

LUDLOW BENTHONIC ASSEMBLAGES

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ABSTRACT. The communities recently described by Calef and Hancock are considered to provide an inadequate picture of Ludlow faunas and their palaeoecological significance. Alternative assemblages, including the important non-brachiopod benthos, have been compiled from the evidence of published faunal lists. It is here maintained that these four assemblages reflect more accurately than those of Calef and Hancock the faunal distribution within the Ludlow rocks but no special significance is claimed for them; each contains subdivisions which may be more readily explained in palaeoecological terms. It is suggested that the recent emphasis on depth-communities has led to neglect of other very important environmental controls, particularly the nature of the substrate. The concept of continuous regression through the Ludlow is considered untenable in the light of sedimentological evidence. The degree of diachronism of the shelly faunas is assessed. It is concluded that the picture drawn by Calef and Hancock is an oversimplification resulting, perhaps, from the attempt to impose a relatively straightforward Llandovery pattern on to the more complex Ludlow rocks.

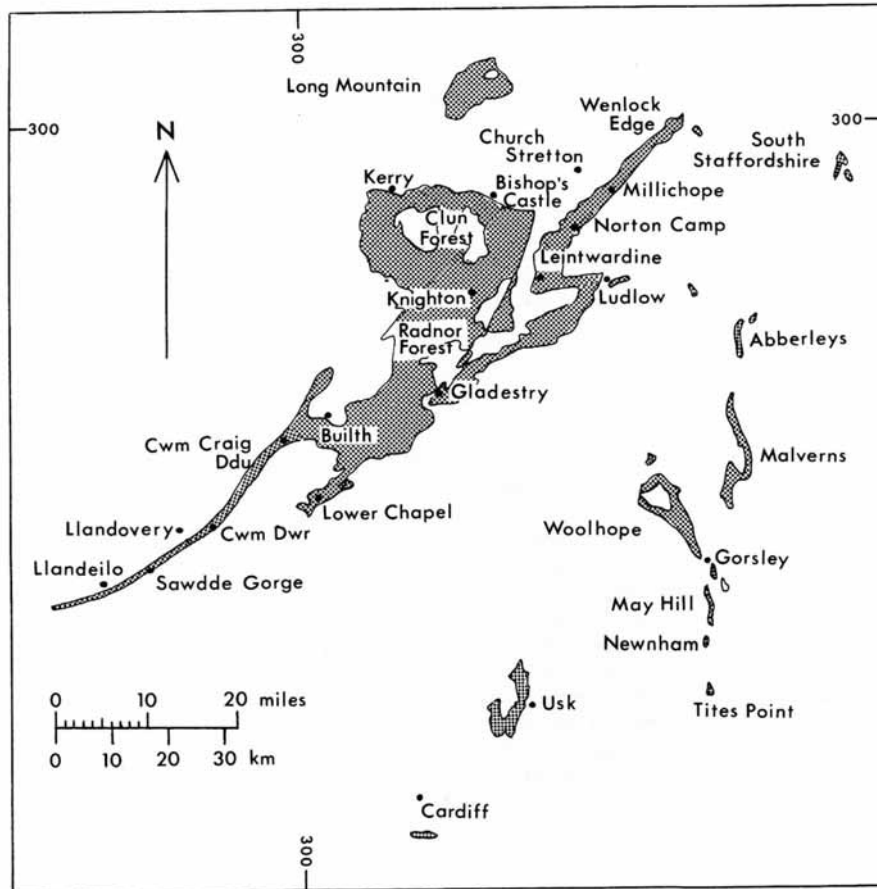
A RECENT paper in *Palaeontology* by Calef and Hancock (1974) describes five major marine benthonic communities occurring in clastic (i.e. terrigenous) sediments laid down in areas of increasing depth of water 'from the shoreline to deep areas in Wales and the Welsh Borderland during Wenlock and Ludlow times'. Only four of these communities are well developed in the Ludlow rocks, mainly on the stable eastern margin of the Welsh basin. They are named after characteristic brachiopod genera as follows: (1) *Salopina*, (2) *Sphaerirhynchia*, (3) *Isorthis*, and (4) *Dicoelosia* communities. They are considered as approximate equivalents of the upper Llandovery depth-communities: (1) *Eocoelia*, (2) *Pentamerus*, (3) *Stricklandia*, and (4) *Clorinda*, the last-named being the deepest of the four. A fifth, deeper *Visbyella* community has only been recognized at one locality in the Ludlow rocks.

The purpose of this paper is to critically examine some of Calef and Hancock's conclusions in the light of the very detailed published evidence on Ludlow faunas and sediments. Text-fig. 1 shows the localities mentioned in this paper.

RECOGNITION OF COMMUNITIES

The statistical description of their communities by Calef and Hancock is most welcome but it is not clear how collections were assigned to a particular community in the first place. Perhaps the allocation was made on the basis of survivors from Llandovery communities but these form a small proportion of the faunas and some genera apparently change their modal communities (Calef and Hancock 1974, Table 12). It is stated that the communities completely intergrade and that the community boundaries are arbitrary lines through a continuum (Calef and Hancock 1974, p. 779). The number of divisions is therefore a matter of practical convenience and ten communities could have been postulated instead of five. The recognition of five communities has proved to be of value in the upper Llandovery and this fact has presumably influenced the choice of five for the Wenlock and Ludlow.

Although it is at first reassuring to have the presence percentage and frequency



TEXT-FIG. 1. Map of south-east Wales and the Welsh Borderland showing the outcrops of Ludlow rocks (stippled) and localities mentioned in the text.

presence recorded for each fossil in each community it is not clear how a geologist attempting to use these tables is expected to allocate a particular fauna to one of these communities. For instance, in the Wenlock *Salopina* community (Calef and Hancock 1974, Table 2) five of the seven *prevalent* fossils are present in less than one-third of the seventeen localities examined—evidently not prevailing very successfully.

ASSEMBLAGES AS LIFE-ASSEMBLAGES

Calef and Hancock follow the practice of Ziegler, Cocks and Bambach (1968, p. 3) in accepting the shell assemblages as reasonably representative of the preservable

elements of the communities. This seems well justified in the Llandovery for the following reasons:

1. Analysis of shells suggests only limited post-mortem transport.
2. The faunal associations are so frequently repeated.
3. Life-assemblages of similar composition to the transported assemblages have been recorded.
4. The community belts are about ten miles wide and only extensive shell transport could confuse the basic pattern.

Points (1) and (2) apply also to the Wenlock and Ludlow rocks (Calef and Hancock 1974, p. 781) but so far no depth-patterns have been established or life-assemblages described. Although it seems likely that Calef and Hancock's thesis does apply to most of the shelf Ludlow faunas, it should be accepted with caution until broad distribution belts have been established, life-assemblages recognized, and further analysis of shell wear and distribution carried out.

COMPOSITION OF ASSEMBLAGES

If, however, the above contention *is* broadly acceptable it means that previously described Ludlow assemblages may now merit consideration as life-assemblages and deserve close comparison with the communities listed by Calef and Hancock. Straw (1937, p. 411) and Lawson (1960) both described Ludlow faunas but much new information has been published since those papers and it is now possible, using detailed faunal lists, to draw up tables of four major Ludlow benthonic assemblages occupying the main shelf area of the Welsh Borderlands and the English Midlands. They characterize the four Ludlow stages (Eltonian, Bringewoodian, Leintwardinian, and Whitcliffian) on the shelf and, therefore, succeed each other vertically in any particular area. Unlike the intergrading communities postulated by Calef and Hancock three of these four assemblages suffer abrupt vertical changes in faunal content. This can be most clearly seen in the range charts included in the papers on Usk (Walmsley 1959, p. 490), Woolhope (Squirrell and Tucker 1960, p. 144), Malvern (Phipps and Reeve 1967, p. 354), Wenlock Edge (Shergold and Shirley 1968, p. 135), and in text-fig. 2 of this paper. This apparent distinction between the faunas is probably due to breaks in deposition or slow deposition between the main stratigraphical units. There is a widespread conglomerate at the junction of the Bringewood and Leintwardine Beds, a frequently developed phosphatized fragment-bed at the Leintwardine-Whitcliffe junction and the Ludlow Bone-Bed where the Whitcliffe Beds join the Downton Castle Sandstone.

The term 'assemblage' is here used in its most general sense to denote those fossils which tend to be found together in the rocks, without drawing any conclusions about the life-assemblages from which they might have been derived or implying any statistically proved separation from an adjacent assemblage. The scope of the word 'together' is also important. If only four assemblages are to be recognized in a shelf thickness of over 360 m of Ludlow rocks then the average thickness per assemblage is at least 90 m. If the thickness examined is limited to about 20 m then the collection of fossils occurring 'together' has a different composition; these are here called 'minor

assemblages'. If the thickness is restricted to one or two metres the fossil composition is again different and much more limited; these are here called faunal units and are, perhaps, the associations of Calef and Hancock (1974, p. 796). The significance of these distinctions is discussed after the assemblage lists.

It must be made clear that no particular significance is claimed in this paper for the four major assemblages described. Calef and Hancock, however, claim that there are four successive intergrading communities related to depth. It is here agreed that four successive assemblages are present and this contention is supported by records from previous papers but it is maintained that there are substantial differences in composition from the community lists of Calef and Hancock. It is further maintained that only one pair of assemblages intergrade and that their ecological significance is more complex than Calef and Hancock realize. It is agreed that the highest assemblage almost certainly represents much shallower water than the lowest and earliest assemblage but the two intermediate assemblages are more complex and contain subdivisions of considerable palaeoecological significance. The changes in the major assemblages may be due to some major environmental factors, such as changes in late Silurian palaeogeography causing restriction of seas and closing and opening of connections to other regions.

The major assemblages listed below have been named after two characteristic genera—not necessarily the most abundant. Although generic names change, they have been preferred to species names which are more likely to be duplicated (e.g. *ludloviensis* or *lewisii*). Ideally, both generic and specific names should be used as different species of the same genus may have different ecological preferences. This procedure would make the titles of the assemblages cumbersome and has not been adopted. However, species names have been given in the assemblage lists. The lists have been compiled from faunal lists from the following eight areas on the shelf: May Hill (Lawson 1955), Usk (Walmsley 1959), Woolhope (Squirrell and Tucker 1960), Malverns (Phipps and Reeve 1967; Penn 1969), Aymestrey (Lawson 1973), Ludlow (Holland, Lawson and Walmsley 1963), Leintwardine (Whitaker 1962), and Wenlock Edge (Shergold and Shirley 1968). Three points have been allocated to a fossil recorded as common, two for fairly common, and one for present, giving a possible top score of twenty-four for 'commonness'. Because the major Ludlow divisions each contain two or three subdivisions, usually with separate recordings of species abundance, average values have had to be taken resulting in non-integers. The figure after the stroke (maximum eight) indicates the number of areas of occurrence. Only benthonic forms are listed, i.e. graptolites and cephalopods are omitted. These lists differ in intent from those of Calef and Hancock in that non-brachiopod benthos is listed (indicated by an asterisk), and often seems of greater importance than they allow. Fossils collected from the limestones as well as the terrigenous sediments are included and are considered to be essential if an over-all picture of Ludlow palaeoecology is required. The brachiopod contents of these assemblages are sufficiently similar to those of the communities of Calef and Hancock to invite closer comparison. A more detailed examination, however, reveals some important disparities, which are briefly discussed.

The author's name is provided only at the first mention of a species but, in the interests of clarity, generic names are repeated in subsequent lists. Text-fig. 2 provides

a graphic presentation of these faunal changes. Most of the important fossils are figured in Holland, Lawson and Walmsley (1963, pls. 3-7), and in Calef and Hancock (1974, pl. 106).

BENTHONIC ASSEMBLAGES

A. *Dicoelosia-Skenidioides* assemblage

1.	<i>Aegiria grayi</i> (Davidson)	14-3/8
*2.	<i>Dalmanites myops</i> (König)	13-6/8
*3.	<i>Hemsiella maccoyana</i> (Jones)	12-2/7
4.	isorthid	10-7/7
5.	<i>Atrypa reticularis</i> (Linnaeus)	9-7/8
6.	<i>Craniops implicata</i> (J. de C. Sowerby)	9-4/8
7.	<i>Shagamella ludloviensis</i> Boucot and Harper	8-0/8
8.	<i>Howellella elegans</i> (Muir-Wood)	8-0/6
9.	<i>Mesopholidostrophia</i> sp.	6-9/6
10.	<i>Dicoelosia biloba</i> (Linnaeus)	6-3/6
11.	<i>Protochonetes minimus</i> (J. de C. Sowerby)	6-3/5
*12.	<i>Calymene</i> sp.	6-1/8
13.	<i>Leptaena depressa</i> (J. de C. Sowerby)	5-9/6
14.	<i>Strophonella euglypha</i> (Hisinger)	5-8/6
15.	<i>Amphistrophia funiculata</i> (M'Coy)	5-8/6
*16.	<i>Leonaspsis</i> sp.	5-5/7
17.	<i>Skenidioides lewisii</i> (Davidson)	5-2/6
18.	<i>Leptostrophia filosa</i> (J. de C. Sowerby)	5-0/5
19.	<i>Eospirifer</i> spp.	5-0/5
20.	<i>Sphaerirhynchia wilsoni</i> (J. Sowerby)	4-7/6
*21.	proetid	4-6/6
22.	<i>Dalejina</i> cf. <i>hybrida</i> (J. de C. Sowerby)	4-5/4
23.	<i>Orbiculoidea rugata</i> (J. de C. Sowerby)	4-4/5
24.	<i>Gypidula</i> cf. <i>galeata</i> (Dalman)	4-3/6
25.	<i>Glassia</i> sp.	4-1/5
26.	<i>Coolinia pecten</i> (Linnaeus)	4-0/5

This list compares well with the *Dicoelosia* community of Calef and Hancock but contains four trilobites and one ostracod. As they indicate, it is a high-diversity, low-density assemblage of predominantly small brachiopods. *Dalejina*, *Skenidioides*, *Nucleospira*, *Cyrtia*, and *Leangella* are more important in their list, perhaps because seven (maybe eight) of their nine *Dicoelosia* localities are in the Lower Elton Beds where these forms are commoner. The Eltonian succession has, therefore, been sampled very unevenly by Calef and Hancock.

B. *Strophonella-Gypidula* assemblage

1.	<i>Atrypa reticularis</i>	20-5/8
2.	<i>Strophonella euglypha</i>	19-8/8
3.	<i>Leptaena depressa</i>	19-3/8
4.	<i>Sphaerirhynchia wilsoni</i>	15-5/8
5.	<i>Gypidula lata</i> Alexander	15-0/8
6.	<i>Leptostrophia filosa</i>	15-0/8
7.	<i>Shagamella ludloviensis</i>	14-0/8
8.	<i>Isorthis orbicularis</i> (J. de C. Sowerby)	13-8/8
*9.	solitary trochoid coral	13-5/8

*10. }	<i>Poleumita globosa</i> (Schlotheim)	11-3/8
*11. }	<i>Dalmanites myops</i>	11-3/8
12.	<i>Howellella elegans</i>	11-0/8
13.	<i>Amphistrophia funiculata</i>	10-3/8
14.	<i>Mesopholidostrophia</i> sp.	10-3/7
*15.	<i>Hemsiella maccoyana</i>	10-0/7
16.	<i>Camarotoechia nucula</i> (J. de C. Sowerby)	9-5/8
17.	<i>Craniops implicata</i>	9-5/8
*18.	<i>Favosites</i> spp.	9-3/8
19.	<i>Shaleria</i> sp. nov.	8-5/7
20.	<i>Coolinia pecten</i>	7-5/7
*21.	<i>Cypricardina</i> spp.	7-5/7
*22.	<i>Ptilodictya</i> spp.	7-5/6
23.	<i>Kirkidium knightii</i> (J. de C. Sowerby)	6-5/5
24.	<i>Eospirifer</i> spp.	6-3/8
*25.	<i>Protochonetes ludloviensis</i> Muir-Wood	6-3/7
26.	<i>Encrinurus</i> sp.	6-3/6
*27.	<i>Calymene</i> sp.	6-0/8
28.	<i>Aegiria grayi</i>	6-0/6
29.	<i>Dayia navicula</i> (J. de C. Sowerby)	5-5/6
30. }	<i>Protochonetes minimus</i>	5-0/6
*31. }	<i>Halysites</i> sp.	5-0/6
*32.	<i>Rhabdocyclus porpitoides</i> (Lang and Smith)	5-0/4

This is a diverse, high-density assemblage dominated by brachiopods, particularly strophomenids, but with quite a significant variety of other groups, i.e. trilobites, corals, bivalve, gastropod, ostracod, and bryozoan. It most closely resembles the *Isorthis* community of Calef and Hancock but the order of abundance is very different. At least two of their samples are from Elton Beds which may explain the records of *Dalejina*, *Homeospira*, *Glassia*, and *Skenidioides*.

C. *Dayia-Isorthis* assemblage

1.	<i>Camarotoechia nucula</i>	21-5/8
2.	<i>Dayia navicula</i>	17-8/8
3.	<i>Protochonetes ludloviensis</i>	16-8/8
4.	<i>Sphaerirhynchia wilsoni</i>	14-8/8
5.	<i>Isorthis orbicularis</i>	14-6/8
6.	<i>Atrypa reticularis</i>	14-2/8
7. }	<i>Shaleria ornatella</i> (Davidson)	13-3/8
8. }	<i>Shagamella ludloviensis</i>	13-3/8
9.	<i>Howellella elegans</i>	13-0/7
10.	<i>Salopina lunata</i> (J. de C. Sowerby)	11-7/7
11.	<i>Leptaena depressa</i>	10-5/8
12.	<i>Whitfieldella canalis</i> (J. de C. Sowerby)	10-3/7
13.	<i>Craniops implicata</i>	10-0/8
14.	<i>Orbiculoidea rugata</i> (J. de C. Sowerby)	9-5/8
*15.	<i>Bythocypris siliqua</i> (Jones)	9-2/6
*16.	<i>Sedgwickia</i> [<i>Fuchsella</i>] <i>amygdalina</i> (J. de C. Sowerby)	8-9/8
*17.	<i>Calymene neointermedia</i> (R. & E. Richter)	8-4/8
18.	<i>Leptostrophia filosa</i>	8-3/7
19. }	<i>Aegiria grayi</i>	7-7/7
*20. }	<i>Pteronitella retroflexa</i> (Wahlenberg)	7-7/7
*21.	<i>Goniophora cymbaeformis</i> (J. de C. Sowerby)	7-6/7
*22.	<i>Serpulites longissimus</i> (J. de C. Sowerby)	7-5/8

*23.	<i>Hemsiella maccoyana</i>	7-2/6
*24.	<i>Neobeyrichia torosa</i> (Jones)	6-7/7
*25.	proetid	6-2/8
*26.	<i>Bembexia lloydii</i> (J. de C. Sowerby)	6-1/7
*27.	<i>Cyclonema corallii</i>	5-2/6
28.	<i>Lingula lewisii</i>	5-0/6

This is a diverse, high-density assemblage, still with brachiopods dominant but the non-brachiopod benthos (ostracods, trilobites, bivalves, gastropods, worm) becoming important in the 'second division'. The brachiopod component compares most closely with the *Sphaerirhynchia* community of Calef and Hancock. Their list omits *Shaleria* and *Aegiria*, presumably because the Upper Leintwardine Beds were not sampled at all. It includes, however, *Mesopholidostrophia*, *Gypidula*, *Strophonella*, and *Amphistrophia*—genera which do *not*, in fact, occur with an abundance of *Dayia*, *Protochonetes*, and *Salopina*.

D. *Protochonetes-Salopina* assemblage

1.	<i>Protochonetes ludloviensis</i>	22-5/8
2.	<i>Camarotoechia nucula</i>	21-5/8
3.	<i>Salopina lumata</i>	20-0/8
*4.	<i>Sedgwickia</i> [<i>Fuchsella</i>] <i>amygdalina</i>	16-7/8
*5.	<i>Serpulites longissimus</i>	15-0/7
*6.	<i>Neobeyrichia torosa</i> (Jones)	12-3/8
*7.	<i>Pteronitella retroflexa</i>	10-8/6
*8.	<i>Goniophora cymbaeformis</i>	10-3/6
*9.	<i>Cornulites serpularius</i> Schlotheim	9-7/8
10.	<i>Orbiculoidea rugata</i>	9-5/6
*11.	<i>Nuculites</i> spp.	9-0/6
12.	<i>Craniops implicata</i>	8-0/6
13.	<i>Howellella elegans</i>	7-3/7
*14.	} <i>Loxonema</i> spp.	5-8/6
*15.	} <i>Tentaculites tenuis</i> (J. de C. Sowerby)	5-8/6
16.	<i>Dayia navicula</i>	5-7/5
*17.	<i>Bythocypris siliqua</i>	5-7/4

This is a low diversity, high-density assemblage with three brachiopods dominant but ten of the seventeen commonest fossils are not brachiopods. Bivalves are particularly important. This fauna corresponds reasonably closely with the *Salopina* community of Calef and Hancock in its brachiopod content but they report *Sphaerirhynchia* and *Dayia* as being prevalent. This may be due partly to their four samples from the atypical Llandeilo-Llandovery area and partly to their three Leintwardinian localities out of a total of twelve localities. It is difficult to comprehend why these seven samples should be grouped with the five from the Whitcliffian in the first place.

Text-fig. 2 presents the same data in graphic form but with more detailed information on the variation in abundance of the various taxa with time. The following points should be noted:

1. The four assemblage-zones (or, perhaps, concurrent-range zones) correspond with the four main divisions of the Ludlow Series into Elton, Bringewood, Leintwardine, and Whitcliffe Beds.

2. The chart is confined to benthonic forms so that the graptolites and the cephalopods are important absentees. Because of the more refined presentation of the vertical



TEXT-FIG. 2. Range chart of benthonic fossils in the Ludlow rocks of the Welsh Borderland shelf facies: based on records from May Hill, Usk, Woolhope, Malvern, Aymestrey, Ludlow, Leintwardine, and Wenlock Edge (see p. 515 for discussion).

variation, the stratigraphically important fossils *Neobeyrichia lauensis* and *Lingula lata* become eligible for inclusion on this chart, although not in the assemblage lists.

3. Most of the species and almost all the genera have longer ranges and different abundance patterns outside this region; in other words, these are mostly local ranges and local acmes due to ecological controls.

4. The common constituents of these assemblages do not necessarily enter and depart, or wax and wane, together, e.g. *Howellella elegans* is prevalent in four assemblages, *Atrypa reticularis* in three, *Salopina lunata* in two, *Shaleria ornatella* in one, whilst *Kirkidium knightii* and *Dicoelosia biloba* are dominant only for part of an assemblage. This suggests that these species are not all reacting to one ecological factor, such as depth of water—as is implied in Calef and Hancock's account. It also seems inappropriate to group species of varying tolerances in the same community; the components of a community should come and go together.

5. There is quite a degree of lateral faunal variation not evident from this chart of vertical abundance; the main contrast is between the inner and outer shelf areas.

There are obviously important differences between these two versions of the four major Ludlow benthonic assemblages—even if the comparison is restricted to the brachiopod content. At first sight, it might be thought that the conclusions of Calef and Hancock have the greater objective validity as they have described the communities statistically, counting all macrofossils in collections of 100–200 specimens. Their records are therefore more objective and precise than the familiar categories of 'common', 'fairly common', and 'present'. On the other hand, presumably because of the time involved in rock-splitting and counting, only 53 localities were collected—usually represented by single beds or up to 20 cm of rock. This means a possible maximum thickness sampled of 10.6 m in a succession at least 360 m thick, i.e. a percentage of only 3.4 in a series of rocks characterized by many vertical and lateral facies and faunal changes. The four major communities are based on only 44 localities, an average of 11 per community. Of these 44, 14 are from the Sawdde Gorge which is just one of the four main sections in the Llandovery–Llandeilo area, where the shelf facies is atypical.

In contrast, in the eight areas from which the alternative lists have been compiled, a total of 2600 Ludlovian localities has been examined—an average of 325 per area. Although it is improbable that any single bed was collected and studied as thoroughly as those examined by Calef and Hancock it is certain that a large percentage of these 2600 localities were studied bed by bed in order to establish the faunal succession and subdivisions and to delimit accurately the boundaries between them.

A close look at the locality list in their Appendix (p. 810) reveals some important differences in faunal records between Calef and Hancock and previous authors. For instance, they record three examples of *Isorthis* communities from the Leintwardine Beds of Ludlow but Holland, Lawson and Walmsley (1963) did not record any occurrences of the supposedly prevalent *Isorthis* community fossils *Mesopholidostrophia* spp., *Dalejina*, and *Amphistrophia* in their Leintwardine Beds. The collections from these three localities have now been examined by the present author at the British Museum (Natural History), by courtesy of Dr. L. R. M. Cocks. Locality Lud 2 evidently yielded abundant *Kirkidium knightii* and is undoubtedly in Upper

Bringewood Beds and *not* Leintwardine Beds; it is hardly a very good example of an *Isorthis* community in that 7 out of the 10 prevalent fossils are missing, the most notable absence being *Isorthis* itself with its statistically assessed presence percentage of 100. Lud 7 and Lud 8 are, however, correctly assigned to the Leintwardine Beds but are again not very convincing representatives of the *Isorthis* community. Indeed, Lud 7 yielded only 4 of the 10 prevalent forms of the *Isorthis* community but contained 8 of the 10 prevalent fossils of the *Sphaerirhynchia* community. This locality is Sunnyhill Quarry, which has recently been studied in detail by Miss Lesley Cherns of Glasgow University. She reports that there are about 15 m of Leintwardine Beds at this exposure of which only 20 cm were sampled by Calef and Hancock (i.e. 1.33%). At this level in the quarry successive bands are dominated by different fossils, e.g. *Isorthis*, *Sphaerirhynchia*, *Dayia*, and *Shagamella*. Calef and Hancock evidently struck a band rich in *Isorthis* but if they had collected a metre above or a metre below they might well have hit a *Sphaerirhynchia* band, and allocated their collection to that community. Indeed, Miss Cherns has studied another locality in the Leintwardine Beds of the Ludlow area (4619 7360) where, in a thickness of 3 m, the four community index fossils *Lingula*, *Salopina*, *Sphaerirhynchia*, and *Isorthis* are all very common, taking it in turn to dominate different bands. Such a faunal pattern might be expected to instil some doubt in the mind of even the strictest devotee of the depth-community relation.

Equally anomalous is the record of a *Sphaerirhynchia* community from the Lower Perton Beds of Woolhope (i.e. Lower Whitcliffe Beds). The prevalent fossils of this community include *Sphaerirhynchia wilsoni* (with a presence percentage of 100), *Whitfieldella* and *Leptostrophia filosa*, none of which are recorded from their Lower Perton Beds by Squirrell and Tucker. This collection has also been examined by the present author and a list of fossils, with numbers present, was submitted to Dr. E. V. Tucker for his expert opinion. He places the fauna in his lowest Lower Bodenham Beds (Lower Leintwardine Beds). He also points out that the locality map reference given by Calef and Hancock appears to indicate a collection from the southern face of the extended Perton Quarry where Perton Beds do not occur at all.

The above lists are supported by less complete evidence in the following publications on the areas of Usk (Squirrell and Downing *et al.* 1969), Church Stretton (Greig *et al.* 1968), Tites Point and Newnham (Cave and White 1971), and Gorsley (Lawson 1954).

The Llandovery-Llandeilo district has been excluded from this analysis as it represents an unusual and 'sandy variety of the shelf facies' (Potter and Price 1965, p. 396) and the faunas display variations which may relate to the sandy, shallow-water facies. Calef and Hancock, however, include fourteen localities from this area in their community analysis based on fifty-three Ludlow localities and this may explain some of the peculiarities in the associations recorded by them. Presumably because of their commitment to brachiopod communities they fail to recognize what is probably the most significant assemblage palaeogeographically in this area. This is a strong molluscan fauna which Potter and Price (1965, p. 390) considered to be 'well adapted for sandy, shallower and possibly less saline conditions'. It occurs in sandstones of middle Ludlow age and includes the bivalve genera *Grammysia* and *Modiolopsis* and the gastropods *Loxonema*, *Platyschisma*, and *Bucanopsis*. *Lingula* and *Orbiculoidea*

also occur in association with this fauna, which resembles that of the Downton Castle Sandstone and also the persistent Palaeozoic linguloid-molluscan community described by Bretsky (1969) as characterizing near-shore sandy and silty environments.

Although Calef and Hancock (1974, p. 779) refer to shelly faunas occurring in the basin they record collections only from Builth Wells (four localities) and Denbighshire (one), and none from Clun Forest, Knighton, Long Mountain, and Radnor Forest. They would certainly not have found a simple succession of their four shallowing benthonic communities. In many places, as at Bishop's Castle, the *Dicoelosia-Skenidioides* assemblage is well developed at the base of the Ludlow succeeded by *Diversograptus nilssoni* shales. Above follows a *Dayia-Isorthis* fauna with some elements of the *Strophonella-Gypidula* fauna in the more calcareous siltstones (e.g. *Gypidula*, *Poleumita*, and *Favosites* at Builth). Then succeeds a normal *Dayia-Isorthis* fauna followed by shales with *Lingula lata* and *Saetograptus leintwardinensis*. This latter association is very interesting when it is recalled that in the upper Llandovery the *Lingula* community is in the shallowest belt and the graptolitic beds in the deepest belt. Above this fauna comes the distinctive *Aegiria grayi-Neobeyrichia lauensis* assemblage, followed by a *Dayia-Protochonetes-Fuchsella* assemblage and then a typical *Protochonetes-Salopina* assemblage as on the shelf. This is only a very generalized pattern covering a large area but it serves to demonstrate the limitations of a palaeoecological interpretation based only on brachiopod communities and also includes some distinctive associations not recognized by Calef and Hancock.

ASSEMBLAGES AS COMMUNITIES

If four major benthonic assemblages are worthy of recognition in the shelf Ludlow it is here maintained that the above lists are a more accurate record of the associations of the fossils than are the lists of Calef and Hancock, even allowing for their restriction to brachiopods. The palaeoecological significance of these major assemblages must, however, be questioned. Are they, for instance, communities?

In its normal, non-biological usage the term 'community' suggests that the components have something in common, some interdependence, which results in a nucleated gathering. In palaeontology the term has come to be used quite commonly, as in Calef and Hancock's paper for a completely intergrading life-assemblage. It consists of a number of species inhabiting the same area at the same time. In the case of the major shelf assemblages listed above it should be realized that the forms recorded occur over an area of 12 000 sq km and each assemblage spans at least 30 m of strata, i.e. at least one million years of time. The same applies to the communities of Calef and Hancock. They might claim that this is not a serious objection if one is concerned with the regional palaeogeographical picture. There are, however, lateral and vertical faunal variations within these major assemblages which may have greater palaeoecological and palaeogeographical significance than the differences between the major faunal units. An example of significant lateral variation occurs in the *Dayia-Isorthis* assemblage of Leintwardinian age; the eastern shelf is characterized by the common occurrence of *Protochonetes ludloviensis* and *Salopina lunata* in the siltier near-shore shallow-water facies (Holland and Lawson 1963, p. 287)

whereas the shelf-edge area, muddier and perhaps deeper, shows a reduced abundance of these species and the increased importance of *Dayia navicula* and *Shagamella ludloviensis*. Vertical variation is well illustrated in the Bringewoodian of the western shelf where the *Strophonella-Gypidula* assemblage can be divided into a lower *Amphistrophia funiculata* fauna and an upper *Kirkidium-Favosites* fauna. Are these minor assemblages communities in the sense that the constituent species inhabited the same place at the same time—in the same depth of water? It is doubtful, for Newall (1966) has subdivided the *Kirkidium-Favosites* fauna into three units of palaeoecological significance viz.:

1. *Atrypa-Strophonella* units formed in conditions of least turbulence.
2. Coral units of tabulate coral colonies formed in the shallow photic zone in conditions of fairly high turbulence.
3. *Kirkidium* units formed in a high-energy environment and possibly within the breaker zone.

Such faunal units, of depth significance, are completely masked by being lumped together in major assemblages or communities. Even the units mentioned above, usually several feet thick, may benefit from refinement. Contrary to the statement by Calef and Hancock (1974, p. 780), Ludlow fossils commonly occur in bands, often dominated by particular fossils. Studies of these bedding-plane assemblages would probably repay study; there may even be more than one community on one bedding plane! In the Leintwardinian of the eastern shelf successive bedding planes are often dominated by *Isorthis*, *Sphaerirhynchia*, and *Protochonetes* with *Salopina* in turn; it is surely too much to postulate depth changes every few centimetres through the succession to explain the repetition of Calef and Hancock's communities.

The ultimate degree of refinement is to investigate the palaeoecology of the individual species, paying particular attention to its relationship to the sediment and to the possible functional significance of some of its morphological characters. Mr. John Hurst, of Oxford University, has already derived significant results from some such studies on Silurian brachiopods (Fürsich and Hurst 1974).

BRACHIOPOD COMMUNITIES

The community tables published by Calef and Hancock (1974, p. 783) are based solely on the brachiopod fraction of the fauna for two reasons: (1) brachiopods generally make up at least 90% of the total fauna, (2) the taxonomic uncertainty is less with brachiopods than with most other groups. This second reason is particularly unconvincing as the trilobites and ostracods have been quite well studied and even the neglected groups, such as corals, bivalves, gastropods, worms, bryozoa, can often yield information of palaeoecological significance in spite of their nomenclatorial imprecision. The first point, on the dominance of brachiopods, can be seen to be well justified from the lists published here. Nevertheless, non-brachiopods are evidently not unimportant. Indeed, in the *Protochonetes-Salopina* fauna here listed, ten out of the seventeen fossils are *not* brachiopods, bivalves being particularly important. It has already been pointed out that there are important coral units on the main shelf

and a bivalve assemblage in the Llandeilo-Llandovery area during Bringewoodian times.

It must, however, be appreciated that the study of brachiopod communities has yielded important ideas on Silurian palaeogeography in recent years. It would be interesting to see to what extent the study of the non-brachiopods will confirm, refine, or contradict these ideas. Corals, stromatoporoids, and algae should certainly be helpful as depth-indicators particularly in the Wenlock and in the carbonate developments. It should be emphasized in this respect that Calef and Hancock's study is restricted to the clastic rocks.

DEPTH COMMUNITIES

Calef and Hancock wisely refer to depth-related communities rather than depth-controlled communities. It is difficult to understand how depth can directly control the distribution of organisms in the sea. Nevertheless, most of the controlling factors normally vary with depth—some directly, such as pressure, light, and temperature and some less inevitably such as substrate, sedimentation, turbulence, salinity, and food supply. Muddy substrate and still water are commonest at greater depth but are not uncommon in shallow water; hence the need for caution.

The depth-patterns plotted for the upper Llandovery (Ziegler 1965) nevertheless seem convincing proof of the depth-relationship of the communities. Even here there is need for some caution as a progression from onshore to offshore does not always correlate with increasing depth. Indeed, in the case of the middle Ludlow, Alexander (1963, pp. 111–112) adduced evidence that the shell-banks of *Kirkidium* accumulated on a shelf-edge ridge, i.e. in very shallow water even though far off shore.

Calef and Hancock do not, however, produce such depth-pattern maps for the Ludlovian, to demonstrate their communities succeeding each other laterally and basinwards at particular times. The main reason for this (Hancock, pers. comm.) is their uncertainty about precise time-correlations in the Ludlow rocks of the Welsh Borderlands. Presumably, they require lineage zones such as have been established for the upper Llandovery based on the evolution of *Eocoelia*, etc. These zones did not, however, prove the established graptolite zones to be inadequate or diachronous and it is therefore not clear why the widespread graptolite zones of *Diversograptus nilssoni* and *Saetograptus leintwardinensis* are not acceptable in the Ludlovian. If the correlation by Holland, Lawson and Walmsley (1963, p. 150, Table 2) is followed, Calef and Hancock's communities can be plotted for each of the stages of the Ludlow. No clear patterns emerge, partly because more data are needed and partly because single communities tend to spread over most of the shelf, perhaps because the slope was much more gentle than in the Llandovery. There are also some puzzling anomalies. In the lower Eltonian the south-eastern inliers of Usk, May Hill, and Woolhope display a *Dicoelosia* community whereas the further offshore area of Wenlock Edge has a 'shallower' *Isorthis* community. In the Bringewoodian the *Isorthis* community occurs at Ludlow and Wenlock Edge but the 'deeper-water' *Dicoelosia* community is reported from May Hill, which is well on to the shelf. The Leintwardinian plots show an equal mixture of *Sphaerirhynchia* and *Salopina* communities at Usk and

May Hill—apparently completely, not merely marginally, overlapping. The *Isorthis* community is reported from Ludlow, which is indeed further offshore in the traditional interpretation. In the Whitcliffian, the *Salopina* community is widespread, occurring at Usk and May Hill on the inner shelf, at Ludlow on the outer shelf, and at Bult in the basin. At Woolhope, however, on the inner shelf a *Sphaerirhynchia* community is recorded. The direct interpretation of these communities in terms of depths therefore results in inconsistent and confusing patterns.

Calef and Hancock state (1974, p. 797) that 'no good correlation has been seen between sediment type and community within the clastic facies covered by this paper'. This is contrary to the experience of previous workers who have felt compelled to refer informally to the '*Dicoelosia* mudstones' (actually fine siltstones), the 'strophomenid siltstones', the '*Dayia* shales', and the '*Chonetes* flags'. It would be interesting to know whether the *Dicoelosia* community of Calef and Hancock has ever been found other than in fine olive siltstones with irregular bedding.

Nevertheless, the suggestion that the *Salopina* community normally inhabited shallower water than the *Dicoelosia* community is not disputed. Also, Calef and Hancock's use of density and diversity indices to interpret depths is a welcome new approach, to be used with caution.

CONTINUOUS REGRESSION

Calef and Hancock contend that the upward Ludlow succession represents a single regression and (1974, p. 800) 'have found no evidence of widespread cyclic transgressions and regressions such as those postulated by Phipps and Reeve (1967, fig. 6) for the Malvern Hills area'. It is here maintained that there is adequate evidence from both the sediments and the fauna that the pattern figured by Phipps and Reeve is the regional picture for the shelf area. The Main Outcrop (Wenlock Edge to Aymestrey) confirms this. The *Dicoelosia* mudstones of the Lower Elton Beds obviously accumulated in still water with a muddy substrate; the high faunal diversity and low density lead Calef and Hancock to the conclusion that the water was relatively deep. This seems quite acceptable.

The succeeding Middle Elton Beds are characterized by graptolites and orthocones with a very small benthonic fauna. It has usually been considered that these deposits probably represent a further deepening of the sea. Calef and Hancock record a *Visbyella* community from the Middle Elton Beds of Ludlow and presumably agree on this continued deepening (perhaps to 1000 or 1500 m according to Hancock, Hurst and Fürsich 1974) rather than a regression. The graptolitic Upper Elton Beds contain slumps and few benthonic forms. They pass up into the richly benthonic *Strophonella-Gypidula* calcareous siltstones of the Lower Bringewood Beds which are succeeded by the *Kirkidium-Favosites* limestones of the Upper Bringewood Beds. Newall (1966) has concluded, from detailed palaeoecological studies, that the tabulate corals lived in moderately turbulent water and that the *Kirkidium* banks were probably within the breaker zone. Cross-bedding is fairly common (Whitaker 1962, p. 339) and is indicative of current action. Lawson has found algal remains in these beds at Aymestrey (Elliott 1971) suggesting water no deeper than 30 m. These indications of extreme shallowing are confirmed by the widespread occurrence of

a limestone conglomerate at the base of the succeeding Lower Leintwardine Beds, suggesting actual emergence of most of the shelf area. Oolites have been found at this level on Wenlock Edge (Shergold and Shirley 1968, pl. 126) and the occurrence there of the large ostracod *Leperditia* might be taken to indicate extreme shallowing as Berdan (1968) suggests that these ostracods were adapted to temporary subaerial exposure. The dark shales of the Lower Leintwardine Beds at Aymestrey containing a *Dayia navicula*-*Shagamella ludloviensis* sub-fauna plus *Saetograptus leintwardinensis* must therefore represent some degree of deepening as postulated by Phipps and Reeve (1967) not continued regression. This period of emergence in the middle Ludlow is even more convincingly demonstrated by Potter and Price (1965, p. 398) in the Llandovery-Llandeilo area where the Old Red Sandstone facies in the Bringewoodian Trichrûg Beds is succeeded by the fully marine *Dayia-Isorthis* assemblage (the *Sphaerirhynchia* community of Calef and Hancock) of the Leintwardinian. There is then general agreement on progressive shallowing up through the Whitcliffe Beds into the Downton Castle Sandstone, with its *Lingula*-mollusc assemblage.

The regional pattern for the shelf is therefore of two periods of maximum transgression (Middle Elton Beds and Lower Leintwardine Beds) and two periods of maximum regression (tops of the Bringewood Beds and Whitcliffe Beds), approximately as depicted by Phipps and Reeve (1967, fig. 6). The recognition of this pattern raises serious problems for the believers in depth communities. It means that the same depth of water probably obtained three, or even four, times in the Ludlovian period and yet there is no repetition of Calef and Hancock's depth-communities. The *Dicoelosia* mudstones, the strophomenid siltstones, and the *Dayia* shales may all have been deposited at similar depths and it may have been the difference in substrate (or some other factors) which resulted in the differences in faunal assemblage.

DIACHRONOUS COMMUNITIES

Although Calef and Hancock postulate a succession of regressive benthonic communities they do not explicitly suggest that these are diachronous in the way that the upper Llandovery communities are. This reticence may be due to their uncertainty about the precise time correlation of the Ludlow rocks. It has for long been recognized that the shelly faunas are largely facies dependent and the present Ludlow correlation from basin to shelf has therefore been based on the occurrences of graptolites, trilobites, and ostracods rather than brachiopods. The internationally recognizable graptolite zones of *Diversograptus nilssoni* and *Saetograptus leintwardinensis*, although best developed in the basin facies, spread well on to the shelf and interdigitate with the shelly divisions, particularly along Wenlock Edge. Furthermore, at the top of the Leintwardinian there occur not only the highest specimens of *Saetograptus leintwardinensis* but also the short-range species *Neobeyrichia lauensis* and *Calymene neointermedia* which occur together at a similar level on the Baltic island of Gotland.

If this correlation is accepted some of the brachiopod assemblages are seen to be diachronous. The brachiopods characteristic of the *Strophonella-Gypidula* assemblage appear in the Eltonian of the basin but in the Bringewoodian of the shelf. The *Protochonetes-Salopina* assemblage is strongly developed in the Leintwardinian of

the southern and eastern shelf but does not reach the basin areas of Kerry and Knighton until Whitcliffian times. Within the main shelf area diachronism of the shelly divisions is less easily demonstrated, perhaps because of fairly uniform conditions, including depth, over most of the area.

CONCLUSIONS

The four successive benthonic assemblages here listed for the Ludlow are considered to give a fuller and more accurate picture of the shelf faunas than the communities listed by Calef and Hancock, which seem to be based on inadequate sampling and are inevitably limited by restriction to brachiopods in clastic sediments. The palaeoecological significance of these four major assemblages is not clear. The minor assemblages, characterizing smaller thicknesses of rock, are likely to be closer to the life assemblages. The study of the functional morphology and facies preference of particular species is also a promising approach.

The recent emphasis on depth-communities has led to a neglect of other important, and more direct, environmental controls, particularly the nature of the substrate.

A consideration of sedimentary evidence demonstrates that Calef and Hancock's postulation of continuous regression throughout the Ludlow is unacceptable.

The present correlation of the Ludlow rocks, based mainly on graptolites, trilobites, and ostracods, is thought to be reasonably sound. Some of the shelly assemblages are, however, markedly diachronous from shelf to basin but not noticeably so on the main shelf.

It is concluded that the picture drawn by Calef and Hancock is an over-simplification resulting, perhaps, from an attempt to impose a relatively straightforward Llandovery pattern on to the more complex Ludlow rocks.

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