

A PHENETIC STRATEGY MODEL FOR DALMANELLID BRACHIOPODS

by J. M. HURST

ABSTRACT. A detailed morphological study, through a sequence of nearshore to offshore sedimentary facies, of the Ordovician dalmanellid *Onniella* and the Silurian *Isorthis*, suggests that there is a positive correlation between environment and morphotype. A phenetic strategy model is proposed in which offshore dalmanellid populations are characterized by deep, rounded sulcate shells, V-shaped deep pedicle muscle fields, strong crural fossettes, strongly impressed dorsal adductor muscle fields (i.e. quadripartite), large non-restricted brachial valve sockets, and coarse costellae. By contrast, nearshore dalmanellid populations are characterized by transverse, shallow, non-sulcate shells with U-shaped shallow pedicle muscle fields, weak crural fossettes, weakly impressed dorsal adductor muscle fields, restricted brachial valve sockets, buttressed brachioophores, and fine costellae. There are exceptions to the model but generally the positive correlation, which is explained in terms of functional necessity, has repercussions on previously proposed species phylogenies and their use as biostratigraphic indicators.

DALMANELLID brachiopods are abundant in most Lower Palaeozoic facies, and individual genera and species are often very widespread spatially as well as temporally. These two factors, combined with the morphological simplicity of the group (see Williams and Wright 1963), provide an ideal opportunity to study aspects of phenetic variation.

The aim of this report is to present a basic phenetic model for various dalmanellid genera in Lower Palaeozoic clastic facies, and is organized around two basic topics. The first of these involves the documentation of phenetic variability patterns of populations of *Onniella* through the type upper Caradoc (Ordovician) rocks of south Shropshire (text-fig. 1). These patterns are then compared directly with the Silurian genus *Isorthis*, again based mainly on populations from the Ludlow clastics of the Welsh Borderland. The utility of any model depends upon the extent to which it can be tested: that presented here is eminently testable.

SAMPLING AND METHODS

The samples used for the *Onniella* and *Isorthis* part of the study were obtained for bulk collections of fossils made for quantitative palaeoecological purposes (see Hurst and Hewitt 1977; Hurst and Watkins 1978). Sampling was carried out through continuous profiles with a maximum of 1 m stratigraphically between adjacent samples, and additional bed-by-bed collecting was undertaken at transition points between sedimentary facies.

The majority of *Onniella* and *Isorthis* samples were derived from bioturbated muds and silts in which current-produced sedimentary structures were absent. These occurrences correspond to the 'disturbed neighbourhood assemblages' of Scott (1974) and, despite their 'time-averaged' nature, are the nearest approximation to a local species population in the sense of Mayr (1963). The main difference between the biological population and the disturbed neighbourhood assemblage sample is that

the latter is probably composed of several generations of interbreeding individuals. A very small number of samples derive from coquinas and concentrated swell lags, and these relate directly to mixing of bottom faunas due to the passage of storms (Brenner and Davies 1973; Goldring and Bridges 1973).

The taxonomic basis for this report is twofold. First, the upper Caradoc *Onniella* species of Bancroft (1928, 1945) have been revised by Hurst (1978), and secondly, Ludlow *Isorthis* species have been dealt with by Hurst and Watkins (1978). Briefly, samples of individuals, as qualified above, were statistically analysed following the procedure outlined by Williams (1962, 1963, 1974), in which the morphological variation is expressed quantitatively. Only samples or groups of samples which showed statistically significant morphological gaps (i.e. morphological non-overlap at the 95% confidence interval level) were considered to represent different morpho-species.

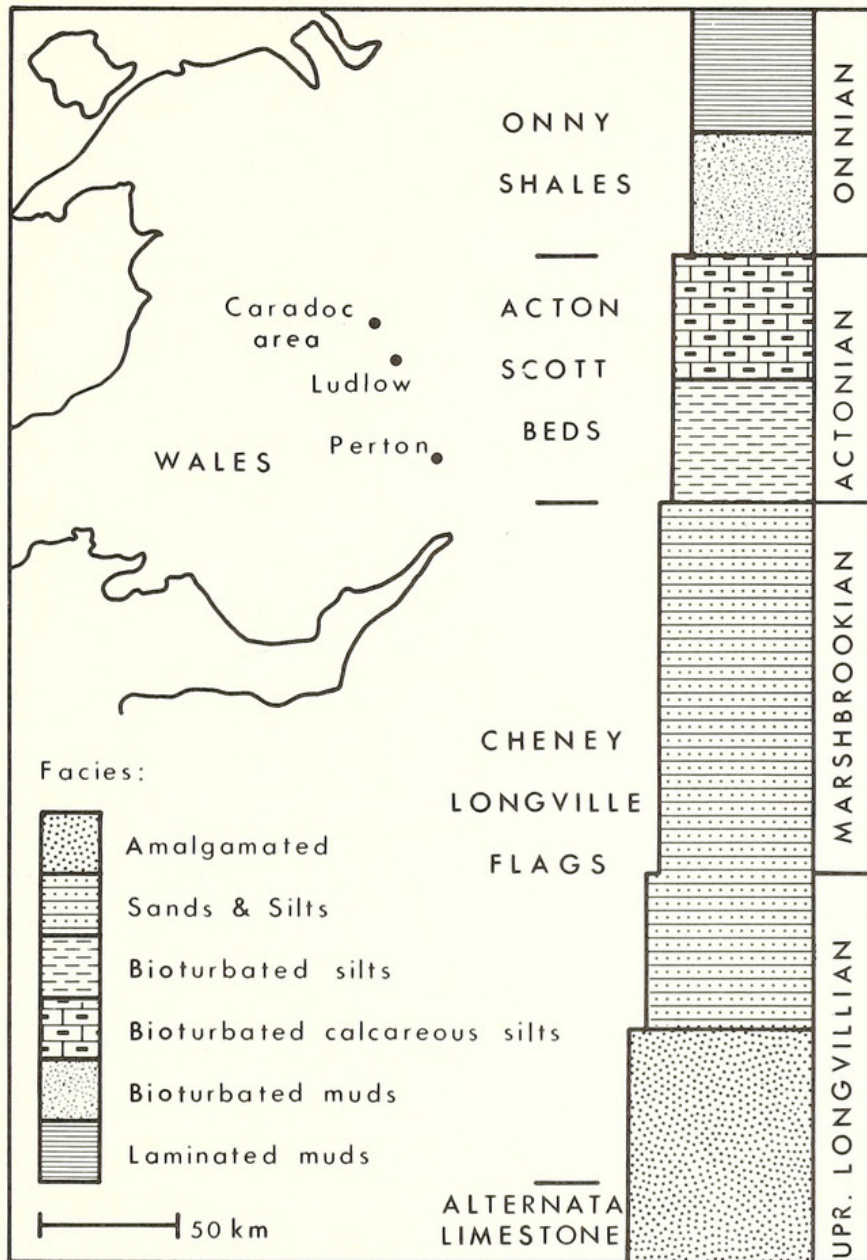
None of the *Onniella* or *Isorthis* statistical data will be reproduced here, but all of it has been placed in the British Museum (Natural History), London depository and is freely available from there, as well as on request from the author. It has also been deposited with the British Library, Boston Spa, Wetherby, Yorkshire, LS23 7BQ, U.K. as Supplementary Publication No. SUP 14010 (20 pages). Figured specimens prefixed by BB are deposited in the British Museum (Natural History), London, MGUH in the Mineralogisk and Geologisk Museum, Copenhagen, USNM in the United States National Museum, Washington, and OUMC in the University Museum, Oxford. Locality details of samples referred to in the text and diagrams (e.g. DH1) have been deposited, along with the collections themselves, in the British Museum (Natural History), London.

SEDIMENTARY FACIES

Major sedimentary facies in the upper Caradoc are shown in text-fig. 1, and those of the Ludlow in text-fig. 2. These vertical sequences of facies, which essentially represent a movement from nearshore to offshore environments in the Caradoc and vice versa in the Ludlow, have direct implications for the evolution of *Onniella* and *Isorthis*. Briefly the facies include:

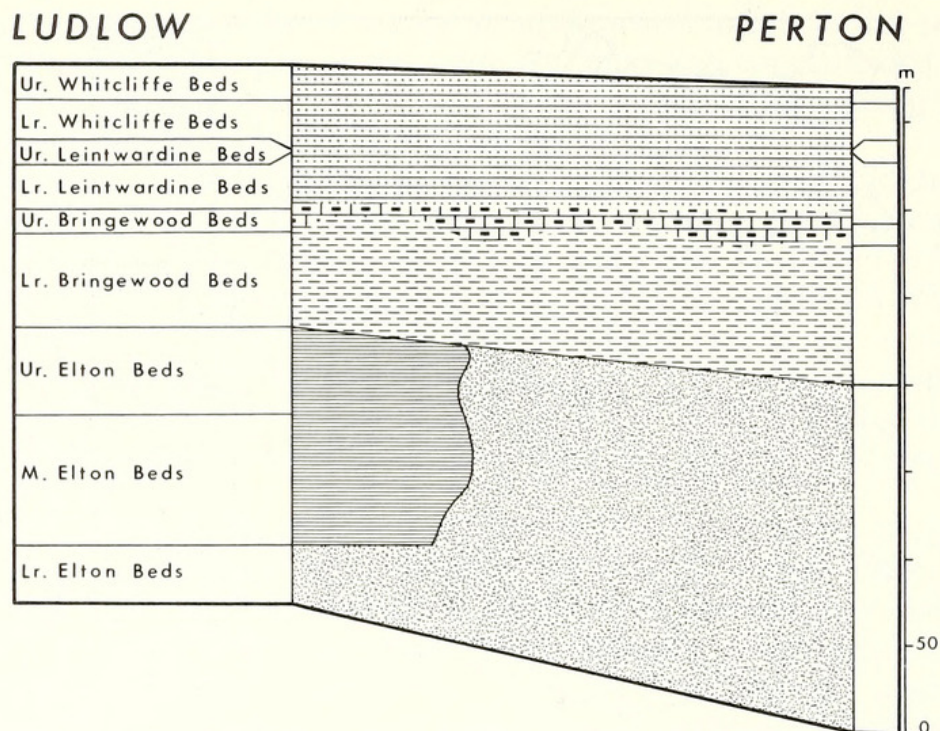
1. *Amalgamated facies* (text-fig. 1). This is known only from the Caradoc and consists of nearshore amalgamated beds of storm-deposited sandy silts and sands, with very occasional thin bioturbated silt partings. The bulk of the sediments are parallel or low angle cross laminated and contain shell lags, up to 50 cm thick in the *Alternata* Limestone, but which decrease in thickness and frequency into the lowest part of the Cheney Longville Flags. These shelf sediments were deposited totally under conditions of high energy and have been related to mass transport during storms (Gadow and Reineck 1969; Howard and Reineck 1972; Goldring and Bridges 1973; Reineck and Singh 1973).

2. *Sands and silt facies* (text-figs. 1 and 2). This consists of a sequence of bioturbated fine sands and sandy silts interbedded with discrete tabular sheets of laminated fine sand. The thickness and frequency of these tabular sand sheets decrease upwards through the Cheney Longville Flags (text-fig. 1), but increase upwards from the Lower Leintwardine Beds into the Whitcliffe Beds in the Ludlow (text-fig. 2). At the



TEXT-FIG. 1. Sketch map of Wales showing the location of the Caradoc area, and giving a generalized stratigraphic facies sequence of the upper Caradoc rocks, based on the Onny Valley section.

same time there is an increase (Caradoc) and decrease (Ludlow) of interbedded bioturbated sediments. The bioturbated sands and sandy silts contain a scattered, low-diversity shelly fauna dominated by articulate brachiopods, which is similar to a 'disturbed neighbourhood assemblage' of Scott (1974). The tabular laminated sand sheets, which are also the result of storm action (Goldring and Bridges 1973) have erosional bases and often contain basal lags of transported shells. The uppermost Cheney Longville Flags consist of bioturbated sandy silts with rare, isolated, thin, and partially bioturbated tabular sand layers. Numerous thin layers of convex-upward shells form swell lags which are similar to the ones described from the Jurassic of America by Brenner and Davies (1973) and result from distal storm action.



TEXT-FIG. 2. Ludlow stratigraphy and facies of the shelf areas of the Welsh Borderland (redrawn from Watkins 1978). See text-fig. 1 for facies symbols and geographic location of Ludlow and Perton. Note that the Ludlow bioturbated calcareous siltstone facies is drawn for the sake of convenience to include the Aymestry Limestone, which is a purer carbonate facies (see Watkins 1978).

3. *Bioturbated silt facies* (text-figs. 1 and 2). This facies is the more distal equivalent of the nearshore storm-deposited facies, and is formed by the low-energy settling of suspended silt and mud, which is subsequently thoroughly reworked by infauna. Swell lags are present, as are thin (2–5 cm) laminated silt layers in the Ludlow equivalent.

4. *Bioturbated calcareous silt facies* (text-figs. 1 and 2). This facies displays the same general features as the previous one, except that it has a very high carbonate content, and no swell lags are known from the Caradoc.

5. *Bioturbated mud facies* (text-figs. 1 and 2). These are probably the most quiet-water offshore deposits in the upper Caradoc and Ludlow sequences, and consist of somewhat calcareous, thoroughly bioturbated muds. This facies corresponds to the shelf mud facies of Reineck and Singh (1973). Occasionally, thin laminated silt layers (2–5 cm) occur in the Ludlow.

6. *Laminated shale facies* (text-figs. 1 and 2). This facies is characterized by parallel lamination; the laminae are formed of different grain sizes of silt and mud a few millimetres thick. Bioturbation is low or absent. The grain size and composition are similar to those in the bioturbated mud facies, and these two facies probably represent lateral equivalents of each other. The lamination is probably due to the inhibition of infauna, a feature which on modern shelves is related to very low concentrations of dissolved oxygen (Emery and Hüslemann 1961; Calvert 1964). Fauna is rare and

consists primarily of trilobites and graptolites. Benthic shells, primarily species from the bioturbated mud facies, are very rare.

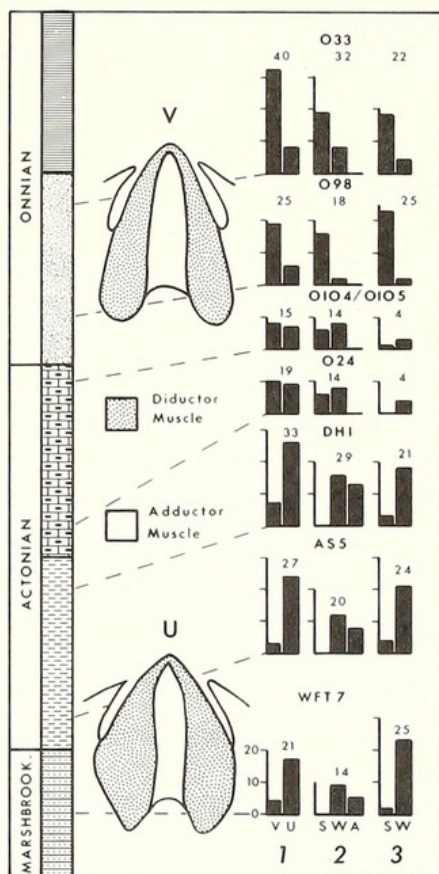
These sedimentary facies represent a movement from nearshore, shallow-water, high-energy areas, subject to frequent episodic rates of sediment deposition (amalgamated facies), through to offshore, deeper, quiet-water areas with slower, probably more constant sedimentation rates (bioturbated mud facies). The intermediate facies represent a combination of environmental factors. Examination of text-figs. 1 and 2 reveals that the upper Caradoc represents a transgressive sequence whilst the shelf Ludlow represents a regressive sequence.

ONNIELLA PHENETIC PATTERNS

The morphological and population trends of the component species of upper Caradoc *Onniella* are shown in Plate 57. Populations show a stratigraphic sequence of *O. reuschi* → *O. depressa* → *O. broeggeri*, which directly corresponds to a transgressive depositional sequence of sands and silts/bioturbated silts → bioturbated carbonate silts → bioturbated muds. *O. reuschi* is a member of the middle shelf communities, whilst *O. depressa* and *O. broeggeri* are members of the more distal shelf communities. The main morphological trends seen in *Onniella* involve: a decrease in shell size and an increase in pedicle valve depth; less transverse shells; a change from population predominantly with a U- to ones with a V-shaped pedicle diductor muscle field (Pl. 57; text-fig. 3); a complementary increase in pedicle diductor muscle field depth (i.e. increase to strongly impressed forms; Pl. 57); an increase in members of the population with strong crural fossettes (text-fig. 3); an increase in size of the sockets adjacent to the brachiorhynchophores (this is often masked in large specimens of *O. broeggeri* by secondary calcite deposition around the brachiorhynchophore) and related to this is the fairly common occurrence of incipient fulcral plate development in *O. reuschi* specimens (Pl. 57, fig. 23); increase in dorsal adductor muscle field impression, resulting in quadripartite appearance and increase in coarseness of ribs and sulcal development (Pl. 57; text-fig. 3; Hurst 1978).

The above data suggest a positive correlation between species morphology and sedimentary facies. Further, the above information on *Onniella* is based on analysis of sections in and around the Onny Valley (see Dean 1958, 1964 and Greig *et al.* 1968 for local stratigraphic and geographic details). However, to the north of the Onny Valley, in the vicinity of Acton Scott (see Dean 1958), the middle Actonian consists of bioturbated sandy silts, similar to the uppermost Cheney Longville Flags sediments. These sediments follow on from the bioturbated calcareous silt facies and indicate a local slight regressive event. Not only is the fauna of this restricted Actonian facies identical in species composition and relative abundances to that of the uppermost Cheney Longville Flags, but the species of *Onniella* present is *O. reuschi* (see Pl. 57; Hurst 1978). Thus, in the Acton Scott area the stratigraphic sequence of *Onniella* is *O. reuschi* → *O. depressa* → *O. reuschi*. The bioturbated mud facies is not developed in the Acton Scott area and *O. broeggeri* is therefore absent. Consequently, during middle Actonian times *O. reuschi* exists contemporaneously with *O. depressa*, the former in the Acton Scott area and the latter in the Onny Valley region. As far as upper Caradoc *Onniella* are concerned, the morphological changes

and distribution patterns seen can be interpreted in one of two ways. First, the directional changes may represent simple ecological clines of characters (Mayr 1963) or, secondly, three distinct species may be restricted to certain sedimentary facies. Thus, as the facies migrates so does the species. The only way the problem may possibly be resolved is by examination of species at facies/ecological boundaries.



TEXT-FIG. 3. Histograms showing the stratigraphic change in V/U pedicle muscle field shape (1), strong, weak or absent crural fossettes (2), and strong or weak quadripartite dorsal muscle field (3), in progressive populations of *Onniella reuschi* (collections WFT7, AS5, and DH1), *O. depressa* (collections O24 and O104/O105) and *O. broeggeri* (collections O98 and O33). Note increase in proportion of population with a V-shaped muscle field, stronger crural fossettes, and quadripartite dorsal muscle field, from *O. reuschi* to *O. broeggeri*. Facies symbols explained in text-fig. 1. Collection localities explained in Hurst (1978) and deposited in the British Museum. Muscle-field diagrams schematically represent internal moulds of pedicle valves showing the classes V and U employed in this paper.

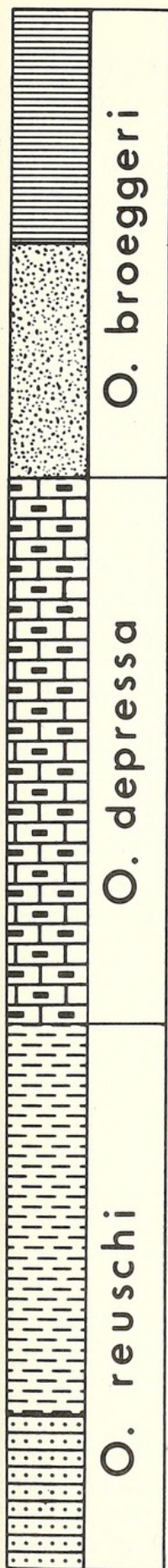
EXPLANATION OF PLATE 57

Upper Caradoc *Onniella* ecological clines. Note the morphological change from *O. reuschi* to *O. broeggeri* which, as far as can be ascertained, is continuous and positively correlated with changing sedimentary facies. Facies symbols explained in text-fig. 1. Stratigraphic extent of facies is not to scale.

Figs. 1–8. *O. broeggeri* Bancroft, 1928. Internal moulds of pedicle valves: 1, BB72463 $\times 4$; 2, BB72459 $\times 2.5$; 3, BB72451 $\times 2.5$; 4, BB72452 $\times 2.5$. Internal moulds of brachial valves: 5, BB72449 $\times 2.5$; 6, BB72457 $\times 2.5$; 7, BB72448 $\times 2.5$; 8, BB72455 $\times 3$. All specimens from Onny Shales, Grid ref. SO 4254 8538.

Figs. 9–16. *O. depressa* Bancroft, 1945. Internal moulds of pedicle valves: 9, BB72433 $\times 2.5$; 10, BB72435 $\times 4$; 11, BB72466 $\times 5$; 12, BB72444 $\times 2.5$. Internal moulds of brachial valves: 13, BB72445 $\times 2.5$; 14, BB72446 $\times 3$; 15, BB72440 $\times 3$; 16, BB72439 $\times 2.5$. Figured specimens 9 and 10 from the Acton Scott Beds, Grid ref. SO 4238 8538; 11 from the Acton Scott Beds, Grid ref. SO 4505 9053; and the remaining specimens from the Acton Scott Beds, Grid ref. SO 4249 8538.

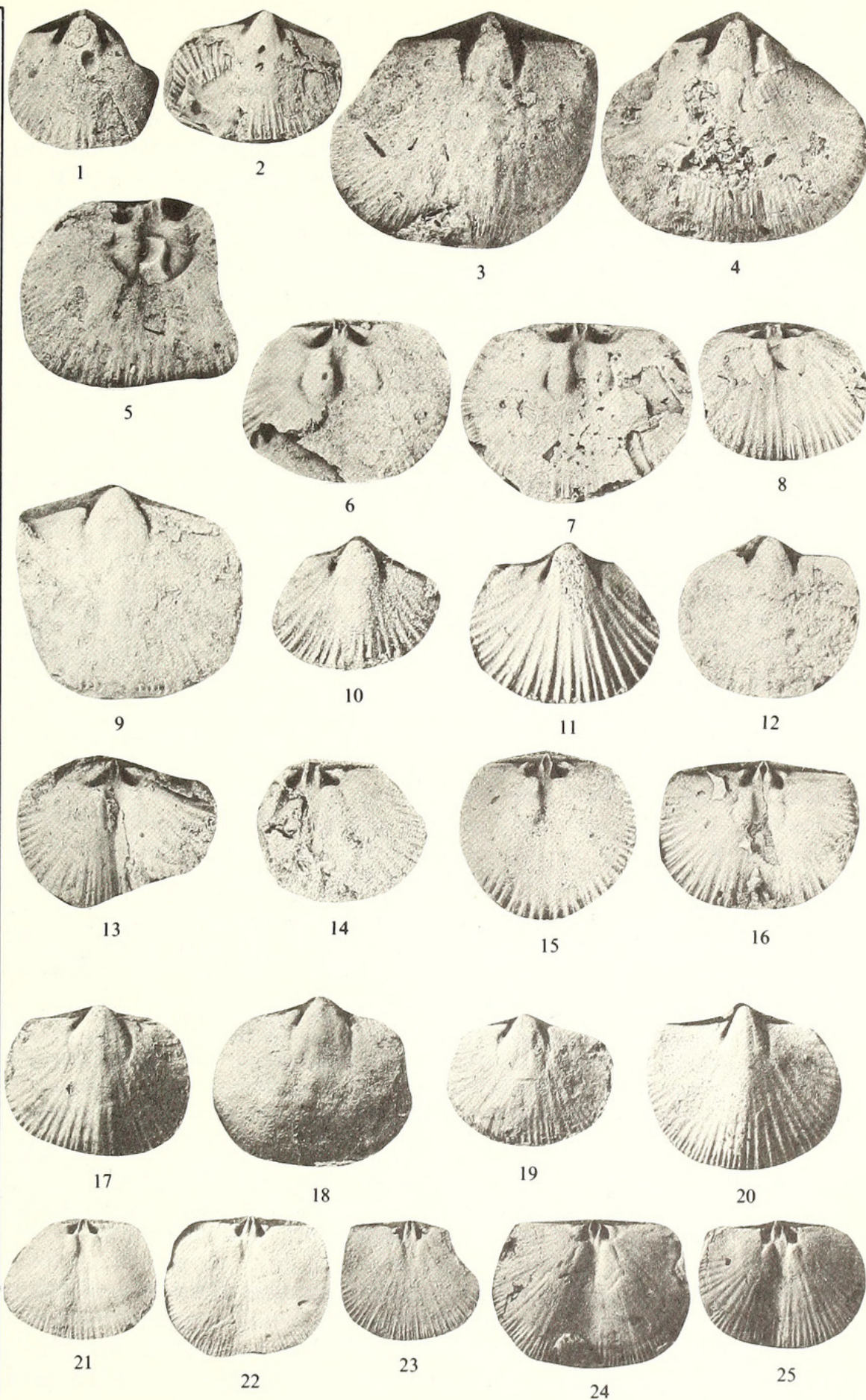
Figs. 17–25. *O. reuschi* Bancroft, 1928. Internal moulds of pedicle valves: 17, BB72419 $\times 2.2$; 18, BB72408 $\times 1.7$; 19, BB72421 $\times 2$; 20, BB72426 $\times 3$. Internal moulds of brachial valves: 21, BB72414 $\times 1.7$; 22, BB72415 $\times 1.8$; 23, BB72412 $\times 1.5$; 24, BB72423 $\times 1.9$; 25, BB72424 $\times 2.4$. Figured specimens 17 and 19 from the Acton Scott Beds, Grid ref. SO 4645 9025, and 20, 24, and 25 from the Acton Scott Beds, Grid ref. SO 4252 8600. Remaining figured specimens from the Cheney Longville Flags: 18, Grid ref. SO 4250 8729; 21, 22, and 23, Grid ref. SO 4448 8900.



O. broeggeri

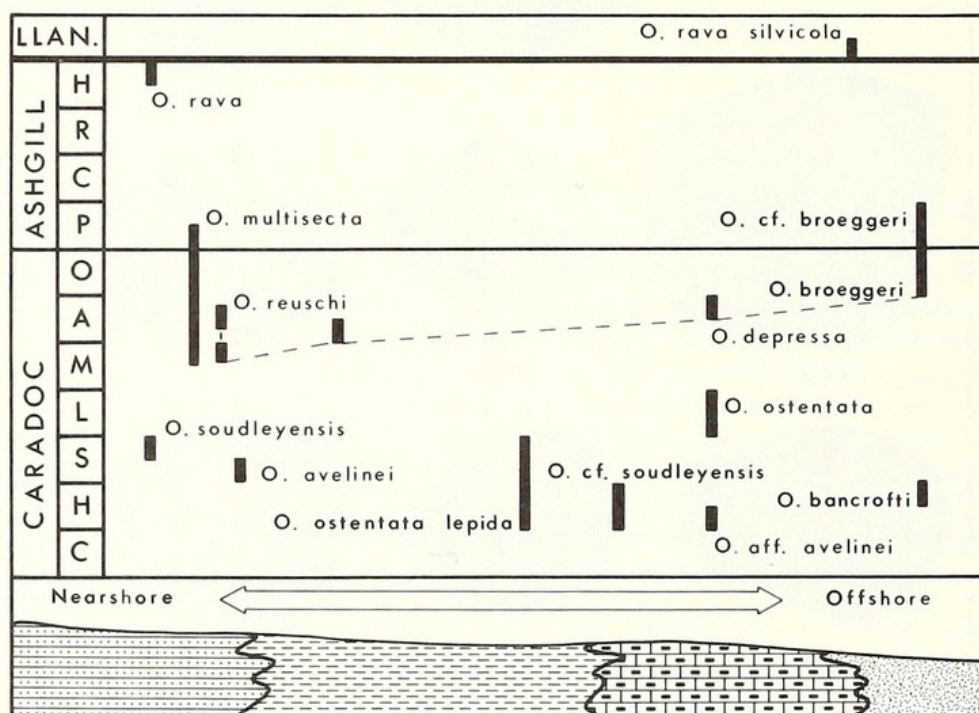
O. depressa

O. reuschi



This has not been possible in the area under discussion. However, these arguments are not critical to the central theme, that of a positive correlation between species, phenetic expression, and environmental/ecological occurrence.

With the intimate association of *Onniella* and sedimentary facies established in the upper Caradoc sequence, it may be possible to recognize such patterns of phenetic expression in other geographic areas and at different times. Comparing the same or similar environments through time may throw some light on differential rates of evolution in the *Onniella* complex. However, at the outset a word of caution must be given. The foregoing discussion is based on morphological species comparisons in which often little is known about the variability of the stocks involved and where their facies occurrences are sometimes ignored. Nevertheless, as some close comparisons are apparent, they are worth pursuing as they are pertinent to the central arguments presented here.



TEXT-FIG. 4. Clastic facies distribution and stratigraphic occurrence of some European and American Ordovician and Silurian *Onniella*. Data compiled from Bancroft (1928, 1945), Bassett *et al.* (1966), Bretsky (1969, 1970), Cave (1965), Dean (1958, 1964), Hurst (1978), Hurst and Hewitt (1977), Ingham (1966), Lindström (1953), Marek and Havlíček (1967), Temple (1970), Whittington and Williams (1955), and Williams (1963, 1974). Stage symbols, Caradoc: C = Costonian, H = Harnagian, S = Soudleyan, L = Longvillian, M = Marshbrookian, A = Actonian, O = Onnian; Ashgill: P = Pusgillian, C = Cautleyan, R = Rawtheyan, H = Hirnantian. Note the predominance of the species in the more offshore facies. Facies symbols explained in text-fig. 1.

Text-fig. 4 summarizes the facies and stratigraphic occurrence of many of the species of *Onniella* described from the western European Ordovician and early Llandovery (Silurian). Little data is included from north America, as most described species occur in carbonates (see Cooper 1956) making precise internal morphological comparison

difficult. Basically, for the ecological phenetic expression sequence to be maintained temporally, *Onniella* species occurring in bioturbated muds should phenetically resemble *O. broeggeri*, whilst those in bioturbated silts and sands and silts should compare closely with *O. reuschi*. Most of the nominal species in the Caradoc of Britain, shown in text-fig. 4, conform to the prescribed patterns (e.g. Pl. 59, fig. 2). To date the one exception is *O. soudleyensis* (Pl. 59, fig. 1), which occurs in the most proximal environment of any *Onniella* and cannot really be fitted into a scheme, although it does resemble *O. reuschi* in pedicle valve musculature, ribbing, dorsal muscle impression and valve depth.

Outside Britain, similar patterns are recognizable. Lindström (1953) described a fauna from the low Caradoc, Lower *Chasmops* Beds (bioturbated muds) of south Sweden, in which the dominance of *O. bancrofti* Lindström and *Sericoidea restricta* (Hadding) is a parallel feature of the bioturbated mud facies of the upper Caradoc (Dean 1958; Hurst 1978). *O. bancrofti* is morphologically very similar to *O. broeggeri* (see Lindström 1953, pl. 1), a fact Lindström commented on (*ibid.*, p. 133).

A further example which lends support to the correlation can be found in the work of Bretsky (1969, 1970) and Bretsky *et al.* (1969). In the Martinsburg Formation (Upper Ordovician) of America, Bretsky (1969, p. 201) described a *Sowerbyella-Onniella* community in a sands and silts facies very similar to that in the upper Cheney Longville Flags (see Hurst 1978); this is a parallel in the sense of Thorson (1957). The specimens of *O. multisecta* figured by Bretsky (1970, pl. 11) fall within the variation range of *O. reuschi* populations. Probably the most striking features of *O. multisecta* are the U-shaped pedicle muscle field, shallow pedicle valve, and weakly impressed dorsal muscle field, features diagnostic of *O. reuschi* (Hurst 1978).

In the late Ordovician there is the *O. rava* Marek and Havlíček species group (text-fig. 4), which appears morphologically distinct from the Caradoc complex. *O. rava* occurs in the Kosov Formation (Hirnantian, Ashgill) of Bohemia in near-shore sediments (Marek and Havlíček 1967). Temple (1970, pl. 4) erected the subspecies, *O. rava silvicola*, from Lower Llandovery blue siltstones with interbedded micaceous layers of Wales (text-fig. 4). This sedimentary description probably indicates that the subspecies occupied an offshore facies; the associated fauna indicates the offshore *Clorinda* community of Ziegler *et al.* (1968a). Temple (1970, p. 22) emphasizes that *O. rava silvicola* differs from *O. rava* as follows: a stronger fold and sulcus; more convex valves; coarser ribbing; and more massive supporting plates (cardinalia). These differences correlate with a gradient from middle to offshore shelf sedimentary environments, and exactly parallel the morphological trends seen between *O. reuschi* and *O. broeggeri*.

To summarize, the gross pattern of evolution of upper Caradoc *Onniella* is complex and may be accounted for in two ways: ecological clinal variation or species migration with sedimentary facies movement. If the complex is clinal, then by implication the genus is probably monospecific with all the described species simply representing morphotypes. The fact that the *O. rava* group also varies along an environmental gradient in a manner similar to that within the Caradoc complex, appears at first sight to lend support to the concept of clinally varying characters. However, the positive correlation between phenetic expression and environmental/ecological

occurrence may simply imply convergent adaptive evolution, with species proliferation related to facies. Most described *Onniella* species from clastic environments occur in offshore facies (text-fig. 4), and it is probable that the more proximal shelf species are episodically derived from the offshore population plexus. The late Ashgill *O. rava* group (text-fig. 4) also varies clinally in a manner similar to that within the Caradoc group, but it appears morphologically distinct.

ISORTHIS PHENETIC PATTERNS

The phenetic trends observed in upper Caradoc *Onniella* are also observed in the Siluro-Devonian dalmanellid *Isorthis*. Such features can be adequately explained with reference to the type Ludlow sections of the Welsh Borderland (text-fig. 2). A more comprehensive account of Siluro-Devonian *Isorthis* evolutionary trends can be found in Hurst and Watkins (1978).

The morphological and population trends of the component species of Welsh Borderland Ludlow *Isorthis* are shown in Plate 58. In short, populations of *I. clivosa* in the lowest Ludlow Elton Beds (text-fig. 2) show progressive and continuous shifts in range of morphological variation to *I. orbicularis* in the Leintwardine Beds. This change corresponds to a prograding depositional sequence of bioturbated muds → bioturbated silts and carbonate silts → sands and silts. The facies (see Watkins 1978) correspond directly to the Caradoc ones, except for the sands and silts (coquinoid siltstone facies of Watkins 1978), which are finer grained than those of the Caradoc. Stratigraphically above *I. orbicularis*, an *I. clivosa* population variant abruptly

EXPLANATION OF PLATE 58

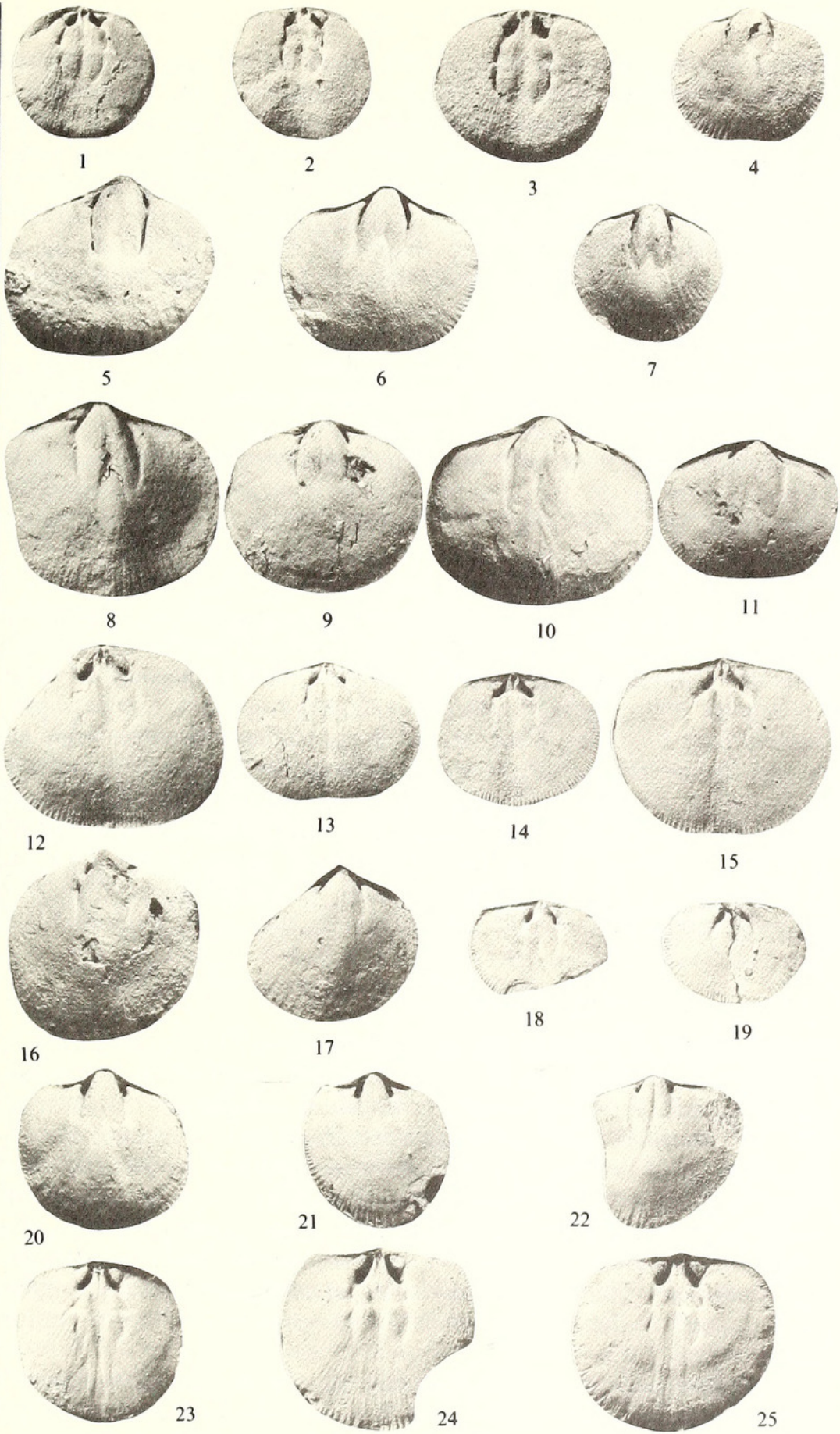
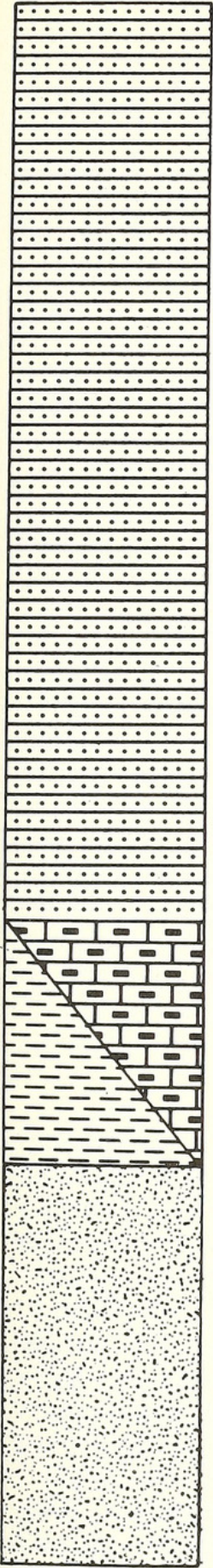
Welsh Borderland Ludlow ecological clines of *Isorthis*. Note the gradual morphological change from the bioturbated muds of the Elton Beds into the lower part of the sands and silts facies of the Lower Leintwardine Beds, followed by an abrupt morphological change in the Upper Leintwardine Beds. Also note the similar phenetics of *Isorthis* and *Onniella* in similar environments. Facies symbols explained in text-fig. 1. Stratigraphic extent of the facies is not to scale. The species terminology used here is taken from Walmsley and Boucot (1975), but this has been revised (see Hurst and Watkins 1978); a copy of the synonymies and the statistical data for that work has been placed in the British Museum (see p. 536).

Figs. 1–7. *I. clivosa* Walmsley, 1965. Internal moulds of brachial valves: 1, BB73647 × 2; 2, MGUH13762 × 2.2; 3, MGUH 13761 × 3. Internal moulds of pedicle valves: 4, MGUH13769 × 2.5; 5, MGUH13767 × 3.5; 6, MGUH13765 × 3; 7, MGUH13766 × 2.3. All from the Upper Leintwardine Beds of the Welsh Borderland, Grid ref. SO 4922 7407.

Figs. 8–15. *I. orbicularis* (J. de C. Sowerby, 1839). Internal moulds of pedicle valve: 8, BB73648 × 2.5; 9, BB73649 × 2.5; 10, OUMC23093 × 1.8; 11, MGUH13759 × 2.2. Internal moulds of brachial valves: 12, OUMC23134 × 2; 13, MGUH13755 × 2; 14, MGUH13756 × 2; 15, MGUH13754 × 2.1. Figured specimens 8, 9, and 11 from the Lower Leintwardine Beds, Grid ref. SO 7230 4024; 13, 14, and 15 from the Lower Leintwardine Beds, Grid ref. SO 7230 4024; and 10 and 12 from the Lower Leintwardine Beds, Grid ref. SO 6944 1663.

Figs. 16–19. *I. clivosa*. Internal mould of pedicle valve: 16, MGUH13752 × 2.6; 17, BB73650 × 2.7. Internal moulds of brachial valves: 18, MGUH13746 × 2; 19, MGUH13748 × 2.1. All figured specimens from the Lower Bringewood Beds, Grid ref. SO 7131 3858.

Figs. 20–25. *I. clivosa*. Internal moulds of pedicle valves: 20, MGUH13741 × 2.6; 21, MGUH13744 × 2.3; 22, MGUH13745 × 2.3. Internal mould of brachial valve: 23, MGUH13739 × 2.6; 24, MGUH13737 × 2.9; 25, MGUH13740 × 2.8. All figured specimens from the Elton Beds, Grid ref. SO 3860 7240.



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appears in the sands and silts of the Upper Leintwardine Beds (text-fig. 2) and is undoubtedly derived from *I. clivosa* populations in the Elton Beds (Pl. 58). These populations show a mixture of characters common to both *I. clivosa* in the Elton Beds and *I. orbicularis* in the Lower Leintwardine Beds, indicating the phenetic plasticity of the *Isorthis* stock. The reappearance of *I. clivosa* populations in the Upper Leintwardine Beds coincides with a major faunal turnover, in which species typical of more offshore facies fleetingly reappear (Watkins 1978). As far as can be ascertained, in the Leintwardine Beds there is a sharp morphological break between *I. clivosa* and *I. orbicularis*.

The stratigraphic trends in morphology from *I. clivosa* to *I. orbicularis* involve all the features listed earlier for the transition *O. reuschi* to *O. broeggeri*. The only difference involves the nature of change of the brachiophores and sockets. True fulcral plates (see Williams and Wright 1963) are not known in *Isorthis*, but small lateral shell ridges develop to augment the splaying brachiophores as well as buttressing anterior ridges (Pl. 58). The lateral ridge restricts the socket into which the ventral tooth slides, and in that respect is analogous to the fulcral plate. Such a feature is well seen in the Upper Leintwardine *I. clivosa* populations (Pl. 58).

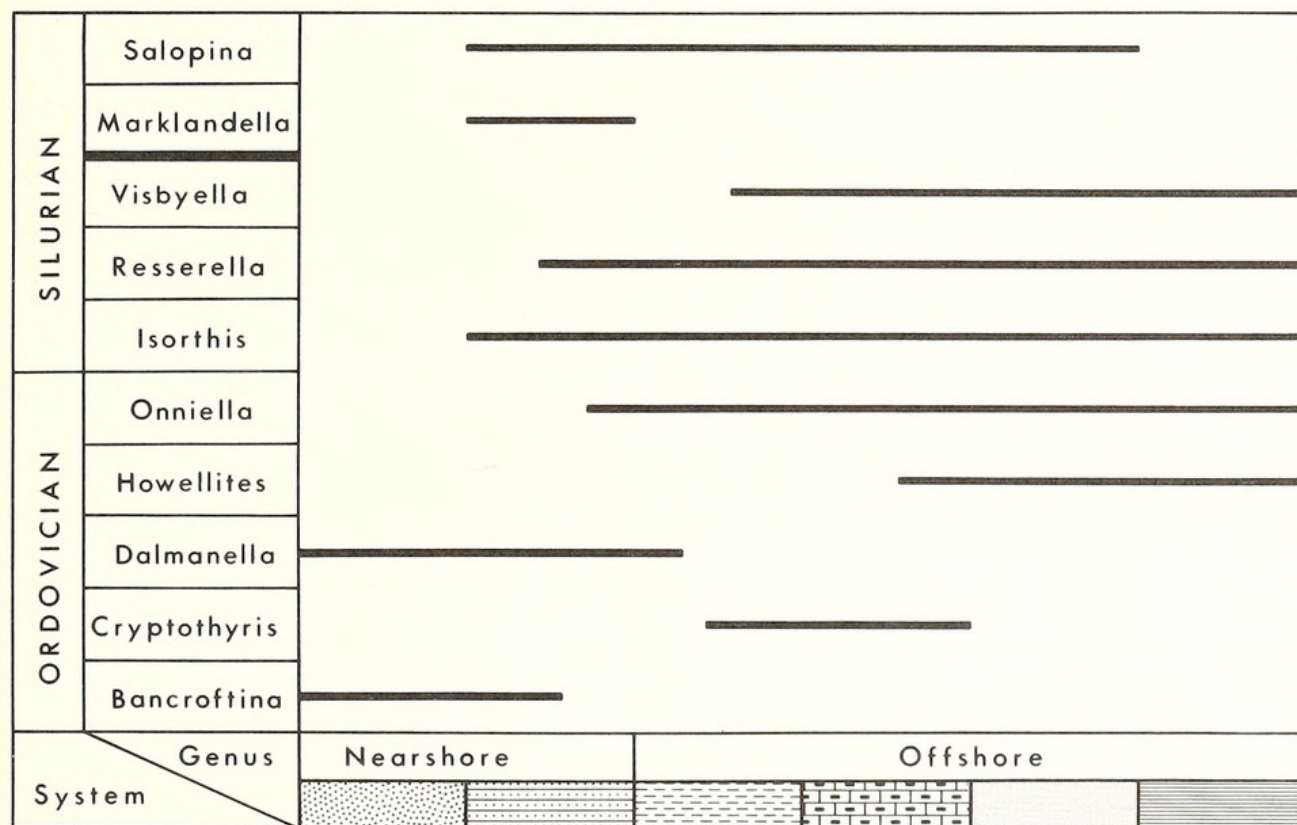
Again, as with *Onniella*, such phenetic patterns can be traced in clastic facies in other geographic areas at different times. For example, *I. fornicatimcurvata* (Pl. 59) occurs in the nearshore sands and silts facies (*Quadrifarius rugaecosta* and *Protonetes novascoticus* Communities) of the Pridoli Stonehouse Formation (Watkins and Boucot 1975); morphologically it closely resembles *I. orbicularis* and the Upper Leintwardine *I. clivosa*. There are some contradictions to the basic model. *I. amplificata* occurs in fairly nearshore storm-influenced environments in the Wenlock (Hurst 1975a, b) but, however, examination of Plate 59 reveals that the species is a mixture of onshore and offshore population characteristics. The ventral and dorsal cardinalia development (except for the crural fossette) is typical of nearshore populations, but the valve and muscle field configurations are more typical of offshore populations. For a comprehensive review of *Isorthis* phenetics see Hurst and Watkins (1978).

DISCUSSION: EXTENT OF THE TRENDS

How far are the *Onniella* and *Isorthis* phenetic patterns paralleled in other closely related dalmanellids? The following discussion is limited to clastic facies occurrences for two reasons: so that direct environmental comparisons may be made with *Onniella* and *Isorthis*, and because carbonates present a completely new set of problems within themselves (see Hurst 1975a). Also, for ease of reference, the shallow marine environmental gradient in which dalmanellids occur is divided into nearshore and offshore, as depicted in text-fig. 5. Further subdivisions are not practical, especially in the wider context of this discussion, due to the inadequacies of facies descriptions and their depth inference. The principal division between nearshore and offshore corresponds approximately to the point of last common occurrence of storm-laminated sandstones and siltstones.

Ordovician genera which are mainly limited to offshore facies include *Howellites* (M. Lockley, pers. comm. 1977) and *Cryptothyris* (Dean 1958; Hurst 1978), and they phenetically resemble offshore *Isorthis* and *Onniella* (Pl. 59). Similarly in the Silurian,

Visbyella prefers offshore quiet-water areas (see Ziegler *et al.* 1968a; Cocks and Rickards 1969; Hurst 1975c), e.g. *V. pygmaea* in the Llandovery Purple Shales of Shropshire (Ziegler *et al.* 1968b), a bioturbated mud facies. All known species of *Visbyella* respond phenetically to the set patterns (see Walmsley *et al.* 1968).



TEXT-FIG. 5. Generalized clastic facies distribution of some Ordovician and Silurian enteleletean genera. Main data for the Silurian forms compiled from Boucot (1975), with subsidiary sources explained in the text. Ordovician data for *Onniella* from references listed in caption to text-fig. 4. Data for other genera taken from Williams (1963, 1974), Whittington and Williams (1955), Hurst (1978), and M. Lockley (pers. comm. 1977). Facies symbols explained in text-fig. 1.

Resserella is a more eurytopic Silurian dalmanellid (text-fig. 5), though generally preferring offshore facies (Calef and Hancock 1974; Hurst 1975a; Boucot 1975), where the phenetic expression is similar to that described for *O. broeggeri* and Elton Bed *I. clivosa* populations (e.g. see *R. llandoveryana* Williams in Williams 1951 and Temple 1970; *R. canalis* in Bassett 1972 and Walmsley and Boucot 1971). However, in the lowest Wenlock *Pycnactis* Beds of the Tortworth Inlier (Curtis 1972), *R. whitfieldensis* occurs in a nearshore community and sediments (Calef and Hancock 1974) and its phenetic expression is remarkably similar to *I. orbicularis* and *O. reuschi* (see Bassett 1972, pl. 9), thus underlining the positive correlation between environment and morphotype.

Dalmanella generally occurs in nearshore facies (text-fig. 5) in the Caradoc, being most common in sands and silts (text-fig. 6), and here resembles nearshore *Onniella* in terms of valve configuration, cardinalia, and musculature (Pl. 59). However, in the Caradoc at least it differs most noticeably in shell depth. Williams (1963) described

a *Dalmanella* from an offshore fauna in the middle Caradoc of North Wales, and this is morphologically very similar to offshore *Onniella* and *Isorthis*.

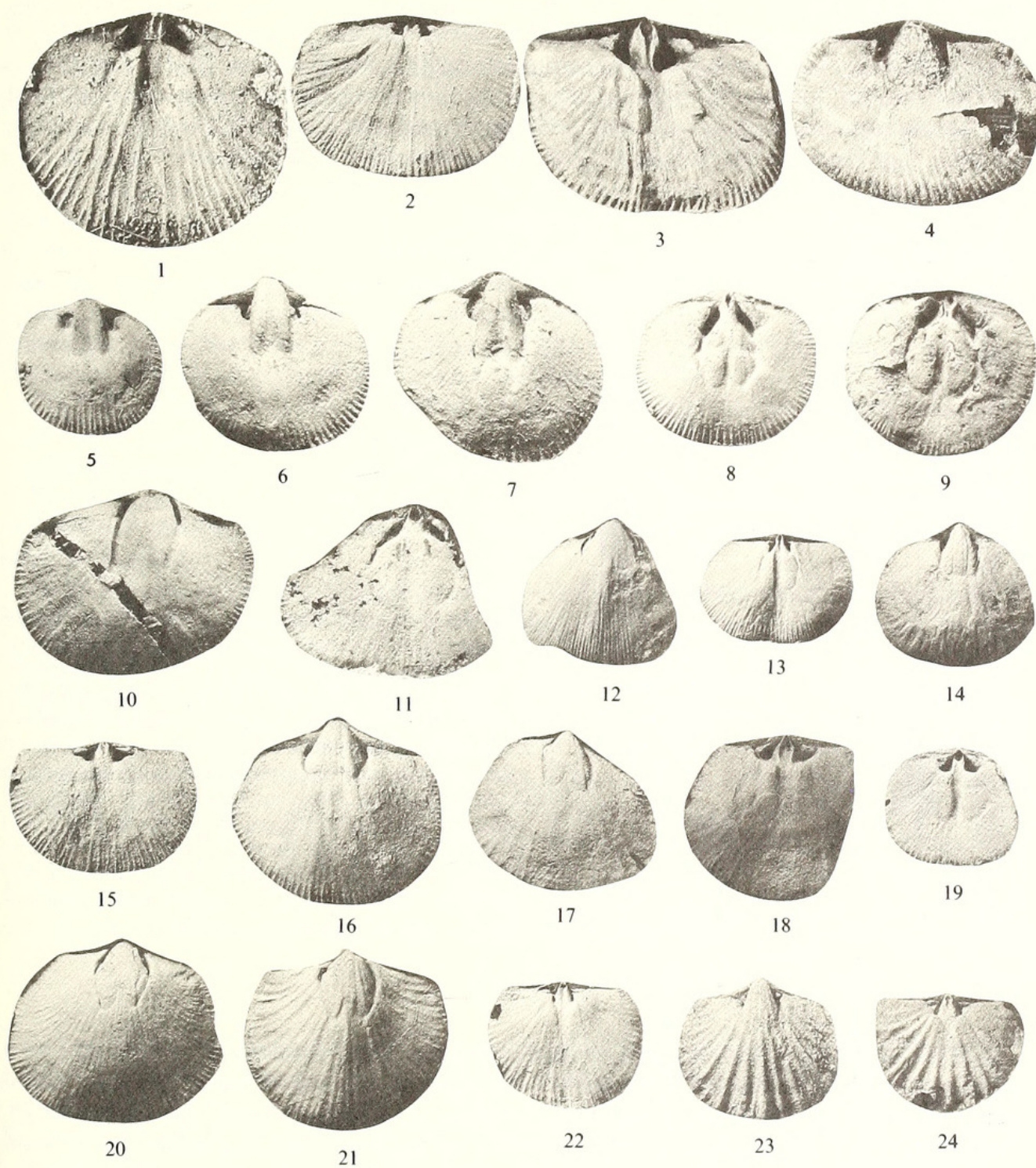
Bancroftina commonly occurs in the amalgamated facies in the Caradoc (text-figs. 5 and 6). Morphologically it is very distinct from any other nearshore dalmanellid (Pl. 59). However, also in the Caradoc a species of *Bancroftina*, *B. hewitti*, occurs in the sands and silts facies, and in terms of muscle and valve configuration and cardinalia (especially socket restriction) it is very similar to *O. reuschi* and *I. orbicularis* (Pl. 59). The most characteristic feature of *Bancroftina* is the widely splayed brachiophores (Williams and Wright 1963) which in effect restricts the sockets, analogous to the lateral ridges in *Isorthis* and *Resserella* and the fulcral plates of *Dalmanella* and *Onniella*.

FUNCTIONAL CONSIDERATIONS

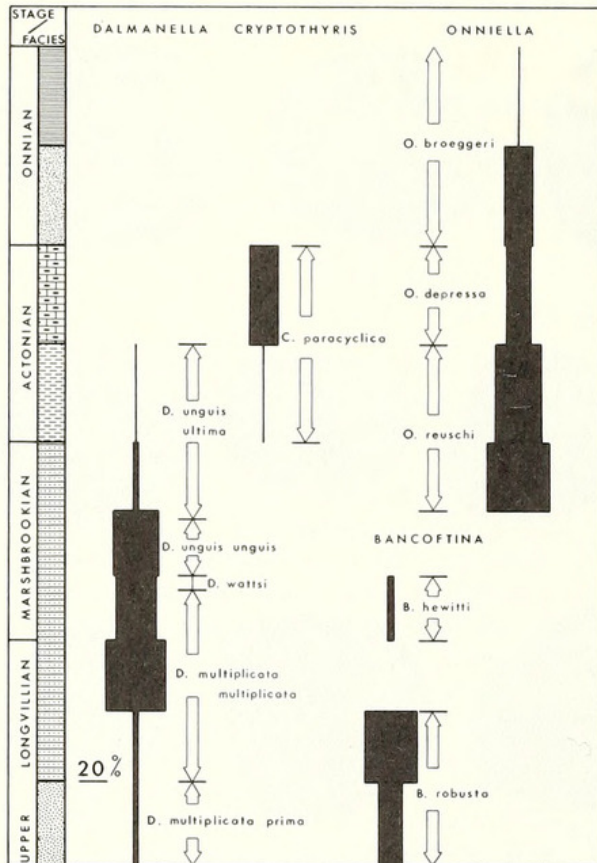
The many morphological parallels seen in dalmanellids indicate that in some instances there must be some common underlying functional causes. One of the most striking

EXPLANATION OF PLATE 59

- Fig. 1. *Onniella soudleyensis* (Bancroft, 1945). Internal mould of brachial valve, BB10271 $\times 4$, lower Horderley Sandstone (lower Caradoc) Shropshire, Grid ref. SO 4105 8523.
- Fig. 2. *O. avelinei* Bancroft, 1928. Internal mould of brachial valve, BB10326 $\times 2.5$, Harnage Shales (lower Caradoc) Shropshire, Grid ref. SO 4140 8620.
- Fig. 3. *Howellites ultima* Bancroft, 1945. Internal mould of brachial valve, BB10286 $\times 3$, Upper Allt Ddu Group (lower Caradoc, North Wales), from the gutter at Craig y Gath (see Williams 1963).
- Fig. 4. *H. striata* Bancroft, 1945. Internal mould of pedicle valve, BB10282 $\times 3$, Allt Ddu Group (lower Caradoc, North Wales), from the gutter at Craig y Gath (see Williams 1963).
- Figs. 5–9. *Isorthis amplificata* Walmsley, 1965. 5–7, internal moulds of pedicle valves, BB73651 $\times 2$, OUMC35644 $\times 2$, and OUMC35648 $\times 2.2$, respectively. 8–9, internal moulds of brachial valves, OUMC35662 $\times 2.3$ and OUMC35663 $\times 2.5$, respectively. All from the lowest Elton Beds (Wenlock/Ludlow?) of the Usk Inlier, Grid ref. ST 3332 0160.
- Figs. 10–11. *I. fornicatimcurvata* (Fuchs, 1919). 10, internal mould of pedicle valve, USNM241687 $\times 3$. 11, internal mould of brachial valve, BB73654 $\times 3$. Specimens from the Stonehouse Formation (Pridoli), Nova Scotia, USNM locality 10185 of Harper (1973).
- Figs. 12–13. *Salopina lunata* (J. de C. Sowerby, 1839). 12, internal mould of pedicle valve, BB73652 $\times 1.8$. 13, internal mould of brachial valve, BB73653 $\times 1.8$. Specimens from the Upper Whitcliffe Beds (Ludlow) of the Welsh Borderland, Grid ref. SO 5096 7414.
- Figs. 14, 19. *Cryptothyris paracyclica* (Bancroft, 1928). 14, internal mould of pedicle valve, BB72501 $\times 1.7$. 19, internal mould of brachial valve, BB73653 $\times 1.8$. Specimens from the Acton Scott Beds (upper Caradoc) of the Welsh Borderland, Grid refs. SO 4460 8992 (14) and SO 4241 8538 (19).
- Figs. 15–16. *Bancroftina robusta* (Bancroft, 1945). 15, internal mould of brachial valve, BB72483 $\times 2$, upper Horderley Sandstone, Shropshire, Grid ref. SO 4180 8590. 16, internal mould of pedicle valve, BB72487 $\times 2$, Cheney Longville Flags, Shropshire, Grid ref. SO 4778 9159.
- Figs. 17–18. *B. hewitti* Hurst, 1978. 17, internal mould of pedicle valve, BB72491 $\times 1.2$. 18, internal mould of brachial valve, BB72488 $\times 1.1$. Specimens from the Cheney Longville Flags, Shropshire, Grid ref. SO 4398 9002.
- Figs. 20–22. *Dalmanella wattsi* (Bancroft, 1929). 20–21, internal moulds of pedicle valves, BB72315 $\times 1.5$ and BB72316 $\times 1.5$, respectively. 22, internal mould of brachial valve, BB72318a $\times 1.4$. Specimens from the Cheney Longville Flags, Shropshire, Grid ref. SO 4446 8901.
- Figs. 23–24. *D. unguis unguis* (J. de C. Sowerby, 1839). 23, internal mould of pedicle valve, BB72320 $\times 2.3$. 24, internal mould of brachial valve, BB72321 $\times 2$. Specimens from the Cheney Longville Flags, Grid ref. SO 4446 8901.



phenetic trends seen in *Isorthis* and *Onniella* is the decrease in shell size and increase in depth from the nearshore sands and silts facies into the offshore bioturbated muds. A simple substrate model may explain such a relationship. Bokuniewicz *et al.* (1975) predict that on softer substrates (i.e. muds) shells must decrease in size to prevent sinking into the substrate. Consequently, a functional relationship may exist between smaller dalmanellid species on softer substrates and larger forms on harder substrates, so as to maintain the commissure above the sediment-water interface.



TEXT-FIG. 6. Quantitative stratigraphic distribution of the genera and component species of upper Caradoc dalmanellids. The relative abundance of a given species is its percentage occurrence relative to all brachiopods in a given sedimentary facies. The step-like nature of the relative abundances in the sands and silts facies reflects subtle sedimentary facies changes resulting in faunal turnovers. These correspond to the five faunal zones for this facies erected by Bancroft (1933) and they correlate directly with the step-like nature of the *Dalmanella* abundance range. Note how the genera are neatly packaged along the environmental gradient. Facies terms are explained in text-fig. 1.

Costellae probably correspond to the position of chitinous rods called setae, which in present-day brachiopods extend from the mantle edge as sensory bristles around the valve edge (Williams and Wright 1963; Rudwick 1970). Greatest densities of ribs, and therefore probably of setae also, occur in offshore genera which invade the sand and silt facies, an environment of higher sedimentation rate. This greater density possibly indicates more protection of the feeding mechanism by the tactile setae. *Bancroftina* and *Dalmanella* in the Caradoc display a similar trend in more nearshore areas (Hurst 1978) and, although this can probably be attributed to the same general cause, the fact that the genera more common in offshore facies have their highest costellae density at the point where *Bancroftina* and *Dalmanella* have their lowest, reflects the different ways in which genera may respond to environmental parameters.

Important differences may be expected in the articulation system of dalmanellid genera in a transect from nearshore to offshore sediments. Dalmanellids possess deltidiodont hinge teeth (Jaanusson 1971) which are characterized by simple distal growth but which are not particularly strong as interlocking devices. Consequently, many accessory characteristics evolved to strengthen the system. In *Bancroftina* the splayed nature of the thickened brachiophores and brachiophore bases (Williams and Wright 1963) restricted the movement of the tooth in the sockets (cf. splayed brachiophores and lateral ridge development of nearshore *Resserella*, *Isorthis*, and *Marklandella*), whilst *Dalmanella* developed fulcral plates to achieve the same effect (cf. some nearshore *Onniella*). Additionally, in all nearshore *Isorthis* and *Resserella* (text-fig. 5; Pl. 58) anterior buttressing of the brachiophores by shell ridges which bound the adductor muscle field is also common. This is also known in *Onniella* (Havlíček 1974). Such socket restriction and articulatory strengthening is an obvious response to life in nearshore agitated environments.

There are a number of morphological patterns which have no obvious explanation. Perhaps the most outstanding concerns the pedicle valve musculature. Why should populations predominantly with U-shaped pedicle muscle fields (concomitantly with shallower scars) prevail in nearshore facies whilst those populations consisting mainly of V-shaped pedicle muscle fields (accompanied by deeper scars) predominate in more offshore facies?

Nevertheless, dalmanellid phenetic patterns are clearly closely related to functional requirements. Also the plasticity of the phenotype plays an important role in the spatial distribution of the genera involved. For instance, text-fig. 6 reveals that, in the upper Caradoc, at least, dalmanellid genera (and species) occur in distinct bands along the environmental gradient which presumably reflects their primary functional adaptations, which is related to the sum of their morphological features. Further, the more restricted (stenotopic?) genera such as *Cryptothyris* are morphologically more compact, whilst the more widespread (eurytopic?) genera such as *Onniella* are phenetically far more variable. The dalmanellids dealt with here appear to support a type of niche variation model (see Van Valen 1965; Soulé 1972; Rothstein 1973; Ashton and Rowell 1975), but this provisional conclusion requires rigorous statistical testing; this is now being carried out.

CONCLUSIONS

A fundamental phenetic strategy model based on a detailed study of *Onniella* and *Isorthis* is proposed for dalmanellid genera. Offshore dalmanellid populations are basically characterized by deep, rounded sulcate shells with V-shaped and deep pedicle muscle fields, strong crural fossettes, coarse costellae, large non-restricted brachial valve sockets, and strongly impressed dorsal adductor muscle fields resulting in quadripartite appearance. Conversely, populations in more nearshore areas (sands and silts facies or equivalent) are characterized by transverse, shallow, non-sulcate shells with U-shaped and shallow pedicle muscle fields, weak crural fossettes, weakly impressed dorsal adductor muscle fields, restricted brachial valve sockets, buttressed brachiophores, and fine costellae. Between the two extremes, all intergradations exist. Further, it must be borne in mind that the above characters refer to the population

trends as a whole and not to the individual, and that not all characters are present at once in a single population.

The phenetic patterns are the consequence of functional considerations. However, there are exceptions to the model (e.g. *I. amplificata*) and also the genus in the amalgamated facies (e.g. *Bancroftina*) appears to react differently to the environmental parameters. Thus, the model needs to be rigorously tested, using more genera, and either modified or abandoned. Further, the model may well be applicable to other closely related enteletaceans. For instance, the eurytopic Siluro-Devonian drabovid *Salopina* (text-fig. 5; see nearshore *S. lunata* on Pl. 59) may follow similar lines, whilst the platyorthiniid *Marklandella* (text-fig. 5) which occurs in nearshore environments also appears to follow some of the patterns (see Walmsley and Bassett 1976).

The fact that at least some dalmanellid genera show positive correlation between morphotype and sedimentary facies has important implications as regards stratigraphic and phylogenetic studies of individual groups. Phylogenies as proposed for *Salopina* (Harper *et al.* 1969), *Resserella* (Walmsley and Boucot 1971), and *Isorthis* (Walmsley and Boucot 1975) should be treated with some scepticism, as no account has been taken of the facies occurrence of the species involved. In such cases, proposed phylogenies may simply consist of the 'linking up' of recurrent morphologies which are a direct result of response to environmental factors rather than of any genuine evolutionary process. Also, due to their morphological plasticity, it is doubtful whether many dalmanellids are useful for precise biostratigraphic correlations.

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