

BRACHIOPOD ECOLOGY AND LOWER GREENSAND PALAEOGEOGRAPHY

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ABSTRACT. Living brachiopod colonies show a marked preponderance of young stages in the population but this is not a necessary criterion of a life-assemblage of fossil brachiopods. The occurrence of well-preserved whole shells of all growth stages is one of the criteria of a life-assemblage. The percentage of disarticulated and broken valves present in a fossil assemblage is roughly proportional to the distance drifted from the original site of life, but this refers to total distance, not necessarily net distance. In the Lower Greensand (Aptian) of Faringdon and the Bargate Beds (Lower Greensand) of Surrey the brachiopod faunas do not occur as life assemblages but as redistributed communities in the immediate neighbourhood of their sites of life. Study of the lithology, fauna, and thickness variations of the Bargate Beds, and of bore-hole evidence, suggests that the beds were deposited very close to shore. This conclusion is extended by analogy to the Faringdon Greensand. Similar evidence is reviewed for the Lower Greensand of Upware and leads to a similar conclusion. The Ferruginous Sands (Aptian) of the Isle of Wight were deposited under neritic conditions but many miles from a shore. Here, in at least two horizons, life assemblages of articulate brachiopods are preserved; their sedimentary environment suggests that shallow, well-oxygenated conditions with currents were necessary for brachiopod life.

INTRODUCTION: LIFE OR DEATH ASSEMBLAGES?

THE first problem which arises in any consideration of palaeoecology is that of determining whether the fossils concerned are preserved where they lived or have been moved after death by current or other agencies, since upon this depend any further deductions concerning conditions of life of the animals.

Articulate pediculate brachiopods, unlike cemented organisms, can never be preserved strictly in the orientation of life because of the decay of the pedicle, but in the absence of powerful disruptive agents, especially of strong currents, a colony of pediculate organisms might be expected to be preserved fossil as a mass of shells occupying the site of the living colony.

Boucot (1953) has suggested criteria for distinguishing such an undisrupted community from a current-drifted assemblage (defined by Craig 1953).

1. *Size/frequency distribution measurements.* A brachiopod life assemblage might show a markedly concave size/frequency curve owing to the large number of young produced and the high mortality rate among immature individuals. Percival (1944) demonstrates this for living brachiopod colonies, but other factors both during and after life may modify the picture. For example, current and wave action may selectively remove shells to leave not a current-drifted assemblage but a current-depleted community, and it is likely that the shells removed will be those of young individuals because of their higher proportional mortality rate and because currents which are not strong enough to break up the biohermal community form might transport the smaller rather than the larger shells (cf. Boucot, Brace, and Demar 1958, p. 323). Subsequent solution, especially in porous rock, should affect small shells rather than larger, owing to their greater surface/volume ratio, and thus change the composition of the assemblage. The physical difficulties of observing very small shells and of separating them from the matrix is another

practical consideration affecting the apparent size/frequency distribution. These three factors could all combine to reduce the proportion of small shells in the fossil assemblage to considerably less than that of young forms in the original community. Thus the occurrence of whole shells of all growth stages may be strong evidence for the presence of a life assemblage (Craig 1954), irrespective of the exact shape of the size/frequency curve. Abrasion would tend to reduce the number of unusually large shells, but this would apply to a current-drifted assemblage rather than to a community virtually in the position of life, since currents powerful enough to bring about abrasion of shells would also be powerful enough to break up the community form.

2. *The ratio of articulated to disarticulated shell valves.* This is an important consideration (Boucot *et al.* 1958). In general, pediculate articulate brachiopods are among the most resistant of bivalves to disarticulation, so that a high proportion of disarticulated valves will indicate drifting about the sea floor for a relatively long period before burial, and in species whose brachial and pedicle valves differ markedly in size or shape the two valves may become differentially current-sorted. Similarly the valves will be more liable to abrasion the longer they are drifting from their place of origin, and a high proportion of broken valves will indicate a still longer period of current-drifting.

These considerations cannot supply more than a small part of the picture of the animals' ecology, but more can be filled in by taking into account the nature of the sediment in its field, petrographic and chemical aspects.

SOME CASES FROM THE ENGLISH LOWER GREENSAND

1. *Faringdon.* The outliers of Lower Greensand at Faringdon, Berkshire, provide a local glimpse of the deposits of a shallow Upper Aptian sea channel (Kirkaldy 1939, Arkell 1947a, Middlemiss 1959). At the base are the Red and Golden Gravels, which are coarse, condensed gravelly sands, current-bedded, and full of organic remains, including, in particular, calcareous sponges and Polyzoa. None of these are in the position of growth and most are to some extent broken but not comminuted. The general aspect is that of a fore-reef deposit which has received current-borne detritus from a very nearby region of luxuriant sponge and polyzoan growth. Brachiopods are also abundant but consist dominantly of separated and often abraded valves. For the species *Gemmarcula aurea*, Elliott (1956) quotes 84 per cent. worn and disconnected valves, but the remaining 16 per cent. of this species present a problem since they are well preserved, even to the delicate terebrateloid brachial apparatus, and could be interpreted as buried in the position of life, especially since Elliott was able to find all growth stages among them. Other species occur in similar proportions. In particular *Sellithyris coxwellensis* Middlemiss, *Cyrthothyris cyrta* (Walker), and *C. uniplicata* (Walker) are present in all growth stages and in all stages of preservation from the whole shells with well-preserved brachial loops to worn single valves.

Elliott quotes the experiments of Menard and Boucot (1951) for a belief that the closed shells of recently dead brachiopods may be transported by gentle currents without damage and also may be current-sorted into species without being current-sorted by size or shape, so that different growth stages of one species may be drifted together, and thus concludes that the whole of the Faringdon deposits must be regarded as a current-accumulation (death assemblage).

This conclusion seems to be inescapable but the presence of very well-preserved shells and of juvenile stages mixed with adult and gerontic indicates that the position of life was in the immediate neighbourhood of the present-day deposits and that we have here a redistributed life assemblage, the great differences in state of preservation among specimens of one species being due to differences in total time of to and fro drifting within a small area. By analogy with the Bargate Beds (below) it is unlikely that the position of life of these species was more than a mile or so from their present locations, probably much less.

We may conclude that, at least in the case of the species *G. aurea*, *S. coxwellensis*, *C. cyrta*, and *C. uniplicata*, the net distance of current-drifting from the original sites of life was very small, although for many individuals the total drifting distance was large. Several other species are comparatively rare and always fragmentary at Faringdon, for example *Praelongithyris praelongiforma* Middlemiss and *Cyrtothyris cantabridgiensis* (Walker); the distance travelled by these shells was presumably much greater.

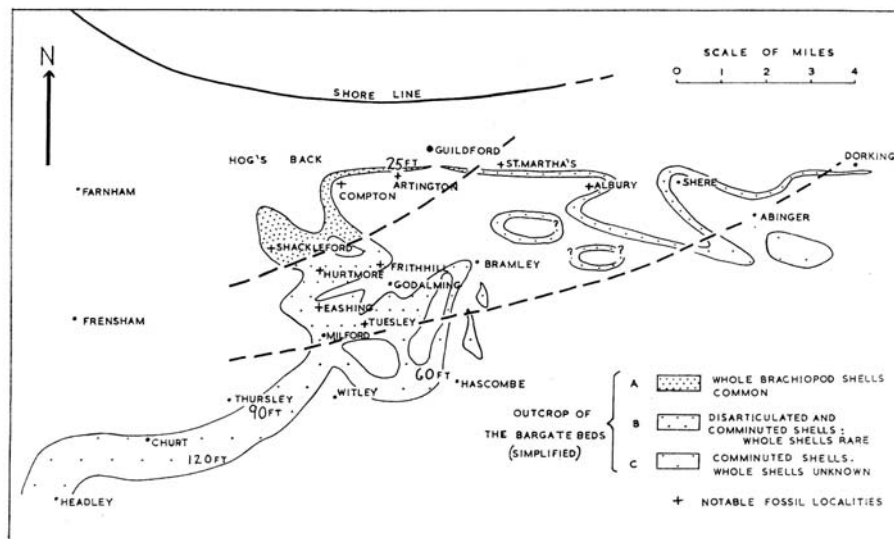
These remarks apply to the Golden Gravel. The overlying Red Gravel is much poorer in brachiopods, but both illustrate observations of Elliott (1950) and Cooper (1937) on the common association of articulate brachiopods with sponges. The sponges presumably formed a very suitable substratum for the attachment of the brachiopods and large specimens of the sponge *Rhaphidonema* can sometimes be found with rhynchonellids still in position between the folds of the sponge skeleton, even though the sponge itself has been transported from its site of life.

2. *The Bargate Beds.* The Bargate Beds of the Lower Greensand just to the south of Guildford, 28 miles south-west of London, carry a fauna mainly of brachiopods (Meyer 1864, 1868; Wright 1939) and present many parallels with Faringdon, where the Sponge Gravels belong to the same ammonite subzone. Exposures with identifiable brachiopods occupy an area of some 12 by 4 miles (text-fig. 1) in which the beds are composed of coarse pebbly sandstones and coarsely arenaceous limestones, all strongly false-bedded. As at Faringdon, the brachiopods found in any one exposure may exhibit all stages of abrasion from whole shells with well-preserved loops to abraded single valves, and beyond this to broken valves more fragmentary than any at Faringdon, and also a mixture of growth stages. Whole and practically unrolled shells are found quite commonly in the coarsest parts of the beds, which must have been deposited under conditions of strong current action.

Here again none of the fossils are in the position of life but are spread along the bedding planes and the foreset planes of the false bedding with different species, different growth stages, and different stages of abrasion intimately mixed. They represent a life assemblage in the sense that they lived in the area in which they are now found but they are all current-drifted to a greater or lesser extent. South-westwards from Guildford the brachiopod shells are progressively more finely comminuted (text-fig. 1), and around Thursley and Headley the only fossils found whole are rare ammonites and nautiloids. The ecological picture is of an area of shallow, current-washed, and hence presumably well-oxygenated sea floor, bearing scattered colonies of brachiopods each of which had a short life before being broken up by currents.

The overall direction of the current-bedding throughout the Bargate Beds of the north-west Weald is from north-west or north (Kirkaldy 1939, Knowles and Middlemiss

1959) but the actual foreset directions are complex and in many exposures no dominant direction is obvious. As a result of rapid variation in detailed current direction, the depedicated shells were washed to and fro and only those which had drifted within area A long enough to be broken into fragments were transported to area B. This, plotted on a map (text-fig. 1), seems to imply that no shell could remain whole if the net distance drifted, from the position of life to the position of final burial, were more than a mile or so.



TEXT-FIG. 1. Palaeogeography of the Bargate Beds near Guildford, Surrey.

Eastwards the Bargate lithology passes near Dorking, 12 miles east of Guildford, into thin unfossiliferous loams, but around Nutfield, 9 miles east of Dorking, these are replaced by fine calcareous sandstone with fuller's earth (Gossling 1929), yielding numerous fossils but not brachiopods (Dines and Edmunds 1933). Wood (1957) has shown that this Nutfield facies was deposited in a sheltered area of the sea floor under conditions leading to the formation of a peculiar assemblage of authigenic heavy minerals; conditions which were not inimical to shelly life but, in contrast to those of the Bargate Beds, must have been unfavourable for brachiopods.

Ecological conditions seem then to have been very similar during *Parahoplites nutfieldensis* times at Faringdon and in the north-west Weald and a further question of considerable importance is how near to a shore these shallow-water, current-washed deposits were laid down. In neither case are the strictly littoral deposits of the sea preserved but the Bargate Beds contain a valuable piece of evidence in the presence of numerous derived Jurassic ammonites (Arkell 1939) which are mainly of Oxfordian age, although some are Callovian and Kimeridgian. They are mostly preserved in rather fragile limonite and are confined to an area immediately south of Guildford corresponding quite closely

with areas A and B in text-fig. 1. Arkell concludes, from their state of preservation, that these fossils cannot have travelled far and that the Bargate Beds were deposited directly upon Oxford Clay north of Compton. The ammonites from the Ampthill and Kimeridge Clays are phosphatized and much more worn, suggesting that the outcrop of these beds was farther away, probably to the west. Arkell postulates a major fault along the line of the Hog's Back to explain the sudden disappearance northwards of the pre-Bargate Cretaceous Beds; he does not discuss the position of the actual shore-line in Bargate Bed times, and previous writers such as Chapman (1894) have taken the supposed presence of Bargate Beds in the Richmond boring as conclusive evidence that the shore-line lay some 20 miles north-east of Guildford.

The Richmond boring (Judd 1884), 8 miles south-west of central London, found, separated by a sharp junction from normal Gault, 10 feet of limestone resting, with a basal phosphatic nodule bed, upon Great Oolite (Bathonian). Judd regarded this rock as 'Neocomian' and as consisting of reworked Great Oolite material with worn Jurassic brachiopods. Whitaker and Jukes-Browne (1894) were apparently the first to compare it lithologically with the Bargate Beds, Chapman (1894) to suggest actual stratigraphic correlation. It would in this case represent the extreme northern extension of the Lower Greensand sea, since in the Chiswick borehole, 3 miles to the north-east, Gault rested on Old Red Sandstone (Geol. Surv. Wartime Water Supply Pamphlet No. 10, part III).

There seems, however, to be no positive evidence for such a correlation. The specimens and thin sections at the Geological Survey differ from the Bargate Beds in the rarity of quartz grains and, in sections from the lower half of the limestone, in the great abundance of ooliths, and they closely resemble the specimens from the Great Oolite part of the core. In fact, the thin section claimed by Chapman to show especial similarity to Bargate rock (E 29128, from 1156 ft. 6 in.) comes from part of the core assigned by both Judd (1884) and Whitaker (1912) to the Great Oolite. There seems to be no real reason for not regarding all 10 feet as Jurassic. If any major division is to be made, the most obvious level for it is at the 'pyritic clay' at 1145 ft. 9 in., which has densely packed bioclastic limestone without ooliths above, oolitic limestone below; the upper division (4 ft. thick) might be Cretaceous. Even assuming all or some of the beds to be reworked Great Oolite and to be of Cretaceous age, they could, on internal evidence, be a shallow-water *Tourtia*-like facies of any part of the Lower Greensand, although the absence of glauconite is notable. A similar limestone in borings at West Bilney and Culford in East Anglia is probably of much earlier Cretaceous age.

At the outcrop the Bargate Beds appear to be of very shallow-water near-shore facies and are succeeded by the Puttenham Beds (higher Upper Aptian), of somewhat more off-shore character (Middlemiss 1962*a*); thus any pre-Gault deposits lapping on to the Palaeozoic platform 20 miles away to the north-east might be expected to represent transgressive horizons younger than the Bargate Beds, either Puttenham Beds or Folkestone Beds (Lower Albian). It is not possible to confirm this directly from well records, since no bores in the intervening area reach the base of the Lower Greensand, but all those which penetrate Lower Greensand at all show sand of Folkestone Beds type underlying the Gault (Whitaker and Jukes-Browne 1894, and Geol. Surv. Wartime Water Supply Pamphlet No. 15, part V).

Figures for the thickness of the Bargate Beds given by Knowles and Middlemiss (1959), Kirkaldy (1932), Meyer (1868), and Dines and Edmunds (1929) indicate north-

ward thinning at a fairly constant rate of 25 feet every 2 miles, which, if extrapolated, would give a zero isopach near the Guildford By-pass road, about 1 mile north of Guildford. Such a position for the shore-line would fit the palaeoecological facts better than one several miles farther north and it is here postulated that Arkell's fault formed a fault-line coast in Bargate Bed times. There had probably been some movement of the fault in immediately pre-Bargate times, causing the slight break between the Hythe and Bargate Beds represented by the basal Bargate pebble beds and causing any pre-Bargate Cretaceous rocks deposited north of the fault to be rapidly stripped off, thus accounting for the fact that the Bargate Beds, although deposited at a time of general marine transgression, are of more littoral facies than the underlying Hythe Beds. It seems probable that this movement of the fault would have been part of the post-Wealden *pre-nutfieldensis* movements which are so important in Dorset and in the southern Midlands (Arkell 1947*b*, Ballance 1960), and which Casey (1961) shows to have been intra-Upper Aptian in age.

At Faringdon there is less evidence bearing upon the position of the shore-line; derived Jurassic fossils occur but are much more rolled than in the Bargate Beds. Arkell (1947) considered the Faringdon deposits to be 'not of littoral origin but accumulated in a clear, shallow, neritic sea' as 'generally there is no comminution of the sponges or shells by wave action'. As shown above, however, the facies is almost exactly the same as in the Bargate Beds, apart from the much greater amount of limonite, and by analogy it seems likely that the nearest shore-line was not more than 4 miles away.

3. *Brickhill and Upware*. The richest assemblages of Lower Greensand brachiopods ever discovered were at Brickhill, Buckinghamshire, 40 miles north-west of London, and Upware, 9 miles north-east of Cambridge, at neither of which are there now any exposures, so that any palaeoecological evidence has to be drawn from old accounts and museum collections. Between these two localities the dominant feature of the Lower Greensand is its attenuation from about 200 feet near Brickhill in the south-west to 8 feet at Upware in the north-east. In general the beds here consist of coarse, variable, current-bedded sands, normally unfossiliferous. Near Great Brickhill, however, old pits yielded abundant brachiopods in lentils of calcareous sandstone scattered through the lowest 30 feet in association with phosphatic nodules, indicating condensation of deposit; the Lower Greensand rests unconformably on Upper Jurassic Oxford Clay. The degree of condensation seems to vary rapidly since at Rushmore, only 2 miles from Brickhill, the basal phosphatic bed was only 7 feet thick (Keeping 1875). When the sands are traced north-eastwards into Bedfordshire and Cambridgeshire a similar process of thinning due to increasing condensation takes place. Between Potton and Sandy very ferruginous sands with phosphatic nodules have yielded indigenous fossils, including brachiopods, in a ferruginous condition in a phosphatic conglomeratic bed (Walker 1866).

Finally on the 'islands' of the Cambridgeshire fens, such as Ely, a few feet of coarse sands with phosphatic nodules represent the Aptian and it was this highly condensed facies which was formerly well exposed at Upware. The main relevant features of the Lower Greensand here are (1) its extreme thinness and great richness in calcium phosphate; (2) the coarseness of the deposits, which include conglomerates with walnut-sized pebbles; (3) the abundance of the fauna in the *coarsest* part of the beds, where yet the fossils were extremely well preserved, especially the brachiopods, whose brachial

loops are usually complete (Walker 1867, Keeping 1868, Bonney 1875, Teall 1875, Keeping 1883).

At Upware the Lower Greensand rests unconformably upon both Kimeridge Clay and Corallian reef limestones (Upper Oxfordian), the reef limestones having been exhumed from their clay cover by erosion immediately prior to Aptian times to form a rocky mound against which the Lower Greensand was laid with distinct depositional dip (Bonney 1875). The indigenous Aptian fossils were confined to two conglomeratic nodule beds, each a few inches thick and separated by a foot or so of sand, the lower of which rested directly upon the Upper Jurassic clays and limestones and was markedly richer both in indigenous fossils and in calcareous cement (Keeping 1883). The brachiopods are not only extremely well preserved but show a wide range of growth stages and tended to occur in masses of cemented 'brachiopod conglomerate', each block consisting of individuals of one species (Sedgwick Museum, Cambridge), which were living in colonies extremely locally, the majority of them probably utilizing the exposed surfaces of Corallian limestone as a hard substratum for attachment. They have been moved by currents no more than a matter of yards at the most. Both Bonney and Keeping correlate the abundance of shelly fauna and of calcareous sponges at Upware with the presence of abundant calcium carbonate derived from the Corallian limestone (the presence of derived ooliths in the internal matrix of the brachiopods is characteristic of Upware) and Keeping (1875) notes the absence of calcareous sponges from Brickhill (no calcareous Jurassic rocks nearby), whereas they are abundant at Faringdon (Corallian limestone again very close).

The derived fossils at Upware were mixed with the indigenous in the same nodule beds (Keeping 1883) and show three different types of preservation: (1) fossils from the Corallian limestone are in their original calcareous condition and lumps of the limestone were commonly found, showing that it was exposed to active erosion at the time; (2) ammonites from the Oxford Clay are well preserved and composed of limonite, as in the Bargate Beds; (3) all other derived fossils are phosphatized, these including forms from the Kimeridge Clay and Portlandian and also from the Lower Cretaceous. These points have a direct bearing upon the habitat of the indigenous brachiopods. Erosion of the hard Jurassic limestone implies wave action upon an immediately adjacent coast-line formed of these rocks, not necessarily the mainland coast—it could have been an island, but at least the brachiopods were here living in an almost littoral environment. The presence of well-preserved limonitized Oxford Clay ammonites suggests, by analogy with the Bargate Beds, the presence of a shore line composed of Oxford Clay not more than 2 or 3 miles from Upware but now hidden beneath the unconformable Gault; in the Cambridge boring the Lower Greensand rested upon Corallian which was only $9\frac{1}{2}$ feet thick (Edmunds 1954). The phosphatized Kimeridgian and Portlandian specimens have been rolled about the Aptian sea floor for a longer period, during which phosphatization took place; Keeping 1883, p. 31, remarks that they are smaller and much more worn than at Potton and that the Portlandian fossils are of southern affinities and are more numerous at Brickhill. The Kimeridge Clay at Upware itself is poorly fossiliferous, thus it is probable that all these forms are derived from the south and represent rocks forming the shore of the Aptian sea at a greater distance from Upware than the Oxford Clay and Corallian. This conclusion is supported by examination of the fossils from the Lower Greensand recently exposed during the construction of the M1 road at

Ridgmont, Bedfordshire, between Potton and Brickhill (Geol. Surv. nos. WA 1924–82). The fossils came from the basal conglomerate of the Lower Greensand and consist very largely of the typical Hartwell Clay (Upper Kimeridgian) ammonite *Pavlovia*, preserved as phosphatic internal casts. The degree of rolling varies much but some have fresh and unworn ribbing, others even show the original iridescence of the shell in the grooves between the ribs—evidently derived from the immediate neighbourhood. There are also traces of indigenous fossils in this collection, including one specimen of *Platythyris* aff. *comptonensis* Middlemiss, not at all rolled, damaged, or disarticulated.

As to the position of the main Upper Aptian shore-line relative to Upware, some negative evidence is obtainable from well records. 'Lower Greensand' is recorded in several well records east of Upware, namely North Creake (Kent 1947), West Bilney (Pringle 1920), Southery (Pringle 1923), Culford (Whitaker and Jukes Browne 1894), and Lowestoft (Strahan 1913), but in each case appears to be of pre-Aptian age. Thus we may at least conclude that, as there is no evidence to the contrary, the Upper Aptian shore-line could have been very close to Upware. The pre-Upper Aptian Cretaceous undoubtedly extended an unknown distance to the east but much of it had been removed prior to the deposition of the Upware Lower Greensand, probably during the period of the intra-Upper Aptian tectonic movements.

4. *The Isle of Wight*. Here the Aptian rocks begin, after a slight break giving rise to a bone-bed, with a richly fossiliferous sandstone, the Perna Bed, 5 feet thick, which is succeeded by the Atherfield Clay, poorly fossiliferous but containing species of the zonal ammonite *Deshayesites* (Casey 1961). The remainder of the Aptian is grouped under the name of Ferruginous Sands (White 1921), a varied series of sediments which show no evidence of having been deposited very close to a shore, but the neritic origin of which is shown by their lateral variability as well as by the nature of their fauna.

The Perna Bed itself is uniform in facies and fauna within the island and its characteristic fauna occurs at the base of the Lower Greensand northwards to the north crop of the Weald. It is a very mixed fauna including lamellibranchs, gastropods, compound corals, and also brachiopods, which are common and moderately well preserved, but there is no suggestion here of any preservation of the life assemblage, since they occur scattered through the bed, intimately mixed with the rest of the fauna. The Perna Bed transgression was succeeded by a phase of quiet sedimentation of fine silts, now the Atherfield Clay, during which conditions throughout most of the south English area seem to have been inimical to brachiopod life.

The clearest and most fossiliferous section of the Ferruginous Sands is that provided by the cliffs from Atherfield to Rocken End, along the south-west coast of the island, where Fitton (1847) divided the beds into Groups III–XV. Brachiopods are known from most of these groups but occur with especial abundance in Group IV (the Lower Gryphaea Bed) and Groups IX and X (The Walpen and Ladder Sands and Upper Gryphaea Bed), which will be described in more detail.

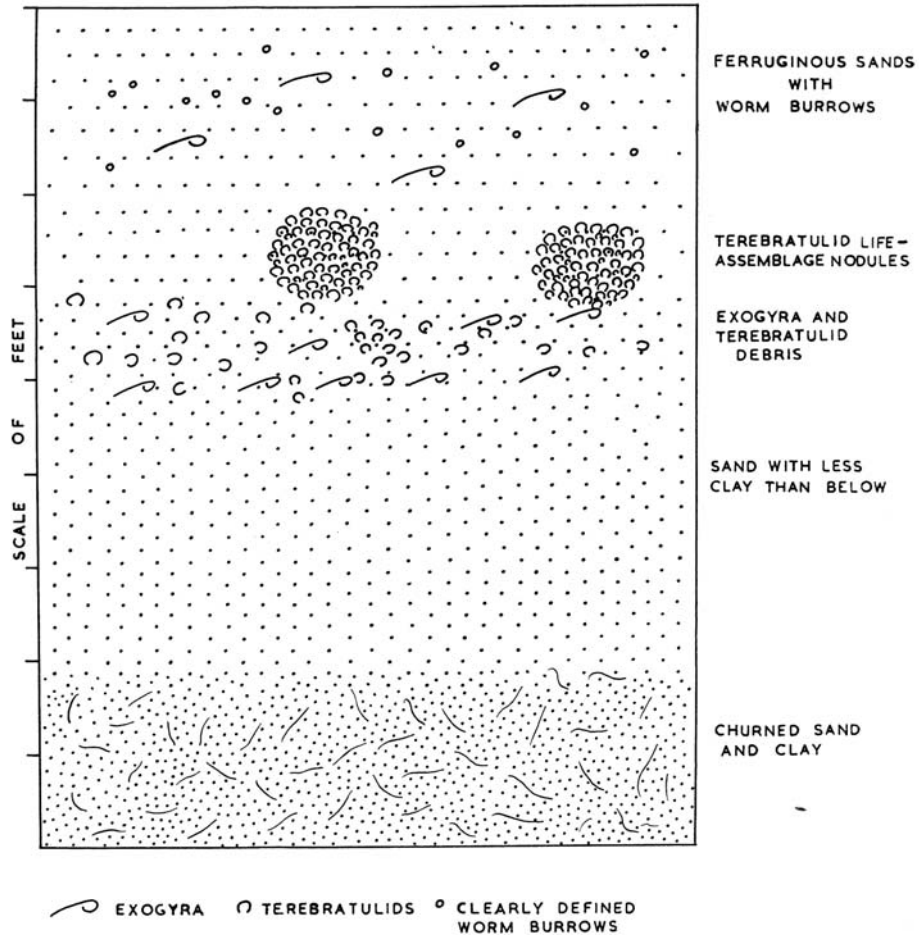
In the Lower Gryphaea Group, *Sellithyris sella* (J. de C. Sow.) occurs abundantly in two distinct kinds of assemblage: (a) accumulations strung out parallel with the bedding but in places forming pockets and (b) knots of closely packed well-preserved shells. Specimens of each of these types of assemblage were removed whole from the cliff face and broken up in an attempt to extract and measure every fossil from them.

The specimen of type (a) was taken from a lenticular thickening of the fossiliferous band and measured $14 \times 12 \times 7$ in. The fauna consisted of a mixture of *Sellithyris sella* with rhynchonellids, pectinids, and *Exogyra*, of which the majority of the brachiopod shells and all the lamellibranch shells were disarticulated, and most were fragmentary.

The specimen of type (b) was a rounded nodular mass $10 \times 8 \times 6$ in. high, consisting of a packed mass of *Sellithyris sella* set in a friable sandstone matrix, the shells exhibiting no preferred orientation. This was broken up manually and yielded 200 whole shells, of which 198 were *S. sella* and two rhynchonellids. There was inevitably some breakage inherent in the method but loss of specimens due to this cause was estimated at not more than 5 per cent.; no broken shells were noticed apart from those broken during extraction. Study of the ontogeny and variation of these forms is in progress; meanwhile the points which are relevant to the criteria mentioned in the Introduction can be stated thus: (a) whole and well-preserved shells representing all growth stages are present; text-fig. 4 shows the distribution of overall size (length+breadth+thickness) and closely comparable histograms are given by these measurements plotted separately; (b) only two disarticulated valves were found; (c) all except two specimens were of one species.

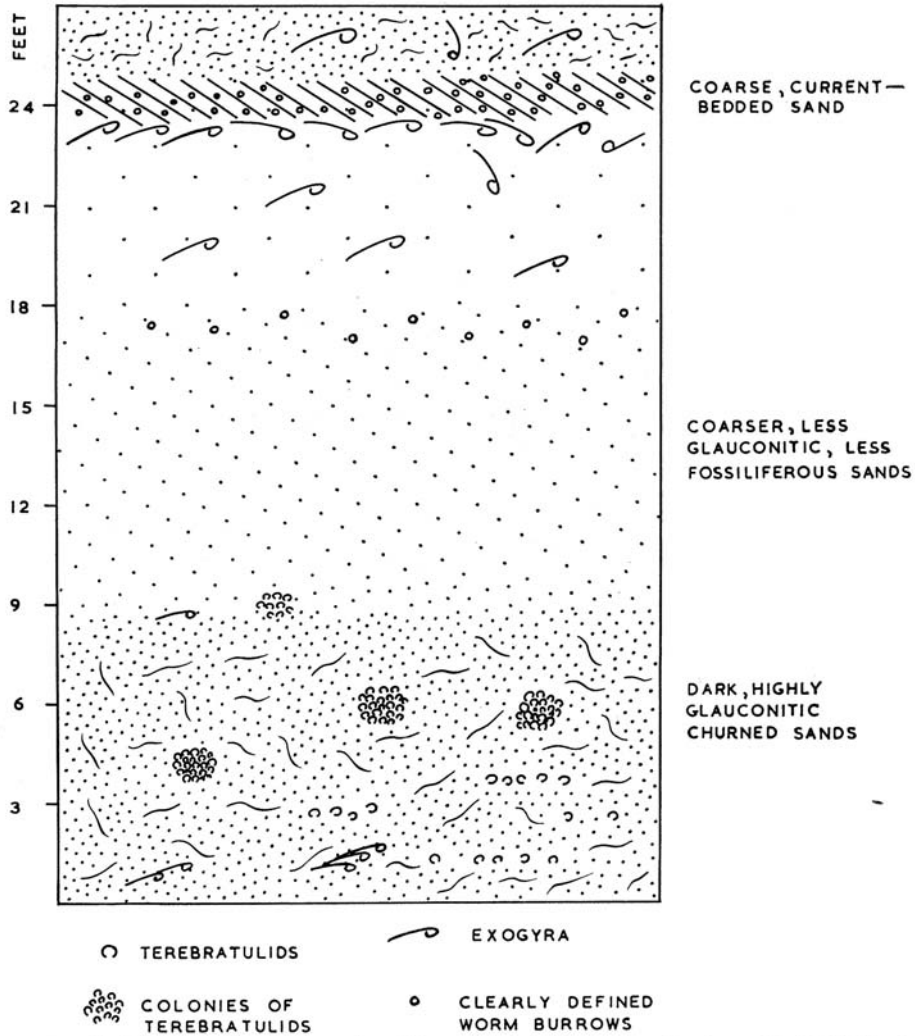
It is concluded from this evidence that the closely packed knots of *Sellithyris sella* (type B) represent biohermal colonies and are as near to being 'life assemblages' as can be expected with this type of animal. We may go on to consider why life assemblages were preserved here but broken contemporaneously in the other examples above. Text-fig. 2 shows the relations of the main fossiliferous horizon in the middle of Group IV, with the 'biohermal' masses of *S. sella* occurring at a slightly, but distinctly, separate level from the current distributed accumulation of shells. The lower part of the group represents relatively slow deposition and relatively poor oxygenation (Middlemiss 1962b). Below the fossil horizon the clay fraction becomes progressively reduced and the fossil horizon then follows abruptly with the appearance of large *Exogyra* and terebratulid debris, in coarser ferruginous non-glaucopitic medium sand. These 4 feet seem to represent increasing current velocity culminating in the main fossil horizon, at which currents were sufficiently powerful to break up nearby brachiopod colonies and transport large shells; this was followed by a short period of quieter conditions during which there were formed, in the water which was still relatively well oxygenated, the brachiopod colonies, some of which can be seen to be founded upon a large *Exogyra* shell as a local hard substratum, just as the modern *Terebratulina retusa* lives on detached scallop shells in the Sound of Jura (Rowell 1960). This would seem to imply that during the period of the main fossil horizon some parts of the sea floor carried living brachiopod colonies, while in other parts these were being broken up and the shells scattered by currents to form the accumulations of type a. The reason why some of the colonies were preserved from dispersal, and now form assemblages of type b, can be seen in the succeeding beds of the upper part of the group, which are relatively coarse sands full of vermiform burrows and represent rapid deposition (Middlemiss 1962b). Thus there was successively (1) inhibition of brachiopod life by poverty in oxygen, (2) colonization by brachiopods encouraged by well-oxygenated water coupled with slow deposition and the presence of large *Exogyra* shells for fixation, (3) rapid deposition which killed off the colonies, prevented their dispersal by currents, and inhibited further colonization.

In the Walpen and Ladder Sands and Upper Gryphaea Group (Groups IX and X)



TEXT-FIG. 2. Diagrammatic representation of the main *Terebratula* horizon in Group IV of the Ferruginous Sands at Atherfield, Isle of Wight.

the evidence is not quite so clear. There is evidence of current action in the presence of streams of serpulids, *Exogyra*, terebratulids, and rhynchonellids spread along certain bedding planes, many of the brachiopods well preserved and not drifted far. Quite separate from these are small ($10 \times 18 \times 6-9$ in.) lenticles packed with *Sellithyris sella shanklinensis*, some with associated serpulids. A smaller one of these ($10 \times 7 \times 6$ in.) was analysed as above. Here again there was no preferred orientation of the shells. Of *S. sella shanklinensis* 214 shells were extracted, in addition to three rhynchonellids (whole shells), three specimens of *Exogyra*, and one gastropod. Percentage loss during extrac-

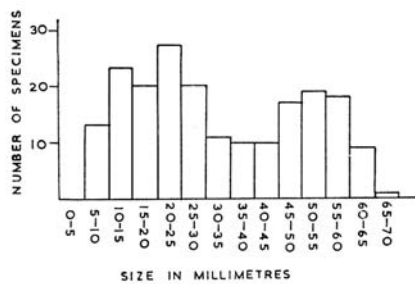


TEXT-FIG. 3. Diagrammatic representation of Group X of the Ferruginous Sands at Atherfield, Isle of Wight, together with the top of Group IX and the base of Group XI.

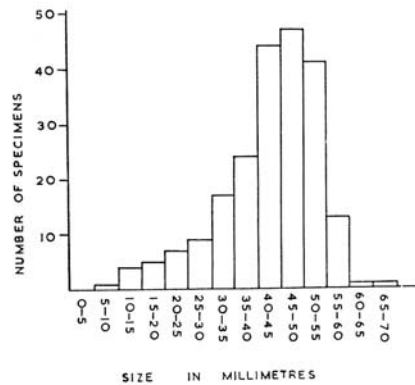
tion was estimated at 8, with again no shells recognized as pene-contemporaneously broken. Text-fig. 5 shows the distribution of overall size, with length, breadth, and thickness separately giving closely similar histograms, indicating that complete shells of all growth stages are present. Only one disarticulated valve was found.

These brachiopod colonies are in medium-grained silty and very glauconitic sand

(glauconite 35–45 per cent.), much disturbed by burrowing organisms. Group X shows evidence of increasing speed of deposition, the sand becoming markedly coarser and lighter in colour upwards with large *Exogyra* and clearly defined vermiform burrows becoming abundant near the top, culminating in the deposition of coarse, current-bedded sands with clearly burrowed foresets (Middlemiss 1962*b*). The factors in common with Group IV seem to be the presence of the large *Exogyra* as substrata, current action, and the increasing rapidity of deposition to preserve the colonies from dispersal. The period during which conditions were favourable for the brachiopods is represented



TEXT-FIG. 4. Frequency distribution of overall size among *Sellithyris sella* from a nodule in Group IV of the Ferruginous Sands, Atherfield, Isle of Wight.



TEXT-FIG. 5. Frequency distribution of overall size among *Sellithyris sella shanklinensis* from a nodule in Group IX of the Ferruginous Sands, Atherfield, Isle of Wight.

by a greater thickness of strata than in Group IV (about 15 ft. as against 2 ft.—see text-fig. 3), conditions in the upper part of the group being presumably unfavourable for colonization because of the rapid accumulation of sediment.

Another locality in the Isle of Wight where conditions seem to have resembled those of Group IV of the Atherfield section is south of Shanklin, on the south-east coast, in beds equivalent to Group XIII (zone of *Parahoplites nutfieldensis*). Here the bed which forms the reef of Horse Ledge is of medium-grained ferruginous sandstone, current-bedded on a small scale (6 in. foresets), with clear vermiform burrows, and is overlain by a highly fossiliferous horizon about 2 feet thick. The upper surface of the ledge provides extensive exposures of bedding surfaces within the fossiliferous horizon, upon which can be seen nests of *Rhynchonella parvirostris*, about 12 inches in diameter, associated with large *Exogyra* and serpulids and mingled with rarer *Ornithella morrisoni*, scattered fairly regularly a few yards apart, as are single specimens of large *Exogyra* and pieces of fossil wood. The brachiopods are well preserved and contain only a small percentage of broken or disarticulated valves and probably are life assemblages in the sense used above. The greensand of the fossil horizon has no apparent sedimentary structure, so that the suggested sequence is rapid sedimentation of the ledge-forming bed (which northwards towards Shanklin becomes much more strongly current-bedded), followed by slow deposition of the fossil horizon and subsequent reversion to rapid

sedimentation of the overlying 20 feet or so of strata, culminating in the ferruginous and strongly current-bedded sands above (equivalent to Group XIV).

CONCLUSIONS: CONDITIONS OF LIFE

These examples converge to the conclusion that the Aptian brachiopods, and particularly the terebratulids, lived in well-oxygenated conditions in shallow water where there was some current action. They formed colonies in which successive offspring fixed themselves to the parental shells to build up miniature brachiopod reefs. The colony in some cases commenced on a hard substratum, in other cases on a soft substratum where a large lamellibranch shell probably formed the initial platform for attachment. Owing to this neritic environment the colony was normally broken up eventually by currents and its members scattered over a greater or smaller area. Thus the optimum environment in which their *fossil* remains are discovered is normally one of quite coarse material—sand and pebbles—the finer fraction of which has been winnowed out and deposited elsewhere, in which the deposits are condensed because they were being constantly scoured and resorted by wave currents. An exception is that in the Ferruginous Sands of the Isle of Wight sedimentation was at times sufficiently rapid to smother some colonies and preserve them in their position of growth.

A point of great importance in the consideration of Aptian palaeogeography is that these conditions favourable to brachiopod life normally occurred close to, or at least within a very few miles of, the coast-line, as Cooper pointed out (Cooper 1937); Percival (1944) and Rowell (1960) also describe living colonies of articulate brachiopods immediately off-shore. Thus in many cases the approximate position of the coasts of the time can be followed by using these coarse condensed deposits, with their often abundant brachiopods, as a guide.

Conditions of life in crowded colonies led to asymmetrical growth in numerous individuals; Cooper (1937) noted this among modern forms and it is well seen among Upware specimens. Crowding may also in some cases have led to stunted growth; at Faringdon a high proportion of small specimens of *Sellithyris coxwellensis*, the commonest species there, show closely spaced exaggerated growth-lines, suggesting stunting (Middlemiss 1959, p. 122 and plate 16, fig. 12), and it has been remarked (e.g. Davidson 1852–5, p. 71) that many species are smaller at that locality than elsewhere. Very large gerontic specimens of several species (*Cyrtothyris cyrta*, *C. uniplicata*, *S. coxwellensis*, *Cyclothyris latissima*) are certainly found there but these are rare. Small size alone is, of course, no evidence of stunted growth, but growth-line evidence seems convincing enough in the case of *S. coxwellensis*. Crowding may have been one cause of stunting but the great abundance of iron present at Faringdon may have been another factor, although the evidence with regard to the effect of iron solutions upon animals is contradictory (Tasch 1953). An interesting point in this connexion is the difference in brachiopod faunas between the Golden and Red Gravels at Faringdon; in the Red Gravel, with its greater ferric iron content, brachiopods are much rarer than in the underlying Golden Gravel but, of those that occur, rhynchonellids greatly outnumber terebratulids, whereas among the abundant Golden Gravel brachiopods terebratulids slightly outnumber rhynchonellids. This apparent greater tolerance by rhynchonellids of iron-depositing conditions can be illustrated by several other instances, including the more ferruginous parts of the Ferruginous Sands in the Isle of Wight, the upper

Sandgate Beds of the south-west Weald (Kirkaldy 1937) and the Puttenham Beds in the north-west Weald (Middlemiss 1962a).

The development of local races of *Sellithyris* in the Upper Aptian probably had an ecological basis. *S. sella*, which dominated the Lower Aptian, became rare in the Upper and apparently found congenial conditions along certain parts of the shore-lines, in very shallow water, where a number of geographical subspecies and species evolved, such as *S. upwarensis*, *S. coxwellensis*, *S. sella shanklinensis*, the local Upper Aptian races of *S. sella* in the Bargate Beds and Sandgate Beds and those in odd corners of the Ardennes coast, such as those recorded by Barrois (1878) from Grand Pré, which probably gave rise to *S. tornacensis*. The latter species itself flourished in Cenomanian times in precisely the conditions favoured by its Upper Aptian ancestors; it is found in the very shallow water Cenomanian of Normandy and of the Ruhr and in the Tourtias, whose origin under almost littoral conditions, where the deposits were as likely to be washed away in one season as built up on the next, is clear (Dehée and Petit 1927, Parent 1928, Stainier 1935).

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