MARINE ECOLOGY AND PALÆOECOLOGY

"TO provide discussion between botanists, zoologists and palaeontologists on subjects of mutual interest by comparing analogous living and fossil assemblages" was the principal purpose of a symposium on marine ecology and palaeoecology which was held by the Systematics Association in the Department of Zoology and Wadham College, Oxford, during September 24-26. The meetings were attended by about 130 people, of whom just more than half were palaeontologists, and there was useful interchange between disciplines that enjoy far too little contact.

The first paper was by Prof. O. M. B. Bulman (Cambridge), who discussed the mode of life of the extinct non-dendroid graptolites. A pelagic habit is immediately suggested by: (1) their wide distribution (in some cases almost world wide); (2) their occurrence in all types of matrix; (3) their most characteristic occurrence in black shales which seem to represent deoxygenated bottom mud lacking in benthonic organisms. There appeared to be very little concrete evidence of attachment of the 'true' (non-dendroid) graptolites to floating weed, or of common floats for synrhabdosomes which had been postulated by Ruedemann. A variety of buoyancy devices had been attributed to them, such as vesicles, webs between the branches and, in some, triple-vaned structures at the end of the nema. Prof. Bulman suggested that, of the various possible buoyancy mechanisms, the most likely in the majority of graptolites was the presence of gas bubbles in the soft tissue which is now generally accepted as covoring the graptolite skeleton in life

In the discussion which followed, Mr. C. W. Wright (London) suggested that the three-vaned structures, said by some to be buoyancy devices, were more likely to be attitude-maintaining devices, particularly since the posture of most graptolite rhabdosomes appear to have been highly important.

Similar ovidence of a pelagic mode of life was presented by Dr. R. P. S. Jefferies (British Museum (Natural History)), for the Jurassic lamellibranch 'Posidonia'. He considered two species, Bositra buchi (= Posidonia ornati et P. alpina auett.) and 'Posidonia' radiata (= P. bronni magna auett.). Like graptolites, they commonly occur in black shales with few benthonic associates, but also occur sporadically in limostones and sandstones with much benthos. This strongly suggests they were not benthonic.

Granted this, Dr. Jefferies thought that both were probably pelagic swimmers, rather than living attached to flotsam. Thus, in *B. buchi* there was an anterior and posterior gape, suggesting swimming ability by analogy with Recent relatives, no sign of attachment in the shell outline at any growth stage and a shell thickness (60μ) comparable with Recent pteropods.

A nekto-planktonic mode of life for 'P.' radiata was suggested by Hauff's observation that it became abundant when normal benthos disappeared but that it was then much more abundant than such 'benthos' as Ostrea, Inoceramus dubius and Pentacrinus that occurred attached to driftwood.

Swimming ability might be primitive in scallops, since Recent *Lima* and *Pecten* both swim in much the same way and also early Pectinacea were probably active as they have few epizoa and the shape of the shell sometimes suggested swimming ability. After the paper, Prof. C. M. Yonge (Glasgow)

After the paper, Prof. C. M. Yonge (Glasgow) commented that Recent scallops could swim only intermittently. Dr. Jefferies replied that experiments suggest that a pelagic mode of life for '*Posidonia*' was as feasible as for a Recent ptoropod. Mr. N. Tebble (London) was sceptical of the evidence for a pelagic habit in '*Posidonia*', remarking that there was just as much evidence that the sand-living species *Tellina tenuis* is planktonic, which it certainly is not. Dr. Jefferies replied that it was facies that showed that '*Posidonia*' was not benthonic.

Dr. J. A. Allen (Cullercoats) pointed out that there was often an epifauna on Recent *Chlamys septemradiata*, a good swimmer. Dr. Jeffories replied that perhaps early Pectinacea were even more active than the species cited.

Turning to a study of living forms which is proving of particular interest to palacontologists, the meeting heard a paper by Dr. E. J. Denton and Dr. J. B. Gilpin-Brown (Plymouth, and the University of Auckland, New Zealand) on the buoyancy of Sepia and Nautilus. They showed that Sepia changed its specific gravity according to the light, and was more buoyant at night time. This buoyancy is controlled by changes in the relative gas and liquid spaces in the chambers of the cuttle bone. In the older chambers the gas pressure is always about 0.8atmospheres whatever the depth, but the liquid inside the chambers becomes less saline as depth increases, indicating an adjustment of osmotic pressure as a buoyancy control. In adult Nautilus, the gas pressure in all chambers is always about 0.9 atmospheres, and the buoyancy control is effected by varying the liquid content of the last-formed chambers. The problem remained as to how the liquid was removed from these chambers, since the septa are impermeable and in the newest chambers the siphuncle is not in contact with most of the liquid when the animal is in its normal swimming position. Dr. Denton and Dr. Gilpin-Brown suggested that the explanation lay in a special wettable layer on the inside walls of the chambers. This layer functions in the manner of blotting paper, holding liquid which once touches it and transporting it to the living tissue of the siphuncle which then pumps it, by way of the circulation, out of the chambers. The liquid almost all disappears by about the fourth or fifth chamber behind the animal proper. Further work is needed on the pumping mechanism, since some cephalopods, such as Spirula, can certainly go deeper than 240 m, which is the limit set by a pump using simple osmosis.

A complementary paper on fossil cophalopods was given by Mr. C. W. Wright (London), who discussed presentday knowledge of ammonite ecology and systematics. He emphasized how great were the gaps in our knowledge of what was thought of as a 'well-known' group: even their attribution to the Tetrabranchiata could not be regarded as proved. Mr. Wright pointed out that modern cephalopods occupy a wide range of ecological niches and there was reason to think that the ammonites may have done the same. Although generally supposed to be freeswimming, buoyant forms, there were even examples of ammonites with asymmetrical sutures and siphuncles which may well have lain on one side on the bottom like flat-fish.

Recent evidence from the United States of assemblages of up to 400 individuals in isolated doggers suggests original gregarious associations, and Mr. Wright compared this with the breeding swarms of certain living cephalopods which migrate *en masse* and are very sensitive to temperature and salinity. Such a tendency for associations in 'schools' might help to explain the problem of the rapid evolution of the ammonites, since a mechanism was required for the isolation of parts of a population as an agent for speciation. Mr. Wright contrasted the supposed two main stocks of Mesozoic ammonoids: the smooth, thin-shelled, 'opensea' forms such as *Phylloceras* and *Lytoceras*, and the ornamented, thick-shelled, 'inshore' forms which constitute the majority. The slow evolution of the former might be due to random oceanic distributions, with little splitting up of the populations, while the more rapid evolution of the inshore forms might have been permitted by a combination of the diversity of habitats available in the inshore regions and the habit of associating in 'schools'.

Rapid evolution and the repeated production of certain morphological types, such as the oxycones which turn up in many families, necessitate a fragmented classification. Mr. Wright concluded by pointing out that ammonite classifications, which can at best be only expressions of the present state of knowledge, must be regarded as experiments, to be tested against new information and material.

A second important theme of the meeting was the relationship between the distribution of various marine animals in present-day seas and that in the fossil record. Mr. Norman Tebble (British Museum (Natural History)) described the distribution of certain present-day zooplankton, notably among the pteropods and polychætes, which particularly show a specificity to certain water masses. He emphasized that temperature and salinity were among the principal controlling factors, with the greatest changes in distribution occurring at the surface hydrological boundaries, the Sub-Tropical Convergence, the Secondary Polar Front and the Antarctic Convergence. He demonstrated a marked asymmetry in the distributions. For example, among the pelagic polychætes of the Atlantic Ocean three were endemic to the Antarctic waters, sixteen extended from the Sub-Tropical Convergence to the Secondary Polar Front and two of these continued into the high boreal waters of the North Atlantic where there were no endemic species.

In discussion, Dr. W. J. Fry (London) remarked that the distribution of the pycnogonids, entirely benthonic, appeared, from available records, to parallel very closely the distribution of polychætes in oceanic waters, and he thought this similarity again underlined the caution necessary in ascribing particular types of aggregation to particular modes of life.

Dr. C. Edwards (Millport) also described modern distributions, with particular reference to the amphipod crustacea, notably 'Gammarus' (sens. lat.), which have spread into brackish and fresh water. Lake Baikal, the Caspian and the Black Sea were probably populated with representatives of this genus from the open sea during the Tertiary era. They have numerous endemic species, but these are still morphologically close to marine forms. On the other hand, the well-known freshwater shrimp G. pulex has probably had a longer freshwater history. The re-opening of the Black Sea to marine conditions has had the effect of driving the endemic species back into brackish water lagoons, deltas and river-mouths. Chaetogammarus tenellus has ascended the Volga, the Danube and the canals of eastern Europe, and descended the Vistula to Gdansk, becoming adapted en route to freshwater conditions, but will not descend into the brackish range at the mouth of the Vistula. Perhaps competition with native brackish species in the Baltic limits its distribution. G. locusta, which is purely marine around the British Isles (where the brackish habitats are occupied by two other species), does go into the lower salinities of the Baltic; it is probably ill-adapted to fluctuating salinities but can adapt to constant low salinities.

Dr. Edwards suggested that it was a general rule that if species have become adapted to lower salinities they would not re-adapt themselves to fully marine conditions again if they could avoid doing so by entering brackish localities such as river-mouths and lagoons. After the paper there was some discussion about how this rule applied in the fossil record, particularly among the invertebrates. Dr. Edwards considered that an important factor was the longevity of marine environments compared with short-lived local freshwater habitats.

A third paper which concerned itself with distribution through time as well as space was one by Dr. F. T. Banner (British Petroleum Co., Ltd.) on heterochronous homeo-These wholly marine morphy in the Globigerinacea. planktonic Foraminifera range in age from Lower Cretaceous to the present day and are found in all parts of the Dr. Banner produced numerous examples of world. Recent forms in which the tests are homeomorphic with those of distantly related Tertiary species. Homeomorphy occurs particularly in species of *Globigerina* and *Globo*rotalia; the geographical distribution of fossil forms was often parallel to that of their present homeomorphs, a relationship that may be of palæoecological significance. Thus, unkeeled Globorotalia (Turborotalia) scitula, of widespread Recent occurrence, parallels the wide geographic distribution of fossil G. (T.) fohsi barisanensis, while heavily keeled G. (G.) tumida, which is recorded only within 20° N. and S. of the equator, is equally similar to the Miocene G. (G.) lobata robusta, a form of limited geographic range within the tropics. Bandy has suggested that keeled Globigerinacea may be indicative of tropical and warm areas in the Cretaceous as well as in the Cainozoic, and noted an apparent relationship between the distribution of keeled Globotruncana and palæotemperatures as estimated by Urey and others. More recent discoveries of heavily keeled species of Globotruncana in the Maestrichtian of Denmark and Sweden do not, however, appear to support his hypothesis of such indications of a general climatic cooling at the end of the Cretaceous.

Another example of homeomorphy was provided by the development of chamber-elongations in almost all groups of the Globigerinacea independently. Eocene Hantkenina and Cretaceous Schackoina, both possessing superficially similar narrow spine-like processes, had a wide geographical distribution, but other homeomorphic groups, such as the clavate Hastigerinella (Recent) and Schackoina (Cretaceous), appear to have a restricted geographic distribution. Generalizations, although hazardous, might be made to suggest that, relative to a morphologically simple and geographically widespread ancestral stock, the more elaborate the test, the more restricted became the habitat of the morphologically most advanced species.

Combining his investigations of both ancient and modern brachiopods, Dr. M. J. S. Rudwick (Cambridge) discussed the development of protective devices in various articulate groups. As with the Globigerinacea. Dr. Rudwick was able to produce numerous examples of deceptively close convergence. He quoted the classic case of the Middle Triassic spiriferoid *Tetractinella* and the Upper Jurassic terebratuloid *Cheirothyris*. In this case he suggested that the prominent projections on the shells served to carry the mantle margin outwards as an 'early warning' device. This fitted in with observations on the extreme tactile sensitivity of the mantle edge in modern brachiopods. Similarly, the hollow spines of such rhynchonelloid genera as *Acanthothiris* might have been another early warning system.

Dr. Rudwick then described his extension of the prewar work of Herta Schmidt on the zigzag margins which are present in many brachiopods, and the probability of their having functioned as filters to prevent the entry of over-large grains into the shell. These zigzag margins developed in several different ways during ontogeny, suggesting that they were evolved independently in different groups. One variety, which is associated with a distinctive pattern of shell ornament, was itself apparently evolved three times, in the Devonian genus Nayunella (= Yunnanella auctt.), the Jurassic Rimirhynchia and some species of the Cretaceous Cyclothyris. All varieties of zigzag margins disappeared at the end of the Mesozoic and are unknown in Cainozoic or living brachiopods. Dr. Rudwick mentioned, however, that a few living species possess another kind of protective device: the edge of the shell is 'guarded' by rows of sensitive setæ. Grooves along the margins of many fossil brachiopods probably indicate the positions of setæ which had the same function.

The final morning of the meeting was devoted to papers and discussion of ancient and modern reefs. The first paper in this session was by Dr. S. A. Wainwright (California) on modern reef coral associations. He started by emphasizing the need for more quantitative field studies of associations. He discussed the various organisms which directly affect coral morphology, such as boring green algae, symbiotic zooxanthellae and predators among the polychætes, gastropods, asteroids, cirripedes, crabs One particularly good example was the and fishes. parrot-fish which eats living coral on the open parts of the reef, and Dr. Wainwright suggested that palgontologists should look out for such features as the teeth marks of fish and gastropod scars (which are often specifically determinable) in fossil coral roofs.

Dr. Wainwright next considered the distribution of corals on the reefs, taking Fanning Island, in the Central Pacific, as an example. He showed graphically the increase in number of species and growth-rate from the reef flat to the edge of the reef slope, at about 10 fathoms, though with a marked break over the reef ridge, where only algae survive in the heavy surf. Normally, in areas of heavy surf many corals are broken and rolled about, and the consequent abrasion provides many a habitat for boring sponges, gastropods and, of course, new corals. Coral fragments and even blocks up to a ton or so are carried up the reef and thrown on to the beach by wave action. On the slope immediately below the ridge there are only massive encrusting corals, but these pass down into the more fragile branching types at the bottom of the slope.

Dr. Wainwright ended by appealing to biologists to examine reefs and their associations in even greater dotail so that not only would the dynamics of reef-building and reof ecology be more clearly understood but also the sort of information available to the palæontologists would be greatly enlarged. From the palæontologists' point of view, what is desired is more information about coral associations in present-day seas, the biological role of their association and the effects of the associations on the growth pattern of the coral skeleton. The weaknesses inherent in the act of extrapolating from living to extinct organisms are greatly reduced when one deals with species-specific associations the manifestations of which are equally specific, or associations which are 'area specific' in relation to the whole coral reef.

Mr. G. F. Elliott (Iraq Petroleum Co.) turned to the other important constituent of reefs in his paper on past and present calcareous algae. He pointed out that calcifving algae at the present day are distributed among many groups and that some fossil ones are similar to living forms which are not calcified. Their maximum development is found in warm waters and they show a great variety of form. There are the delicately beaded types with light calcification, characteristic of the green algae; there are the thread-like masses within the sediment of the blue-green algae; and thore are the massive, heavily calcified structures of the red algae. The fronded forms all occur in sheltered waters. The very common green alga Halimeda, for example, is very abundant in lagoons and also occurs (though less commonly) on the lower part of the reef slopes, down to considerable depths. On the other hand, the massive red algae, for example Lithothamnium, are particularly important on the exposed parts of modern reefs. These algae also perform an even more important function in binding together reef debris. Their tromendous growth-rate makes up for breakage by the surf, and Dr. Wainwright, in discussion, added that it has been estimated that algae extract calcium carbonate from the sea-water up to 100 times faster than corals.

In the fossil record, Mr. Elliott pointed out, an important consideration is the rapid diagenesis of algal calcifications. This is partly due to the fact that the carbonate is laid down as fine particles (not in laminæ, as in other calcareous organisms) and also due to the high proportion (up to 18 per cent) of magnesium carbonate sometimes present, which leads readily to the process of dolomitization: many beds of dolomite are probably algal in origin.

Mr. Elliott then summarized the fossil record of calcareous algae from Precambrian times onwards. He directed particular attention to certain points, notably the importance of the blue-green algae in the carly part of the record, the rarity of algae in the Devonian reefs and the great importance of algae in Carboniferous and Permian reefs as compared with the Mesozoic. The coralline algae appeared in the Upper Cretaceous and came to dominate the reef onvironment in Tertiary times.

Prof. M. Lecompte (Brussels) discussed the building organisms of the Devonian reefs of Belgium, their ecological characteristics and bathymetrical distribution. He confirmed Mr. Elliott's observations on the rarity of algae in Devonian reefs, apart from the problematical Stromatactis, but he demonstrated clearly the regular succession of forms which are seen repeatedly in both bioherms and biostromes, and which can be related to the depth and turbulence of the water. He emphasized the long-term nature and wide extent of reefs in Belgium and adjacent areas, clearly the result of a rhythmic epoirogenic control, which repeatedly brought the seafloor to the right depth for reef growth. The reef periods alternate with periods of shale deposition, and each time a succession can be traced through: (1) a 'deep-water' zone; (2) a 'quiescent' zone; (3) an 'infra-turbulent' zone; (4) a 'sub-turbulent' zone; (5) a 'turbulent' zone. Each of these is characterized by a particular suite of fossils. The deepest zone shows a dominance of brachiopods, notably stunted variants of forms which occur also in other bathymetric zones. These are followed upwards by the appearance of first solitary and then massive corals. Tabulate forms, such as Alveolites and Thamnopora, are the main builders in the 'infra-turbulent' zone; but several of them apparently could not live in the rougher water. Many other forms also appear, such as bryozoans and sponges. Lamellar stromatoporoids come in very strongly in the 'sub-turbulent' zone and are replaced by massive stromatoporoids in the 'turbulent'. Stromatoporoids were apparently excluded from muddy environments, but the pure limestones of the 'turbulent' zone are largely composed of these organisms, associated with a wide variety of other groups, such as corals, brachiopods, crinoids (which are usually underestimated) and Stromatactis. The last-named was probably very important, but is usually not preserved.

The final paper of the meeting was by Dr. W. S. McKerrow (Oxford) on some local Jurassic coral reefs. This was an introduction to an excursion that was held in the afternoon. Dr. McKerrow described two horizons at which corals were found in life position. In the Upper Oxfordian 'Corallian' beds (Upper Jurassic) branching corals were to be seen thus near Faringdon, Berkshiro. The reef rock around Oxford, known as the Coral Rag, is contemporaneous with the dotrital Wheatley Limestone, which is composed of reef debris. The other coral occurrence was in the Great Oolite Series (Middle Jurassic) at Witney, Oxfordshire. The corals in these earlier beds have been attributed to five different genera, belonging, in the latest classification, to three different sub-orders. Dr. McKerrow showed by means of actual specimens that there were transitions between the different types. The simple Montlivaltia clearly passes into the branching Thecosmilia, and among compound massive types Isastraea (with walls between the corallites) passes into Thamnasteria (in which the walls have disappeared), and the latter (with solid septa) passes into Microsolena (with perforate septa). These passages could be seen in the same colonies, with the septa in direct continuation. It appeared

that the taxonomy of these forms was based (at least in this case) on phenotypic rather than genotypic characters.

The excursion in the afternoon, led by Dr. McKerrow and Dr. H. G. Reading, visited first an exposure of the Great Oolite at Crawley Road Quarry, Witney, where members saw a Bradford Fossil Bed reef in the Forest Marble. The presence in this reef of remains of all animal groups except eephalopods suggests a shallow lagoon in which the water was too turbulent for cephalopods. The second quarry visited showed a 'Corallian' reef at Shelling-

FOREST RESEARCH

MANY factors influence the growth of forest trees, and these factors cover a particularly wide range when the practice of forestry is largely concerned with afforestation and the use of exotic trees. Thus it is easy to understand why forest research in Britain is so comprehensive. This is certainly shown by the numerous projects described in the annual report of the Forestry Commission for the year ending March 1962*.

Where so much dependence is placed on seed supply for ensuring the large planting programme, provenance and genetics are very important. Not only are vigorous trees wanted but also especial attention is being directed to those provenances which show resistance to frost. So that the forester may know where to obtain tree seed in Britain of the best of the existing varieties and cultivars, the *Register of Seed Sources* has been brought up to date and it now contains 535 classified seed sources totalling 8,833 acres. Associated with this has been the work of converting the best seed sources into seed stands and thus improving the genetic quality of seed collected in Britain.

Much attention is being directed to the study of soil moisture. Deep peat remains a problem with its poor drainage, the physical instability of the trees, the difficulties of timber extraction and not enough being known about the water and nutrient régimes of the trees. There is another drainage problem on heavy clay soils, but some hope is seen in improved types of mechanical drain diggers.

Exposure is a limiting factor to afforestation on many sites in Britain, and it is not easy of assessment. However, an inexpensive technique has been developed by using the rate of tatter of standard cotton flags set up for a period on the sites being studied. An account of this method is to be published soon. Wind damage is being examined from various aspects, and one project uses a ford Cross Roads Quarry, near Faringdon, where members saw patches of massive corals in early layers give way to mainly loosely-branching corals higher up, suggesting an increase in the depth of the water at this particular locality with time. The detrital Wheatley Limestone in this quarry was seen below the Coral Rag.

In the course of the symposium special thanks were expressed to Prof. J. W. S. Pringle for entertaining the meeting at Oxford. D. V. AGER

D. NICHOLS

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wind tunnel to determine the relationship between wind velocity and the forces acting on a tree. Another project utilizes the 'tree-pulling' technique to test the effect of direction of pull on tree resistance. Both series of experiments should bring out useful information, but they do not seem to take into consideration that trees in a forest are often subjected to gusts and turbulence and not to a steady force of wind.

The annual report for the New Zealand Forest Service[†], covering the period January 1-December 31, 1962, shows an economic flavour. Emphasis is laid on the quality of the end-product so that utilization will be the most profitable possible. Hitherto, New Zealand's high-grade timber has largely come from its indigenous forests, but these resources are now approaching exhaustion. The tools at the disposal of the sylviculturist in order to obtain a better proportion of good-grade timber from the exotic forests are pruning and thinning and, therefore, present investigations are attempting to relate pruning and its effect on grade enhancement and the relationship between green crown depth and the density of the stand. However, the importance of protection forestry is not being forgotten. More watershed surveys have been carried out. and some reveal conditions which are rather disturbing. Active erosion and the resulting outpourings of detritus into streams may be largely due to red deer, goats and opossums destroying the protective vegetation cover. In some of the more accessible areas, hunters appear to exert sufficient control on the deer numbers and so the vegetation cover is in reasonable condition to give adequate protection against soil erosion. C. J. TAYLOR

* Forestry Commission. Report on Forest Research for the year ended March, 1962. Pp. ix+194+12 plates. (London: H.M.S.O., 1963.) 13s. net.

[†] New Zealand Forest Service: Forest Research Institute. Report of the Forest Research Institute, Rotorua, for the period January 1 to December 31, 1962. Pp. 86+9 plates. (Wellington: Government Printers, 1963.)

RETURN OF THE NENE TO HAWAII

F ROM the beginning of the Wildfowl Trust's attempts to rear the Hawaiian geese, *Branta sandvicensis*, in 1950, it had been hoped that it would become possible to return the Hawaii geese reared at Slimbridge. The growth of the stock has been slow and some of the birds raised have been disporsed to other collections in Europe and North America in order to increase the chance of maintaining and developing flourishing stocks in captivity. By 1960, however, enough geese had been reared to allow the return of some of the nenes to Hawaii. It was not until the summer of 1962 that this somewhat complicated and expensive operation could actually be carried out *.

The Division of Fish and Game, Department of Land and Natural Resources of the State of Hawaii, proposed that the Slimbridge-reared geese should be used in an attempt

* The Wildfowl Trust. Fourteenth Annual Report, 1961-62. Edited by Hugh Boyd. Illustrated by Peter Scott. Pp. 180+42 photographs. (Slimbridge: The Wildfowl Trust, 1963.) 17s. 6d. net. to re-establish the species on the Island of Maui, where it had been extinct for many years. A survey of the existing habitat on Maui in June 1960 showed that there were 9,000 acres of excellent nene habitat and a further 30,000 acres likely to be of some value. A release site was selected near Paliku within the Haleakala National Park. There were strong reasons for this choice: the area at the upper end of the Kampo Gap provides excellent nene habitat with food throughout the year; it is remote, ensuring a minimum of disturbance to the birds in the release pen; suitable accommodation exists for the people needed to care for the birds.

In June 1962 thirty geese were despatched by air from Slimbridge to New York. They were taken to the U.S. Federal Quarantine Station at Clinton, New Jersey, where they were held for 21 days. They were then sont on by air freight to Honolulu. There they were kept in the Zoo for three days to recover from the journey and were