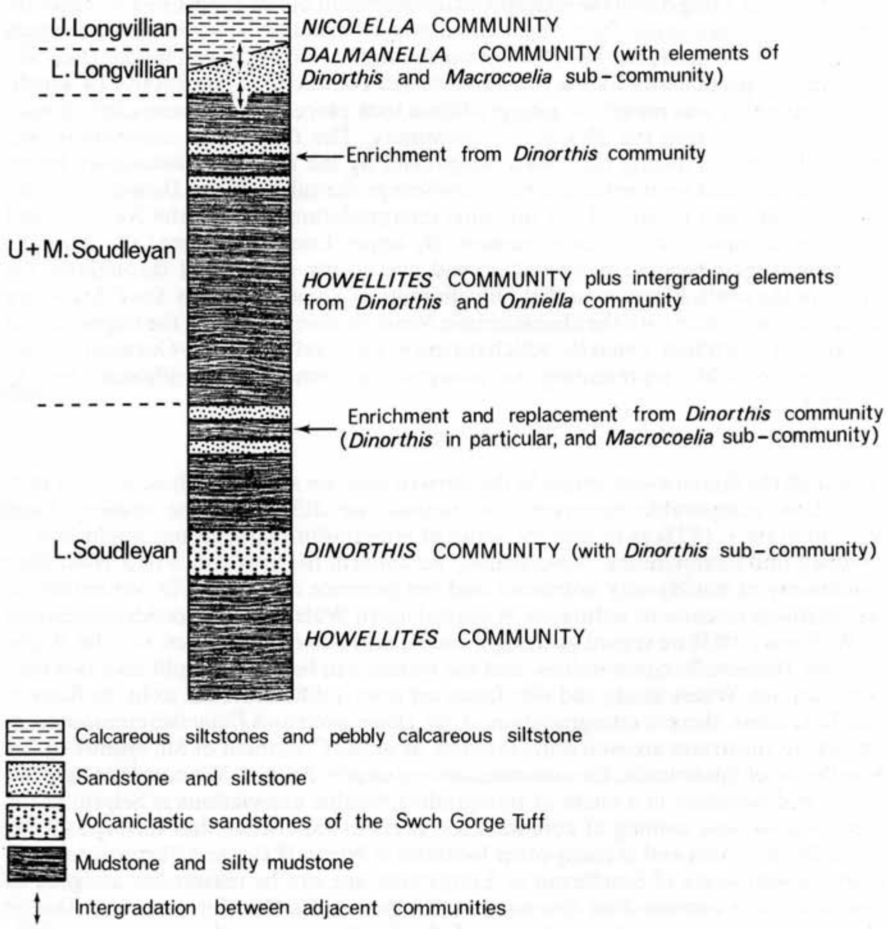
TEXT-FIG. 7. Schematic illustration of the relationship of the Caradoc communities and environmental parameters.

If, however, the associations observed in the Pen-y-Garnedd Shales are representative of the *Onniella* community, it is likely that the community was associated with a mud substrate accumulating under off-shore conditions in a very low-energy environment and with low rates of sedimentation. Lower in the Berwyn succession species of *Onniella* are found occasionally within the *Howellites* community (Table 3), and provisionally might be regarded as intergrading elements from the '*Onniella* community'.

STRATIGRAPHICAL DISTRIBUTION OF COMMUNITIES IN THE SOUTH BERWYNS

The above discussion of Caradoc communities is based essentially on Soudleyan to upper Longvillian assemblages from the south Berwyns. However, similar associations are found in the north Berwyns (Brenchley, in press) and we have found similar communities in Soudleyan and Longvillian rocks of Snowdonia. Communities with the same general composition occur in the Breidden Hills and Shropshire, in rocks ranging in age from Costonian to Longvillian but additional communities are almost certainly present, as for example in the Shelve area of Shropshire where Williams (1974) has described other faunal associations which he assigned (Williams 1976) to a broadly delineated *Bicuspina* Set. We conclude that some of the communities had a relatively stable composition at generic level throughout the lower part of the Caradoc of North Wales and Shropshire, though there were many examples of species replacement and some changes in generic composition (see Williams 1963).

In the south Berwyns the rocks of Soudleyan age characteristically contain the *Howellites* community, which was the indigenous community on muddy-silty substrates throughout this stage. Intergradation from adjacent co-existing communities occurred throughout the succession, particularly when there was intergradation of lithofacies. Thus, at the coarse end of the silt-grade spectrum intergradation took place with genera from the sand-related *Dinorthis* community or *Dalmanella* community. Occasionally, when environmental parameters were suitable, the indigenous *Howellites* community was replaced by the *Dinorthis* community (text-fig. 8). This



TEXT-FIG. 8. Generalized stratigraphical section for the south Berwyns showing the predominance of the *Howellites* community and the periodical invasions of elements from other communities, and finally the establishment of the more off-shore *Dalmanella* and *Nicolella* communities.

occurred when the near-shore volcaniclastic sandstones of the Swch Gorge Tuff were developed in the lower Soudleyan, when virtually monospecific *Dinorthis* assemblages predominated, and again when fine sandstone deposition prevailed throughout the area a short distance (40–50 m) above the tuff, when assemblages dominated by *Heterorthis* together with *Dinorthis* and *Reuschella* prevailed. Near the top of the upper Soudleyan the *Howellites* community was enriched by intergrading elements from both the *Dinorthis* community, such as *Dinorthis*, *Reuschella*, *Macrocoelia*, and *Rostricellula*, and from the *Dalmanella* community, such as *Leptaena* and *Kiaeromena*.

In the lower Longvillian the widespread development of fine sandstones was accompanied by an associated *Dalmanella* community. Periodically, when environmental conditions were amenable, the *Dalmanella* community was replaced by the *Dinorthis* community, particularly by the *Macrocoelia* sub-community. Irrespective of whichever community was prevalent, intergradation took place between these communities themselves and from the *Howellites* community. The *Dalmanella* community was replaced upwards during the lower Longvillian by the *Nicolella* community where there was reduced sedimentation but elsewhere in the substage the *Dalmanella* community continued to prevail. At this time intergradation between the *Nicolella* and *Dalmanella* communities was prominent. By upper Longvillian times the *Nicolella* community had become more widespread and firmly established throughout the whole of the south Berwyns so that only ubiquitous elements such as *Sowerbyella* are found in association with the characteristic *Nicolella* community. In the upper part of the upper Longvillian, *Onniella*, which occurs in the overlying Pen-y-Garnedd Shales, is found, possibly representing an intergrading element from adjacent muddy substrates.

DISCUSSION

Although the faunal assemblages in the Berwyn area are similar to those around Bala and show comparable recurrent associations, we differ in some respects from Williams (1963, 1973) as to how the series of intergrading associations might best be grouped into communities. Nevertheless, we confirm the prevalence of a *Howellites* community in muddy-silty sediments and the presence of a *Nicolella* community in the relatively calcareous sediments of central north Wales. The *Dinorthis* association of Williams (1963) we regard as being divisible into two communities, viz. the *Dinorthis* and *Dalmanella* communities, and the former can be usefully split into two sub-communities. Where sandy and silty facies are poorly differentiated, as in the Berwyn and Bala areas, there is intergradation of the *Dalmanella* and *Dinorthis* communities, but where substrates are well differentiated, as in the Costonian of Shropshire or the Soudleyan of Snowdonia, the communities are clearly defined. We consider that this use of end members in a chain of intergrading benthic associations is helpful in the identification and naming of communities. It is our experience that throughout the whole Berwyn area and at many other localities in North Wales and Shropshire, most faunal assemblages of Soudleyan or Longvillian age can be reasonably assigned to one of the five communities discussed in this paper. We therefore conclude that in spite of the extensive intergradation of the benthic faunas they can be usefully partitioned into communities representing environmentally controlled, re-occurring natural associations.

The degree to which communities intergrade appears to be related to the environmental gradients within a region. Where, as in North Wales, the basin succession is thick and environmental gradients are low, both laterally and vertically, there is considerable intergradation between communities, and mixed assemblages are found. The variable composition of these assemblages implies a high rate of local immigration and extinction, and consequently a high equilibrium number for each community (e.g. Bretsky and Bretsky 1976). In contrast, where a shelf succession is relatively thin, and lateral and vertical environmental gradients are sharp (e.g. east Shropshire) the communities are more clearly partitioned into distinct lithotopes, and the compositions of the communities are less variable. Such communities tend to show a lower equilibrium number and therefore resemble those small, isolated geographical areas such as oceanic islands (MacArthur 1972). Clearly a recognition of the local tectonic and sedimentological framework in which particular communities are found is essential before more generalized models of communities can be framed.

Communities show many temporal changes in their composition as a result of species evolution, the establishment of new niches within the community, the extinction of some species, and the immigration of elements from other areas. Changes of these kinds are found in the communities of the Soudleyan–Longvillian of the Anglo-Welsh area. For example, *Howellites* and *Sowerbyella* are represented by five stratigraphically arranged species (Williams 1963), *Reuschella* by two species and a sub-species, and *Dalmanella* by four species. Most of these new species appear to have arisen indigenously within the Anglo-Welsh area, and indeed most of the Soudleyan and Longvillian brachiopod genera are either represented by earlier species within the area or appear for the first time within this region. In contrast, the appearance of some trilobites, notably *Chasmops* and *Estoniops*, apparently results from immigration from the Baltic region (Dean 1960*a*).

Some of the mid-Caradoc communities, as defined at the generic level, occur more widely within the Ordovician. The *Dinorthis* and *Macrocoelia* sub-communities are well established by Costonian times in south Shropshire and existed until at least the top Soudleyan or lower Longvillian in Wales. Assemblages which are possibly related to the *Dinorthis* community, with *Horderleyella* and *Rafinesquina*, together with coarsely ribbed orthids, such as *Hesperorthis* and *Orthis*, are found as early as the upper Llanvirn of the Llandeilo District (Williams 1953), but these early assemblages also include *Dalmanella* and *Sowerbyella* as major elements. *Dalmanella* is again associated with *Rafinesquina* and *Macrocoelia* in the upper Llandeilo Calcareous Ashes of the Berwyn Hills (MacGregor 1961), which suggests that the *Dalmanella* community might not have become clearly differentiated from the *Dinorthis* community until the Caradoc. Faunas from the Spy Wood Grit (Costonian) of west Shropshire which contain *Dalmanella*, *Bicuspina*, *Kjaerina*, and *Rostricellula* (Williams 1974) are more reminiscent of a mid-Caradoc *Dalmanella* community. Associations apparently similar to the *Dalmanella* community are also present in the Marshbrookian of Shropshire (Dean 1958).

We do not find records of low diversity assemblages dominated by *Howellites* and *Sowerbyella* outside the Soudleyan–Longvillian. In contrast, the *Nicolella* community appears to have a range extending from the Costonian at least into the Ashgill where in zones 1–3 (Cautleyan) of the Cautley area, Ingham (1966) records faunas including *Nicolella*, *Dolerorthis*, *Glyptorthis*, *Platystrophia*, *Sampo*, and *Skenidioides*. Similar faunal associations, with the addition of *Christiania*, are known elsewhere in the Ashgill, e.g. from flank beds of the Boda Limestone of Sweden (personal observation), from Belgium (Sheehan 1975), the Portrane Limestone of east Ireland (Wright 1964), and from the Drummuck Group of Girvan (Lamont 1935). It is possible that this off-shore Ordovician community subsequently developed into the *Dicoelosia-Skenidioides* community of the Lower and Middle Llandovery (Boucot 1975) with the addition of new Silurian elements.

Attempts have been made to generalize Lower Palaeozoic communities into a few major depth related types (Bretsky 1969*a*; Anderson 1971), and in these broad terms the North Wales communities could all be referred to as orthid-strophomenid-trilobite communities. More recently, Boucot (1975) has advocated the use of benthic assemblages which comprise a group of communities that occur repeatedly in different parts of a region in the same position relative to a shoreline. Following this scheme the Caradoc communities could empirically be allocated to the Benthic Assemblages of Boucot, as illustrated in column A below.

Benthic Assemblage 1 is typically represented elsewhere by a linguloid-bivalve dominated community which we have not observed in the south Berwyns. The five communities which we have discussed have been assigned to benthic assemblages according to their relative depth.

	A	B
BENTHIC ASSEMBLAGE 1	Not recognized	Not recognized
BENTHIC ASSEMBLAGE 2	*Dinorthis* community	*Dinorthis* community
BENTHIC ASSEMBLAGE 3	*Dalmanella* and *Howellites* communities	*Dalmanella*, *Howellites*, and *Nicolella* communities
BENTHIC ASSEMBLAGE 4	*Nicolella* community	? *Onniella* community
BENTHIC ASSEMBLAGE 5	*Onniella* community	—

On this interpretation the *Dinorthis* community would be the Anglo-Welsh Caradoc equivalent of the Upper Llandovery *Eocoelia* community, and the *Nicolella* community would equate with the *Costistricklandia* community. However, there are alternative interpretations of the distribution of Caradoc communities relative to benthic assemblages, and we prefer the distribution shown in Column B because, as previously suggested, the depth ranges of the *Dinorthis* to *Nicolella* communities could be as low as 0-30 m. The *Onniella* community in the Pen-y-Garnedd Shales probably occupied a more off-shore position, though this does not necessarily imply substantially greater depths. For example, Cave (1965) interpreted the black graptolitic shales of the Pen-y-Garnedd Shales and its lateral equivalents as occupying a positive area of no great depth within the Welsh Basin.

Sparse faunas comparable to the *Onniella* community, comprising small shells, in particular *Sericoidea*, and found in graptolitic shales, have been interpreted by Sheehan (1977) as being benthic organisms attached to seaweed fronds or other firm areas of the sea floor. Such associations appear to have been some of the deepest in the Ordovician but may, nevertheless, have occurred within normal shelf depths. Sheehan (1977) suggests that the limited biomass and diversity of the fauna might be the result of a deficient nutrient supply deriving from a lower level of marine productivity in the Lower Palaeozoic (Tappan and Loeblich 1973).

The restricted depth range of at least four of the Caradoc communities contrasts with the suggestion of Boucot (1975, p. 50) that Benthic Assemblages 1 to 5 occupy a depth range of 0 to 150–200 m in the Silurian-Devonian, and contrasts even more strongly with the suggested depth range of 0 to 300–500 m for the *Salopina–Visbyella* communities in the Silurian (Hancock *et al.* 1974). It is possible that we have recognized only shallow near-shore faunas, and that other communities existed elsewhere. However, within the Welsh Basin where deeper water facies exist, benthic faunas are sparse or absent. It follows that either we have underestimated the depth range of Caradoc communities or the Silurian depth range has been overestimated (see Hurst 1976), or alternatively there has been a migration of benthic communities into progressively greater water depths during the Lower Palaeozoic and the number of benthic assemblages has increased. We regard it as likely that the comparison of Silurian and modern diversity distributions has led to an overestimate of the absolute depth at which Silurian communities lived. In addition, we also believe that there is evidence for migration of benthic faunas into deeper water during the Lower Palaeozoic. For example, Crimes (1974) has noted a progressive increase in the diversity of ichnofossils in deep-water environments during the Palaeozoic and has commented on the appearance at the beginning of the Ordovician of *Zoophycos* in intermediate depths, and the first significant colonization of the deeper ocean floor. The recorded distribution of sessile epifaunal benthic faunas in the Cambrian also suggests that most such filter-feeding associations were found only in in-shore situations, i.e. the *Skolithos* facies in clastic rocks or the archaeocyathid reefs in carbonate rocks (Copper 1974). Subsequently, the development during the Ordovician of diverse filter-feeding communities composed of brachiopods, bryozoa, echinoderms, and corals changed the ecology of Palaeozoic shelves. The early evolutionary history of these complex communities is still to be determined, but it seems probable that they initially colonized the trophically rich in-shore environments and later migrated into more off-shore situations. The development of an advanced lophophore in the spiriferids and pentamerids may well have been an adaptation to deeper-water environments (see Fürsich and Hurst 1974), and the diversification of these groups in the late Ordovician and early Silurian could be related to the colonization of more oxygen-deficient, trophically poor, off-shore shelf situations.

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REFERENCES

ANDERSON, E. J. 1971. Environmental models for Palaeozoic communities. *Lethaia*, **4**, 287–302.

BASSETT, D. A. 1963. The Welsh Palaeozoic geosyncline: a review of recent work on stratigraphy and sedimentation. Pp. 35–69. *In* JOHNSON, M. R. W. and STEWART, F. H. (eds.). *The British Caledonides*, ix+280 pp. Oliver and Boyd, Edinburgh and London.

—— WHITTINGTON, H. B. and WILLIAMS, A. 1966. The stratigraphy of the Bala district, Merionethshire. *Q. Jl geol. Soc. Lond.* **122**, 219–271.

BERRY, W. B. N. and BOUCOT, A. J. 1967. Pelecypod-graptolite association in the Old World Silurian. *Bull. geol. Soc. Am.* **78**, 1515–1522.

BOUCOT, A. J. 1975. *Evolution and extinction rate controls.* 427 pp. Elsevier, Amsterdam.

BRENCHLEY, P. J. 1969. The relationship between Caradocian volcanicity and sedimentation in North Wales. Pp. 181–202. *In* WOOD, A. (ed.). *The Pre-Cambrian and Lower Palaeozoic rocks of Wales. Report of a symposium. . . .* x+461 pp. University of Wales Press, Cardiff.

—— (in press). The Caradoc rocks of the north and west Berwyn Hills, North Wales. *Geol. J.*

BRETSKY, P. W. 1969*a*. Evolution of Palaeozoic benthic marine invertebrate communities. *Palaeogeogr., Palaeoclimat. Palaeoecol.* **6,** 45–59.

—— 1969*b*. Central Appalachian late Ordovician communities. *Bull. geol. Soc. Am.* **80,** 193–212.

—— 1970*a*. Late Ordovician benthic marine communities in north central New York. *Bull. N.Y. St. Mus. Sci. Serv.* **44,** 1–34.

—— 1970*b*. Upper Ordovician ecology of the Central Appalachians. *Bull. Peabody Mus. nat. Hist.* **34,** 1–150.

—— and BRETSKY, S. S. 1975. Succession and repetition of late Ordovician fossil assemblages from the Nicolet River Valley, Quebec. *Paleobiology,* **1,** 225–237.

—— —— 1976. The maintenance of evolutionary equilibrium in late Ordovician benthic marine invertebrate faunas. *Lethaia,* **9,** 223–233.

—— and LORENZ, D. M. 1970. Adaptive response to environmental stability: a unifying concept in paleoecology. Pp. 522–550. *In* YOCHELSON, E. L. (ed.). *Proceedings of the North American paleontological convention. . . . Chicago, September 5–7, 1969. Vol. 1.* [xiv]+703 pp. Allen Press, Lawrence, Kansas.

CALEF, C. E. and HANCOCK, N. J. 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderlands. *Palaeontology,* **17,** 779–810.

CAVE, R. 1965. The Nod Glas sediments of Caradoc age in North Wales. *Geol. J.* **4,** 279–298.

COPPER, P. 1974. Structure and development of early Paleozoic reefs. *Proc. Second Int. Coral Reef Symp.* **1,** 365–386.

CRAIG, G. Y. and JONES, N. S. 1966. Marine benthos, substrate and palaeoecology. *Palaeontology,* **9,** 30–38.

CRIMES, T. P. 1974. Colonization of the early ocean floor. *Nature, Lond.* **248,** 328–330.

DEAN, W. T. 1958. The faunal succession in the Caradoc Series of south Shropshire. *Bull. Br. Mus. nat. Hist.* (Geol.), **3,** 191–231, pls. 24–26.

—— 1960*a*. The use of shelly faunas in a comparison of the Caradoc Series in England, Wales and parts of Scandinavia. *Rep. 21st session Int. geol. Congr. Norden,* **7,** 82–87.

—— 1960*b*. The Ordovician trilobite faunas of south Shropshire, I. *Bull. Br. Mus. nat. Hist.* (Geol.). **4,** 73–143, pls. 11–19.

—— 1961. The Ordovician trilobite faunas of south Shropshire, II. Ibid. **5,** 313–357, pls. 45–55.

—— 1963*a*. The Ordovician trilobite faunas of south Shropshire, III. Ibid. **7,** 215–254, pls. 37–46.

—— 1963*b*. The Ordovician trilobite faunas of south Shropshire, IV. Ibid. **9,** 3–18, pls. 1, 2.

DIGGINS, J. N. and ROMANO, M. 1968. The Caradoc rocks around Llyn Cowlyd, North Wales. *Geol. J.* **6,** 31–48.

DRISCOLL, E. G. 1967. Attached epifauna—substrate relations. *Limnol. Oceanogr.* **12,** 633–641.

FÜRSICH, F. T. 1976. Fauna-substrate relationships in the Corallian of England and Normandy. *Lethaia,* **9,** 343–356.

—— and HURST, J. M. 1974. Environmental factors determining the distribution of brachiopods. *Palaeontology,* **17,** 879–900.

GREIG, D. C., WRIGHT, J. E., HAINS, B. A. and MITCHELL, G. H. 1968. Geology of the country around Church Stretton, Craven Arms, Wenlock Edge and Brown Clee (Explanation of One-inch Geological Sheet 166). *Mem. geol. Surv. U.K.* i–xiv, 1–380.

HANCOCK, N. J., HURST, J. M. and FÜRSICH, F. T. 1974. The depth inhabited by Silurian brachiopod communities. *Jl geol. Soc. Lond.* **130,** 151–156.

HARRINGTON, H. J. 1959. General description of trilobita. Pp. O38–O117. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology, Part O, Arthropoda.* Geological Society of America and University of Kansas Press.

HURST, J. M. 1975. Wenlock carbonate, level bottom, brachiopod-dominated communities from Wales and the Welsh Borderland. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **17,** 227–255.

—— 1976. The depths inhabited by Silurian brachiopod communities: comment. *Geology,* **4,** 709, 710.

INGHAM, J. K. 1966. The Ordovician rocks in the Cautley and Dent districts of Westmorland and Yorkshire. *Proc. Yorks. geol. Soc.* **35,** 455–505, pls. 25–28.

JOHNSON, R. G. 1960. Models and methods for the mode and formation of fossil assemblages. *Bull. geol. Soc. Am.* **71**, 1075–1086.
—— 1965. Pelecypod death assemblages in Tomales Bay, California. *J. Paleont.* **39**, 80–85.
—— 1971. Animal-sediment relations in shallow water benthic communities. *Mar. Geol.* **11**, 93–104.
—— 1972. Conceptual models of benthic marine communities. Pp. 148–159. *In* SCHOPF, T. J. M. (ed.). *Models in paleobiology*. Freeman-Cooper, San Francisco.
JONES, N. S. 1950. Marine bottom communities. *Biol. Rev.* **25**, 283–313.
KAUFFMAN, E. G. and SCOTT, R. W. 1976. Basic concepts of community ecology and paleoecology. Pp. 1–28. *In* SCOTT, R. W. and WEST, R. R. (eds.). *Structure and classification of paleocommunities*. Dowden, Hutchinson and Ross.
KING, W. B. R. 1923. The Upper Ordovician rocks of the south-west Berwyns. *Q. Jl geol. Soc. Lond.* **84**, 487–507.
LAMONT, A. 1935. The Drummuck Group, Girvan; a stratigraphical revision with descriptions of fossils from the lower part of the Group. *Trans. geol. Soc. Glasg.* **19**, 288–332, pls. 7–9.
LAWRENCE, D. R. 1968. Taphonomy and information losses in fossil communities. *Bull. geol. Soc. Am.* **79**, 1315–1330.
LINDROTH, A. 1935. Die associationen der marinen Weichboden. *Zool. Bidr. Upps.* **15**, 331–366.
MACARTHUR, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. 269 pp. Harper and Row, New York.
MACDONALD, K. B. 1975. Quantitative community analysis: recurrent group and cluster techniques applied to the fauna of the Upper Devonian Sonyea Group, New York. *J. Geol.* **82**, 473–499.
MACGINITIE, G. E. 1939. Littoral marine communities. *Am. Midl. Nat.* **21**, 28–55
MACGREGOR, A. R. 1961. Upper Llandeilo brachiopods from the Berwyn Hills, North Wales. *Palaeontology*, **4**, 177–209, pls. 19–23.
MARSHALL, N. B. 1954. *Aspects of deep sea biology*. 380 pp. Hutchinson, London.
MULLER, C. H. 1958. Science and philosophy of the community concept. *Am. Scient.* **46**, 294–308.
PETERSEN, C. G. J. 1911. Valuation of the sea. I. Animal life of the sea bottom, its food and quantity. *Rep. Dan. biol. Stn*, **20**, 1–81.
—— 1913. Valuation of the sea. II. The animal communities of the sea bottom and their importance for marine zoogeography. Ibid. **21**, 1–44.
PICKERILL, R. K. 1973. *Lingulasma tenuigranulata*—palaeoecology of a large Ordovician linguloid that lived within a strophomenid-trilobite community. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **13**, 143–156.
—— 1974. *Geology of the south Berwyn Hills, North Wales, with particular reference to Upper Ordovician marine benthic communities*. Ph.D. thesis, Univ. of Liverpool.
—— 1975. Application of ichnology to the study of ancient marine benthic community palaeoecology. A discussion and case example. *Marit. Sediments*, **11**, 49–52.
—— 1976. *Vermiforichnus* borings from the Ordovician of central Wales. *Geol. Mag.* **113**, 159–164.
—— 1977. Trace fossils from the Upper Ordovician (Caradoc) of the Berwyn Hills, central Wales. *Geol. J.* **12**, 1–16.
RAMSBOTTOM, W. H. C. 1961. The British Ordovician Crinoidea. *Palaeontogr. Soc.* [*Monogr.*], 1–37, pls. 1–8.
RICHARDS, R. P. 1972. Autecology of Richmondian brachiopods (late Ordovician of Indiana and Ohio). *J. Paleont.* **46**, 386–405.
SHEEHAN, P. M. 1975. Late Ordovician brachiopods from Belgium. *Abstr. Progm geol. Soc. Am.* **7**, 1267.
—— 1977. Ordovician and Silurian brachiopods from graptolitic shales and related deep-water argillaceous rocks. *Lethaia*, **10**, 201–203.
SLOBODKIN, L. B. and SANDERS, H. L. 1969. On the contribution of environmental predictability to species diversity. *In* WOODWELL, G. M. and SMITH, H. H. (eds.). Diversity and stability in ecological systems. *Brookhaven Symp. Biol.* **22**, 82–95.
STANTON, R. J., JR. and EVANS, I. 1972. Community structure and sampling requirements in paleoecology. *J. Paleont.* **46**, 845–858.
TAPPAN, H. and LOEBLICH, A. R. 1973. Smaller protistan evidence and explanation of the Permian–Triassic crisis. *In* LOGAN, A. and HILLS, L. V. (eds.). The Permian and Triassic systems and their mutual boundary. *Mem. Can. Soc. Petrol. Geol.* **2**, 465–480.
THAYER, C. W. 1974. Marine paleoecology in the Upper Devonian of New York. *Lethaia*, **7**, 121–155.

WALKER, K. R. and ALBERSTADT, L. P. 1975. Ecological succession as an aspect of structure in fossil communities. *Paleobiology*, **1**, 238–257.

—— and BAMBACH, R. K. 1971. The significance of fossil assemblages from fine grained sediments—time averaged communities. *Abstr. Progm geol. Soc. Am.* **3**, 783, 784.

—— and LAPORTE, L. F. 1970. Congruent fossil communities from the Ordovician and Devonian of New York. *J. Paleont.* **44**, 928–944.

WATKINS, R. and BOUCOT, A. J. 1975. Evolution of Silurian brachiopod communities along the southeastern coast of Acadia. *Bull. geol. Soc. Am.* **86**, 243–254.

WHITTINGTON, H. B. 1962–1968. The Ordovician trilobites of the Bala area, Merioneth, Part I. *Palaeontogr. Soc.* [*Monogr.*] **116** (1962), 1–32, pls. 1–8; Part II, **118** (1965), 33–62, pls. 9–18; Part III, **120** (1966), 63–92, pls. 19–28; Part IV, **122** (1968), 93–138, pls. 29–32.

WILLIAMS, A. 1953. The geology of the Llandeilo area Carmarthenshire. *Q. Jl geol. Soc. Lond.* **108**, 177–207.

—— 1963. The Caradocian brachiopod faunas of the Bala district, Merionethshire. *Bull. Br. Mus. nat. Hist.* (Geol.), **8**, 327–471, pls. 1–16.

—— 1973. Distribution of brachiopod assemblages in relation to Ordovician palaeogeography. *In* HUGHES, N. F. (ed.). Organisms and continents through time. *Spec. Pap. Palaeont.* **12**, 241–269.

—— 1974. Ordovician brachiopoda from the Shelve district, Shropshire. *Bull. Br. Mus. nat. Hist.* (Geol.), Supp. **11**, 1–163, pls. 1–28.

—— 1976. Plate tectonics and biofacies evolution as factors in Ordovician correlation. Pp. 29–65. *In* BASSETT, M. G. (ed.). *The Ordovician System: proceedings of a Palaeontological Association symposium, Birmingham, September 1974.* 696 pp. University of Wales Press and National Museum of Wales, Cardiff.

WOBBER, F. J. 1968. A faunal analysis of the Lias (Lower Jurassic) of South Wales (Great Britain). *Palaeogeogr. Palaeoclimat. Palaeoecol.* **5**, 269–308.

WORSLEY, D. 1971. Faunal anticipation in the lower Llandovery of the Oslo region, Norway. *Norsk. geol. Tidsskr.* **51**, 161–167.

WRIGHT, A. D. 1964. The fauna of the Portrane Limestone, II. *Bull. Br. Mus. nat. Hist.* (Geol.), **9**, 157–256, pls. 1–11.

ZIEGLER, A. M. 1965. Silurian marine communities and their environmental significance. *Nature, Lond.* **207**, 270–272.

—— COCKS, L. R. M. and BAMBACH, R. K. 1968. The composition and structure of Lower Silurian marine communities. *Lethaia*, **1**, 1–27.

R. K. PICKERILL

Department of Geology
University of New Brunswick
P.O. Box 4400
Fredericton, N.B.
E3B 5A3
Canada

P. J. BRENCHLEY

Department of Geology
University of Liverpool
Liverpool L69 3BX

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