NOTES ON DISTRIBUTION AND MIGRATION OF BRACHIOPODA IN THE BRITISH AND IRISH LOWER PALAEOZOIC FAUNAS.†

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In studying Palaeozoic brachiopods I have been impressed by the fact that, apart from a few light-shelled and laciniate forms which may have drifted attached to seaweeds (*cf.* Ruedemann, 1934), all the others appear to have existed not far from coasts and within reach of currents sufficiently strong to overturn dead shells. Great difficulty is experienced in trying to determine the attitude during life of these fossils; and this corroborates Schuchert's argument that the invasion of deeper bottom waters by the Brachiopoda, where overturning would be less likely to occur, is a comparatively recent development (Schuchert, 1911).

The Lower Palaeozoic species were, it seems, restricted to shallow water, probably mainly within the 100 fathom line, beyond which in the desulphofication zone (Polynov, 1937, pp. 191-192) most graptolitic sediments were deposited. They were sessile save for a brief initial floating life possibly of only about two days if we may judge from modern larvae. Again arguing from present day forms there may have been considerable sensitivity to temperature. Since we are dealing with a marine environment we must also think of the necessity for an adequate supply of oxygen and the adverse influence on shell-growth of an over-abundance of carbon dioxide. We thus realise that wide and deep seas, climate, and muddy belts, as well as land probably served as barriers to migration.

That there was some barrier between Wales and the other Celtic countries in late Arenig and in Llanvirn times is evinced by the brachiopod fauna of the Shanghort and Tourmakeady beds (?Zone of *Didymograptus hirundo*) in Mayo and Galway (Gardiner, Reynolds, and Reed, 1909, pp. 124-5; 1910, p. 265). This fauna has many species which resemble those found apparently at a rather higher horizon in the Tramore Limestone Series in County Waterford, and at what is certainly a higher horizon in the Balcletchie beds, which yield *Dicranograptus tardiusculus*, at Girvan, Scotland. It includes early *Glyptorthis crispa* and

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Leptelloidea grayae, the latter specially characterising muddy beds, and it is very different from the Arenig-Llanvirn Welsh fauna. In parts of Wales *Orthis carausii* (Fig. 1), not recorded in Eire, is a prominent species especially in sandy beds. In fact, like the somewhat homoemorphic Caradocian species *Nicolella actoniae*, it appears to have a long time range, appearing whenever conditions suited it.

The coarse-ribbed, plano-convex *Orthis carausii* finds its *optimum* environment in sands, *e.g.*, in Anglesey; and the narrow body-spaced, fine-ribbed *Leptelloidea grayae* does particularly well in muds, *e.g.*, those at the top of the Tramore Limestone Series where most other brachiopods are absent. In contrast with each of these we may take the bi-convex and rather bulky species of *Porambonites* which in many parts of the Lower Ordovician are abundant in limestones. At the base of the Tramore Limestone Series there is a rich development of *Porambonites filosa* and at the base of the Orthoceras Limestones in Scandinavia there is a similar development of *Porambonites intercedens*. These have been regarded by Davidson as varieties of each other (1869, pp. 195-7), and it might be tempting to correlate the two horizons. But correlation of facies by fossils which depend on facies means begging the stratigraphical question. At Lady Elizabeth's Cove, Tramore, I have recently found *Trinucleus hibernicus* several feet west of the upper margin of the diabase sheet. This seems to be higher than the graptolite horizon in baked sediments from which *Mesograptus foliaceus* and *Nemagraptus gracilis* have been obtained (Reed, 1899, p. 730). The Upper Tramore Limestone fauna thus appears to enclose the graptolite horizon, and if we place emphasis on *N. gracilis*, the top of the Tramore Limestone must reach into the Caradocian.

For the source of the Scots-Irish brachiopods of the early Ordovician one looks westward. The work of Willard and Raymond (1928, pp. 307-309) is important in this connection. It relates Scottish Stinchar and Balcletchie species with those of the Southern Appalachians of like date, although specific identity has in no case been established.

In the case of the Irish dalmanellid, referred to *Orthis argentea*, from the Raheen shales (which succeed the Tramore Limestone and actually contain *Tretaspis* cf. *cerioides*, a trilobite very much earlier in its appearance in Eire than in Scandinavia), it is difficult to draw a clear distinction from primitive dalmanellids in Wales. At some time between Llanvirn and Caradocian the two areas may have been open to immigration from the same source if not at times directly communicating.

Even if this was so, the two zoological provinces were soon separated again, for in the Caradocian generally the Spartan sameness of the Anglo-Welsh fauna, with its repetition of species belonging to a few genera like *Wattsella* and *Kjaerina* contrasts strangely with the Athenian variety of the western fauna. It is not that there are no changes in the Anglo-Welsh environment. We have sand and sandy limestones yielding species like *Dinorthis*

Typical Sandy Facies Species.

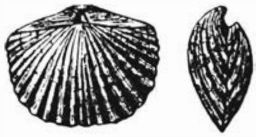

Fig. 1.
Orthis carausii Salter MS,
Tremanhire, near St. David's. x $1\frac{1}{2}$.

Fig. 2.
Nicolella actoniae var. *asteroidea*
Reed, Starfish Bed, Up. Drummuck
Group, Girvan. x $1\frac{1}{2}$.

flabellulum, *Nicolella actoniae*, and *Orthis calligramma*, with large body-volume and coarse ribbing (Figs. 1-2)—all poor horizon markers. We have shales with compressed or diminutive individuals that seem to be adapted to the poverty in oxygen of sea-water above muds. *Sowerbyella*, for instance, with its narrow body, probably used a minimum of oxygen, while its extended apertural margin allowed it to collect oxygen from as

Sowerbyellae Characteristic of Muds.

Fig. 3.
Sowerbyella semirugata
(Reed), Balcletchie mud-
stones, Girvan. x 2.

Fig. 4.
Sowerbyella undulata
(Salter) var., Saugh
Hill shales, Woodland
Point, Girvan. x $1\frac{2}{3}$.

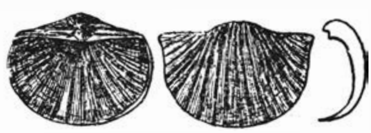

Fig. 5.
*Sowerbyella transver-
salis* (J. de C. Sowerby),
Wenlock shales, Pent-
land Hills. x 2.

large an area of water as possible (Figs. 3-5) (Lamont, 1934 *a*, *b*). In spite, however, of the existence of most types of deposit from coastal sands, through grey shales and limestones, down to the black putrefying graptolite shales in the bathyal* belt where brachiopod life became impossible, the Scots-Irish fauna does not penetrate into the other province.

Till lately palaeontologists have been inclined to try to explain the divergence in faunas by difference of bottom facies and temperature, etc., but the sediments cover so many types and so many genera are involved among brachiopods and more motile groups, that I am driven to agree with Professor O. T. Jones (1938) in favour of an Irish Sea land-mass stretching southwestward from Anglesey. There seems to be evidence of such a barrier having run through the Saltee Islands. A few miles west of these at Carrickadaggan and Fethard we find shallow water deposits including a conglomerate, probably the coastal detritus from the barrier we desire. At the same time we have in the Saltees an ancient granite, associated with dioritic

*From about 600 to 4,500 feet.

intrusions similar to those of known Ordovician date, and foliated especially on its margins apparently by the pressures from the north-east which have thrown the Ordovician rocks of Waterford and Wexford in isoclines against the old coast from which they seem to have been derived.

The later history of the barrier has not been made out fully. One would like to know how it behaved during the time represented by the widespread unconformity between the Caradocian and Ashgillian in the Irish Sea area. We do know, however, that it was effectively breached in Lower Ashgillian times when the contemporary representatives of the Scots-Irish fauna invaded the Anglo-Welsh area. Two good examples of the Ashgillian conquest are the appearance of *Schizophorella fallax,* till now only known at Pomeroy and Girvan, in the Dolhir beds at Glyn Ceiriog, and the occurrence of *Fardenia* cf. *scotica*, a Scottish Lower Drummuck species (Lamont, 1935, pp. 311-2), in the Cyrn-y-brain beds at Llangollen. Equally significant is the arrival of the trilobite genera *Remopleurides* and *Tretaspis* in the Ashgillian of the Pwllheli district (Matley, 1938, p. 593).

That the invading fauna was closely allied to that in North America is shown by Schuchert and Cooper's work (1930) on the Percé, Quebec, fauna which contains species not far removed from some of ours. For example, *Diambonia septata* from Percé is almost identical with *Diambonia discuneata* from the Lower Drummuck beds, and the abundant *Plectatrypae* of Gaspé probably may be compared with those of the Chair of Kildare.

The Silurian brachiopod faunas are rather cosmopolitan. There was land in south-eastern Eire and in the neighbourhood of County Kerry, but it did not prevent migration. Speaking generally the muds of the Silurian had much less volcanic material in them than those of the Ordovician, and were for the most part less oxygen absorptive (*cf.* Miyadi, 1934). Another factor is that there seem to have been wider areas of shallow water, and it is evident that, on the average, oxygen content will rise as surface area in relation to depth increases. Temperature was very prob-

Pentamerids from Limestone.

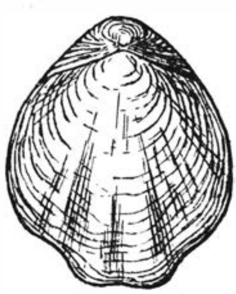

Fig. 6.
Pentamerus oblongus J. de C. Sowerby, Harper's Dingle, Salop. x $\frac{2}{3}$

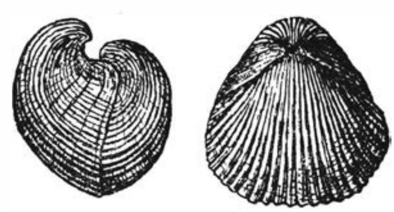

Fig. 7.
Conchidium knightii (J. Sowerby), Aymestry Limestone, Weo Quarry, Salop. Small examples x $\frac{2}{3}$.

ably another factor of importance, especially for heavy shelled forms like *Pentamerus oblongus* and *Conchidium knightii* (Figs. 6-7). These favoured limestone seas where the temperature was high enough to ensure that the amount of dissolved carbon dioxide would be at a minimum and so not hinder the deposition of calcium carbonate in shells; in addition, they are bulky and would require a good deal of oxygen, which also is lost as the temperature of water rises. One therefore thinks that these large species ran the gauntlet between two sets of conditions and could only exist in an area when a certain equilibrium was maintained.

In the maroon Upper Llandovery shales in a boring lately made at Walsall, England, there are well grown specimens of *Brachyprion*, *Schuchertella*, and *Stricklandia*. The last gives giant forms, but one notes that these have a longer anterior-lateral margin in relation to body volume than the numerous individuals of small *Stricklandia lirata* forma α in contemporaneous coastal sand at Rubery. The reddish muds seem to have had no great organic content while the relative absence of volcanicity meant that the sedimentary material was derived mainly from Cambrian shales, etc., which had been exposed on a land area during the whole of Ordovician time and had probably reached an advanced phase of weathering. Furthermore the occurrence of current-bedded silts at many horizons in the Upper Llandovery at Walsall (Butler, 1937, p. 251) points to sufficient disturbance, presumably by wind, to maintain an oxygen supply even in face of considerable absorption by the sea-floor.

The problem still remains, however, why *Pentamerus oblongus* is only present in one thin layer in the 300 feet of Upper Llandovery strata described by A. J. Butler. This problem of the distribution of *P. oblongus* becomes more insistent when we find at Ferriter's Cove, in Kerry, that it and at a slightly lower horizon *Stricklandia lirata* are associated with fossils of Wenlock type (Gardiner, Reynolds, and Reed, 1902, pp. 207-8). It may have been that the Llandovery climate of the Kerry area was warmer than that in England,† and that in this way a low concentration of carbon dioxide in Kerry waters allowed the richly calcitic Wenlock fauna to flourish there earlier than in Shropshire and the English Midlands, whilst the extremely shallow sea probably on an exposed island coast permitted a sufficiency of oxygen for the large-bodied pentamerids.

There are other anomalies in the Silurian of County Kerry which suggest that the appearance of certain Llandovery-Wenlock-Ludlow species, rather than being of zonal significance, may be controlled by temperature, etc. In England a particularly good example of this is provided by the appearance of large *Conchidium knightii* in the Woolhope Limestone near Kington (Garwood and Goodyear, 1919, p. 17) and in the Wenlock Limestone at Dudley (Ketley Collection, University of Birmingham),

†The thick development of the Woolhope Limestone in Radnorshire and Herefordshire probably also indicates warmer conditions as one goes towards the south-west.

as well as in abundance in the Aymestry Limestone. Only a purely local correlation can be based on such a species until we have much more knowledge of mutation in time and response to environment.

While we are dealing with climate one last question suggests itself. What is the significance of the area of very rapid growth recognised by Ma (1937, pp. 177-82), from his work on fossil corals of Ordovician and Silurian date, in Greenland, Huron, Ohio, and Indiana? Did rapid evolution of other groups take place on the borders of this favoured region? Did successive waves of invaders reach our area from it?

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