

THE PALAEOECOLOGY OF THE ACTINOCAMAX PLENUS SUBZONE (LOWEST TURONIAN) IN THE ANGLO-PARIS BASIN

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ABSTRACT. The *plenus* Subzone often conforms to a standard succession of eight beds, numbered 1 to 8 in ascending order. The distribution of aragonitic fossils in the *plenus* Subzone was probably controlled more by preservation than ecology. Preservation was determined firstly by temperature and secondly by turbulence.

In late *subglobosus* times the distribution of macro- and microfauna was governed by depth of water, and the depth preferences of the various species of benthonic foraminifera were like those of their relatives in *varians* times. There was little faunal change at the beginning of Bed 1 times, despite extensive erosion. This indicates that the pre-Bed 1 shallowing, for which there is much lithological evidence, was accompanied by only a small rise in temperature. A sudden change at the beginning of Bed 2 times to a shallower-water type of fauna was due to a considerable rise in temperature which led also to the preservation of aragonitic fossils. The peculiarities of the fauna of Beds 4–6, including the presence of *Actinocamax plenus* and *Oxytoma seminudum*, suggest a moderate decrease in temperature with the appearance of species of Central European Russian affinities. This moderate fall in temperature is reflected in the microfauna. During the deposition of Beds 7 and 8 the temperature rose again slightly.

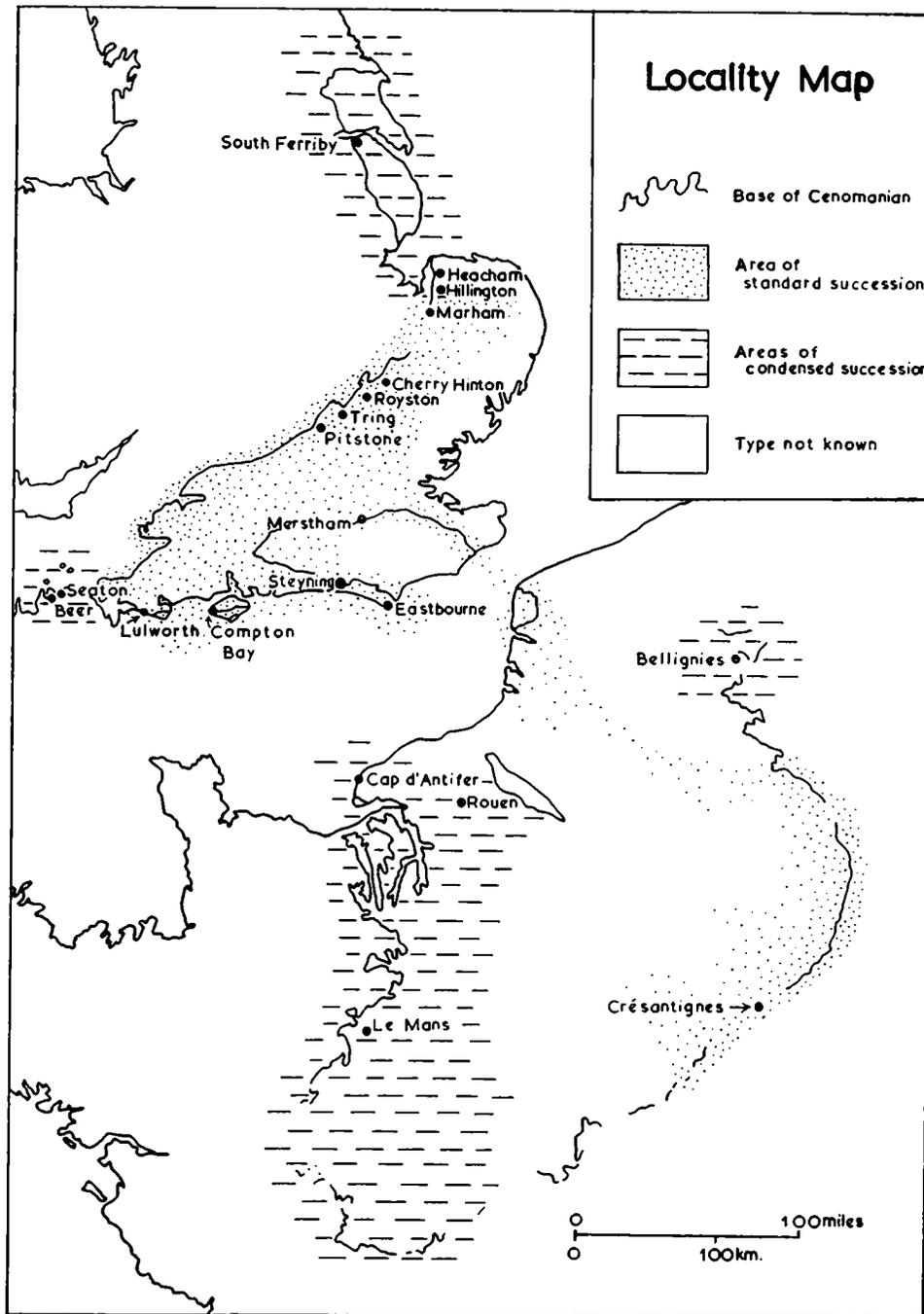
On the basis of certain simplifying assumptions the temperature of deposition of Bed 1 was probably below 5–10° C., that of Beds 4–6 about 16–9° C. and that of Bed 2 considerably higher than 16–9° C.

IN most of the Anglo-Paris Basin the *Actinocamax plenus* Subzone of the *Inoceramus labiatus* Zone is a band of conspicuous marls and marly chalks at the top of the Lower Chalk immediately beneath the Melbourn Rock. It should probably be placed at the base of the Turonian. The stratigraphy of the Subzone has been discussed in detail elsewhere (Jefferies 1961) so that only a short stratigraphical summary is necessary.

In the middle of the Anglo-Paris Basin the *plenus* Subzone conforms more or less to a standard succession of eight beds, numbered 1 to 8 in ascending order and recognizable by fauna and lithology. The type of this standard succession is taken at Merstham in Surrey, on the scarp of the North Downs, and the succession at Merstham is summarized in text-fig. 2. Important features of the succession are (i) the erosion surfaces beneath Beds 1, 2, 4, 6, and 8, especially those beneath Beds 1 and 4; (ii) the marked faunal change at the base of Bed 2; (iii) the occurrence of certain species, including *Actinocamax plenus*, in Beds 4–6; and (iv) the occurrence of the two ammonite faunas—that of *Metoicoceras geslinianum* in Beds 1 to 3 and that of *M. gourdoni* in Beds 4 to 8.

Towards the edges of the Anglo-Paris Basin the *plenus* Subzone is condensed or absent and rests upon, or wedges out against, a sub-*plenus*/*labiatus* erosion surface, homotaxial with the erosion surfaces of the standard succession (text-fig. 1). There is evidence to suggest that the muddiness of the *plenus* Subzone is connected with shallow water and directly associated with the numerous erosion surfaces of the standard succession and with the way in which the Subzone wedges out peripherally (Jefferies 1961).

The purpose of this paper is to discuss the ecology of the *plenus* Subzone fauna, and, in particular, to explain the faunal change at the base of Bed 2, and the faunal peculiarities (including the presence of belemnites) of Beds 4–6. This discussion is based



TEXT-FIG. 1. Locality map. This map shows only those localities from which fossils are mentioned in the present investigation.

partly on detailed bed-by-bed collecting and partly on the application to the foraminifera of those 'pollen-analytical' methods which have been so successful in the study of the Quaternary and which Burnaby (1961) has used in his work on the *varians* Zone.

The Type of the Standard Succession at Merstham.

Scale in ft.	Important Macrofossils (Ammonites excepted).	Aragon. Fossils.	Ammonites.
M.R. — ES	As 7, but without <i>O. wiesti</i> , <i>C. hirudo</i> .	Rare	<u>Gourdoni Zone.</u>
8 — ES	As 4-6 but without fossils marked *.		
7b — c — a	<i>Orbirhynchia wiesti</i> abundant, <i>Cidaris hirudo</i> common.		
6 — ES	As Bed 2, 2-3 & 3 but with <i>Act. plenus</i> *(c.), <i>Oxytoma seminudum</i> *, <i>Aequipecten arlesiensis</i> *, <i>Ditrupea difformis</i> *. <i>Plicatula barroisi</i> much commoner than below or above.	Abundant	<u>Kanabicerias sp.</u> , <u>Sciponoceras sp.</u>
5 — ES	As 2 & 2-3 but all fossils rarer, especially calcitic ones.		
4ii — ES	<i>Rhynchonella</i> ' <i>lineolata carteri</i> , <i>Entolium membranaceum</i> , <i>Calliderma smithiae</i> , <i>Grammatodon</i> cf. <i>cenomanense</i> , <i>Aporthais</i> sp., <i>Solanium</i> sp. <i>Dentalium</i> sp. Large, grypheate <i>O. vesicularis</i> common in Bed 2, absent above.	None	<u>Geslinianum Zone.</u>
4i — ES			
3b — ES	As <u>subglobosus Zone</u> , but <i>Ostrea vesicularis</i> larger (3 cm.), <i>Orbirhynch. multicosata</i> common, <i>Ctenothrissa</i> sp. and <i>Scapanorhynchus subulatus</i> common. <i>Trachyaster</i> ' cf. <i>rugosus</i> present but rare. <i>Holaster trecensis</i> rarer than in <u>subglobosus Zone</u> and <i>Plicatula inflata</i> probably extinct.		
3a — ES	Marked faunal change.	None	
2-3 — ES			
c — ES	Marked faunal change.	None	
2b — a			
1b — ES	Marked faunal change.	None	
1a — ES			
Subg-obosus Zone.	<i>Ostrea vesicularis</i> (c.) (about 1 cm. long) <i>Holaster trecensis</i> (c.), <i>Lingula</i> sp.(c.), <i>Lima globosa</i> , <i>Problematicum</i> sp., <i>Aequipecten beaveri</i> , <i>Entolium orbiculare</i> , <i>Neithea quinquecostata</i> , <i>Plicatula inflata</i> .	None	

TEXT-FIG. 2. The standard succession at Merstham, Surrey (type locality). ES, erosion surface.

PRESERVATION OF ARAGONITIC FOSSILS IN THE PLENUS SUBZONE

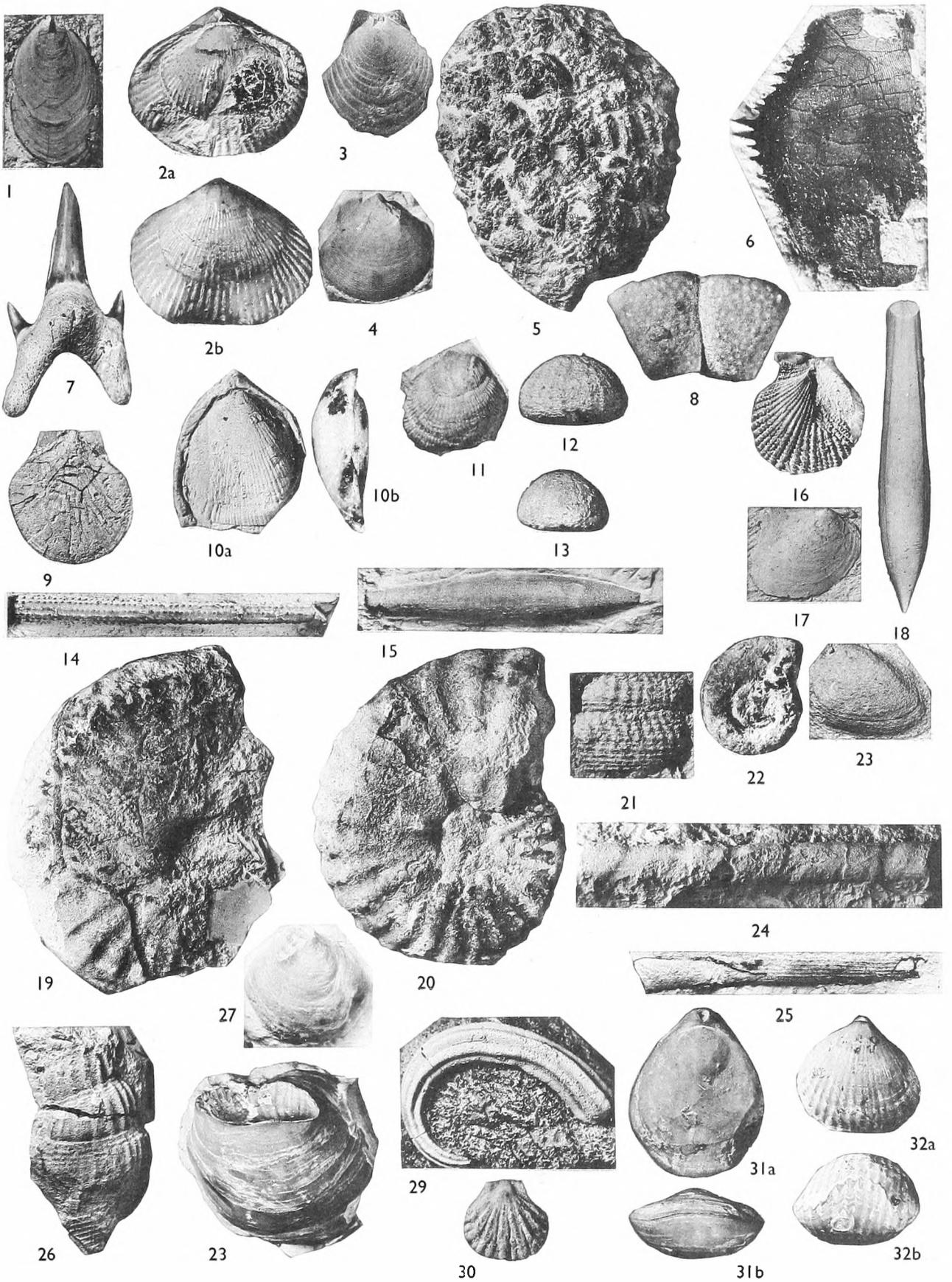
Aragonitic fossils may be preserved in the *plenus* Subzone and Upper *subglobosus* Zone in three main ways which can be called 'normal', 'pebble', and 'oyster-cast' preservation.

'Normal' preservation is the commonest type in the standard succession and also occurs in the *varians* Zone and lower *subglobosus* Zone. Normally preserved aragonitic fossils have the shell converted to marcasite or pyrite (which has since usually turned to limonite) or to chalky calcite and when calcitized are often thinly green-coated. Also they are filled with rock of the same age and type as the matrix, and, except when the matrix is hard, show plastic compression perpendicular to the bedding plane.

'Pebble' preservation is commonest in condensed successions, as in Devon. Pebble fossils are filled with rock which is evidently older and somewhat harder than the matrix and fragments of this older rock may cling to the outside of the fossils. The fossils are usually thickly green-coated or somewhat phosphatized (indicating long exposure on the sea floor), are not plastically compressed, and tend to hammer out rather easily from the matrix.

EXPLANATION OF PLATE 77

- Figs. 1–8. Cold-water group (Bed 1 and the *subglobosus* Zone). 1, *Lingula* sp., $\times 6.7$; Bed 1, Merstham. 2, *Orbirhynchia multicosata* Pettitt, $\times 1.33$; *a* brachial, *b* pedicle valve aspect; Bed 1, Merstham. 3, *Entolium orbiculare* (Sowerby), $\times 2$; Top *subglobosus* Zone, Cernay-en-Dormois (Ardennes). 4, *Lima globosa* (Sowerby), $\times 2$; Top *subglobosus* Zone, Merstham. 5, Problematicum, $\times 1$; Bed 1, Merstham. These structures consist of coarse sand grain-size microfossils bound in a calcite cement and are smooth and flattish on one side and convex and convoluted on the other (the side shown here). 6, *Ctenothrissa* sp., $\times 6.7$; Bed 1, Merstham. 7, *Scapanorhynchus subulatus* (Agassiz), $\times 2$; Top Bed 1, Folkestone (locality 1). 8, *Trachyaster* cf. *rugosus* (Spencer), $\times 6.7$; Bed 1, Steyning.
- Figs. 9–15. Warm-water group (mainly Bed 2 and above). 9, *Entolium membranaceum* (Nilsson), $\times 2$; Bed 2, Eastbourne (locality 1). 10, '*Rhynchonella*' *lineolata* Phillips *carteri* Davidson, $\times 2.67$, somewhat crushed, *a* brachial valve aspect, *b* lateral aspect; Bed 2, Gogs Pit. 11, *Plicatula barroisi* Peron, $\times 2$; Bed 3, Merstham. 12, *Discoidea subuculus* Leske tr. *minima* Agassiz, $\times 2$; lower height and more rounded apex than in fig. 13; Top *subglobosus* Zone, Heacham. 13, *Discoidea minima* Agassiz, $\times 2$; Bed 4, Steyning. 14, *Cidaris perornata* Forbes, $\times 2$, fragment of spine; Bed 4, Winchester. 15, *C. hirudo* Sorignet, $\times 1.33$, spine, slightly abraded; Melbourn Rock, Merstham.
- Figs. 16–18. North Boreal group, with central European Russian affinities, mainly in Beds 4–6. 16, *Aequipecten arlesiensis* (Woods), $\times 2$; Bed 4, Steyning. 17, *Oxytoma seminudum* (Dames), $\times 2$, right valve; Bed 4, Folkestone (locality 1). 18, *Actinocamax plenus* (Blainville), $\times 0.67$; Bed 4, Folkestone (locality 1).
- Figs. 19–26. Aragonitic group; distribution controlled mainly by preservation, not ecology. 19, *Metoicoceras geslinianum* (d'Orbigny), $\times 0.67$; Bed 3, Merstham. 20, *Metoicoceras gourdoni* (Grossouvre), $\times 0.67$; Bed i, Cap d'Antifer. 21, *Cerithium* sp., $\times 2.67$; Bed i (= Bed 4), Crésantignes. 22, *Solarium* sp., $\times 2.67$; found inside a large ammonite, Bed 1, Crésantignes. 23, ? *Grammatodon* cf. *cenomanense* (d'Orbigny), $\times 2$; Bed 3, Merstham. 24, *Sciponoceras* sp., $\times 1$; Melbourn Rock, Merstham. 25, *Dentalium* sp., $\times 1.33$; Bed 7a, Eastbourne (locality 2). 26, *Aporrhais* sp., $\times 1.33$; Bed 3, Merstham.
- Figs. 27–32. Miscellaneous group; forms which do not belong to any of the previous groups, but which have stratigraphical importance or anomalous distribution. 27, *Ostrea vesicularis* Lamarck, $\times 2$; small form typical of the *subglobosus* Zone, with cast of turreted gastropod on attachment area; Top *subglobosus* Zone, Merstham. 28, *O. vesicularis* Lamarck, $\times 1.33$; large form typical of Beds 1 and 2; Bed 1, Merstham. 29, *Ditrupa difformis* (Lamarck), $\times 1.33$; Bed i (tourtia de Mons), Bellignies. 30, *Terebratulina* cf. *nodulosa* Etheridge, $\times 6.7$, pedicle valve aspect. 31, *Ornatothyris* sp., $\times 1.33$, *a* brachial valve aspect, *b* pedicle valve aspect; Base Bed 3, Marham. 32, *Orbirhynchia wiesti* (Quenstedt), $\times 1.33$, *a* brachial valve aspect, *b* anterior aspect.



'Oyster-cast' preservation occurs when the aragonitic fossils are preserved merely as impressions on the attachment areas of *Ostrea vesicularis* (Pl. 77, fig. 27). Oyster casts, usually of small turreted gastropods, are found mainly in the top of the *subglobosus* Zone and Bed 1, in which aragonitic fossils of normal or pebble preservation are almost entirely absent and, together with the presence of the calcitic aptychi of ammonites, they prove that animals with aragonitic shells lived in the sea at the time of deposition of these beds but that their shells were later destroyed.

Distribution of normally preserved Aragonitic fossils. Normally preserved aragonitic fossils are distributed in England as shown in text-fig. 3. Their distribution in the thick sections of standard succession in the eastern Paris Basin (Crésantignes and Cernay-en-Dormois) is similar to that in the South Downs.

In the top of the *subglobosus* Zone and in Bed 1 normally preserved aragonitic fossils are usually rare (except in Bed 1 at Lulworth) although oyster casts are fairly common at these horizons. Normally preserved aragonitic fossils become much commoner at the base of Bed 2 over nearly the whole area of standard succession except near the Wash where the beds are thin (text-fig. 3); Krumbein and Sloss (1951, p. 421), using data from Pike (1947), have noticed a similar tendency for ammonites to be common in thick successions in the Cretaceous of New Mexico. Normal aragonitic fossils continue abundant in Bed 3 but they are rare in Beds 4–8 except when the *plenus* Subzone is more than about 10 feet thick as, for instance, at Eastbourne, Crésantignes, Steyning, Compton Bay (Isle of Wight), and Lulworth.

When the beds are thick and muddy, normally preserved fossils are usually limonitized, e.g. Eastbourne, Crésantignes, and Steyning. This limonitization, however, is probably the result of the recent conversion of marcasite or pyrite. This is suggested by the presence at Eastbourne of ammonites which are partly marcasite or pyrite and partly limonite, for these fossils doubtless owe their only partial conversion to the fact that Recent marine erosion is particularly strong at Eastbourne so that fossils have not long been near enough the surface of the ground to be subject to the action of oxygen-charged, percolating water.

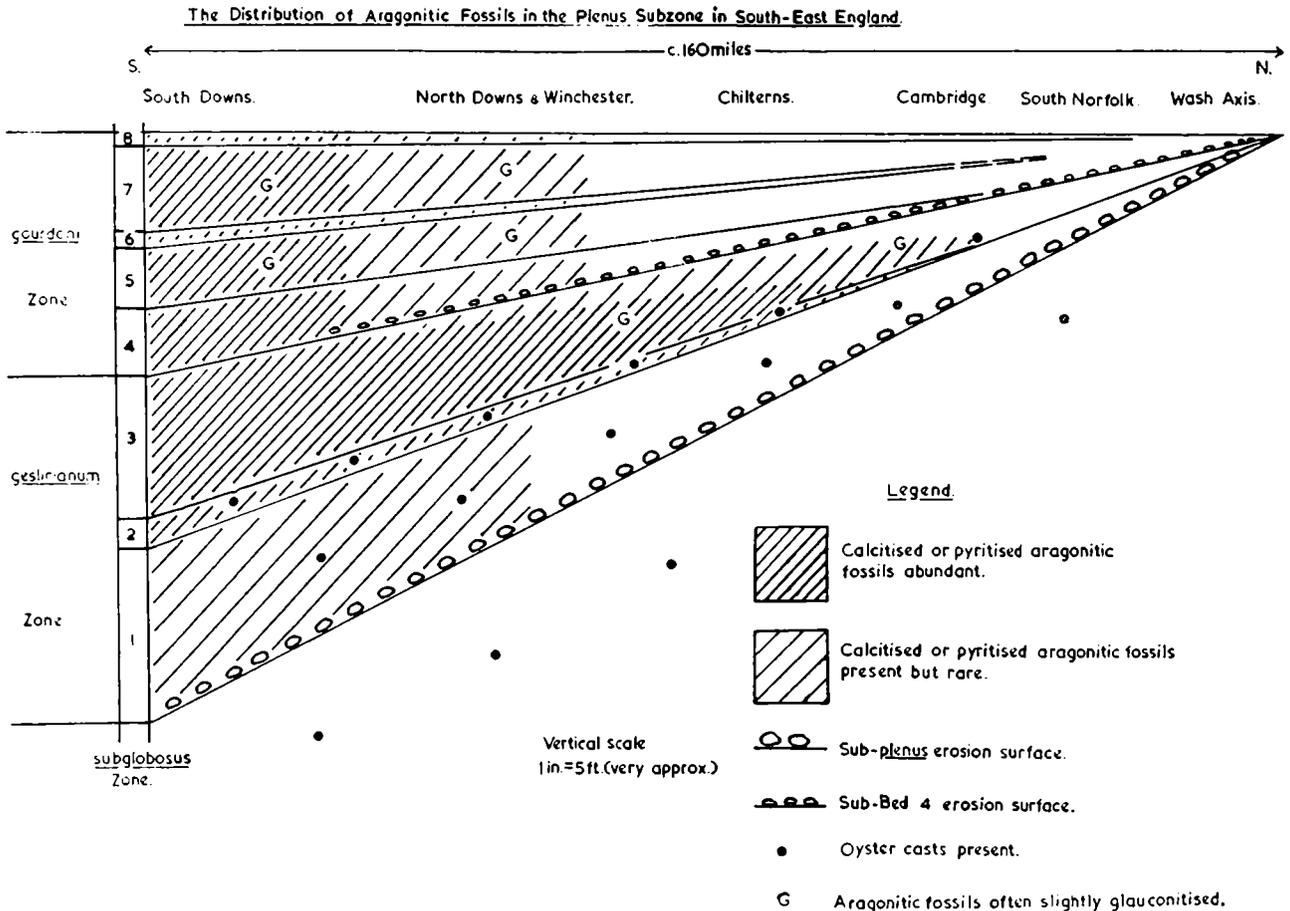
In any given bed the proportion of aragonitic fossils which are slightly glauconitized rises as the bed gets thinner. Thus at Merstham (Subzone 7 ft. 6 in. thick) many of the aragonitic fossils in Beds 2–3 and 3 and nearly all of those in Beds 4–8 are greenish. On the other hand, at Eastbourne (18–25 ft. thick) greenish aragonitic fossils are rare throughout the succession, though commoner in Beds 4–8 than below.

Normally preserved aragonitic fossils are especially common in or near large ammonites. This was noticed in the course of the present work in Bed 1 at Crésantignes (where a *Solarium* was found inside a large ammonite) and also in Beds 2–3 at Royston and Bed 2 at Steyning. The same phenomenon has been noticed by many writers in other beds of the Chalk (Godwin-Austen 1860, Lamplugh 1904, Wright and Wright 1942) and Davis (1926) similarly noted that aragonitic fossils were often found inside echinoids but not in the surrounding matrix.

Factors controlling the preservation of normal Aragonitic fossils. The distribution of normal aragonitic fossils in the *plenus* Subzone and top of the *subglobosus* Zone can largely be explained by variation in temperature (and therefore in CO₂ content of the

sea water), in turbulence of the bottom water, and in length of exposure on the sea-floor (which would be related to rate of deposition and indirectly to turbulence). Other probable, though less important, factors are the rate of pyritisation (or marcasitisation) or calcitisation and the initial strength, weight, and thickness of the shell.

The absence of aragonitic fossils from such beds as Bed 1 and the top of the *subglobosus*



TEXT-FIG. 3. The distribution of aragonitic fossils in the *plenus* Subzone in south-east England.

Zone is probably due to the fact that aragonite, but not calcite, was dissolved by the bottom water, which in this respect was comparable with the bottom water above *Globigerina* Ooze in Recent oceans; this, in turn, was probably connected with low temperature. The solubility of calcium carbonate in sea water has recently been discussed by Revelle and Fairbridge (1957, pp. 250 ff., esp. fig. 5). It appears that in surface sea water of normal salinity and alkalinity (Ca content) aragonite is always more soluble than calcite. A fall in temperature has two effects; it increases the solubility of aragonite or calcite (unlike most other solids) and also increases the solubility of atmospheric CO_2 which lowers the pH (though less than might be expected because of the buffer capacity of sea water). Consequently in equilibrium with an atmospheric partial pressure of about 3×10^{-4} atm. (the present-day value), and neglecting CO_2 produced by organisms, sea water in the laboratory will dissolve aragonite but not calcite at a temperature lower than 5°C .

In trying to apply these results to the Chalk one can presumably neglect the effect of great hydrostatic pressure which appreciably raises the apparent solubility product of both calcite and aragonite at depths of the order of 1,000 metres and also lowers the pH (Revelle and Fairbridge 1957, p. 254). The effect of the production of CO₂ by organisms in the water is more important, however. This is limited under aerobic conditions by the saturation volume of dissolved oxygen per litre (Revelle and Fairbridge 1957, p. 251). At 10° C. and 20‰ chlorinity this is 7.07 c.c./litre (Harvey 1955, table p. 184). Total respiration of this would produce the same volume of CO₂ which, from Revelle and Fairbridge (fig. 5), suggests that aragonite would just be dissolved given a partial atmospheric pressure of CO₂ of 3×10^{-4} atm. Consequently, on the simple though very uncertain assumption that Cretaceous sea water behaved like Recent sea water in this respect, Bed 1 and the top of the *subglobosus* Zone were deposited at a temperature lower than 5° or 10° C.

The widespread appearance of aragonitic fossils at the base of Bed 2, therefore, would suggest a rise in the temperature of the bottom water from below to above the equilibrium temperature of aragonite (which agrees with the change of the fauna towards a more shallow-water type). This level is thus comparable with the Chalk Marl, Chalk Rock, and Top Rock in which aragonitic fossils occur and which are usually regarded as shallow-water bands. By contrast, the southward retreat of aragonitic fossils at the base of Bed 4 may be connected with a decrease in temperature which is also suggested by the fauna. There is a possibility, however, that this southward retreat may also be partly due to an increase in turbulence as indicated by the sub-Bed 4 erosion surface.

Superimposed on the basic pattern connected with temperature is another pattern connected with turbulence and length of exposure on the sea bottom. Even at a period when the temperature of the bottom water was usually higher than the equilibrium temperature of aragonite, aragonitic fossils would still be expected to weaken quicker than calcitic ones because of chemical alteration (to pyrite, marcasite, or calcite) and also, perhaps, by intermittent solution caused by occasional lowering of the temperature below equilibrium for aragonite. This progressive weakening would gradually increase the likelihood that tumbling on the sea floor in turbulent bottom water would destroy the fossil. Consequently preservation of normal aragonitic fossils would be favoured, other things being equal, by rapid burial after death, by the absence of disinterments and by low turbulence in the bottom water during the periods when the fossil was in fact exposed. Areas of rapid and permanent burial would be areas of fast deposition and this explains why normal aragonitic fossils are commonest where the beds are thickest. Isolated points of low turbulence and permanent burial would be found in and underneath large ammonites which would themselves be protected from destruction by the thickness of their shells and their weight (which would prevent them being tumbled on the sea floor). This explains the frequent occurrence of aragonitic fossils in and around large ammonites. That the ammonites acted by producing sites of low turbulence rather than by somehow reducing solution rate is shown by the fact that in the Yorkshire Chalk Rock not only aragonitic fossils, but also certain types of calcitic ones, were preferentially preserved inside large ammonites (Wright and Wright 1942).

Distribution of Pebble preservation. Pebble preservation is commonest in condensed successions and fossils so preserved are older than their present matrix. Instances

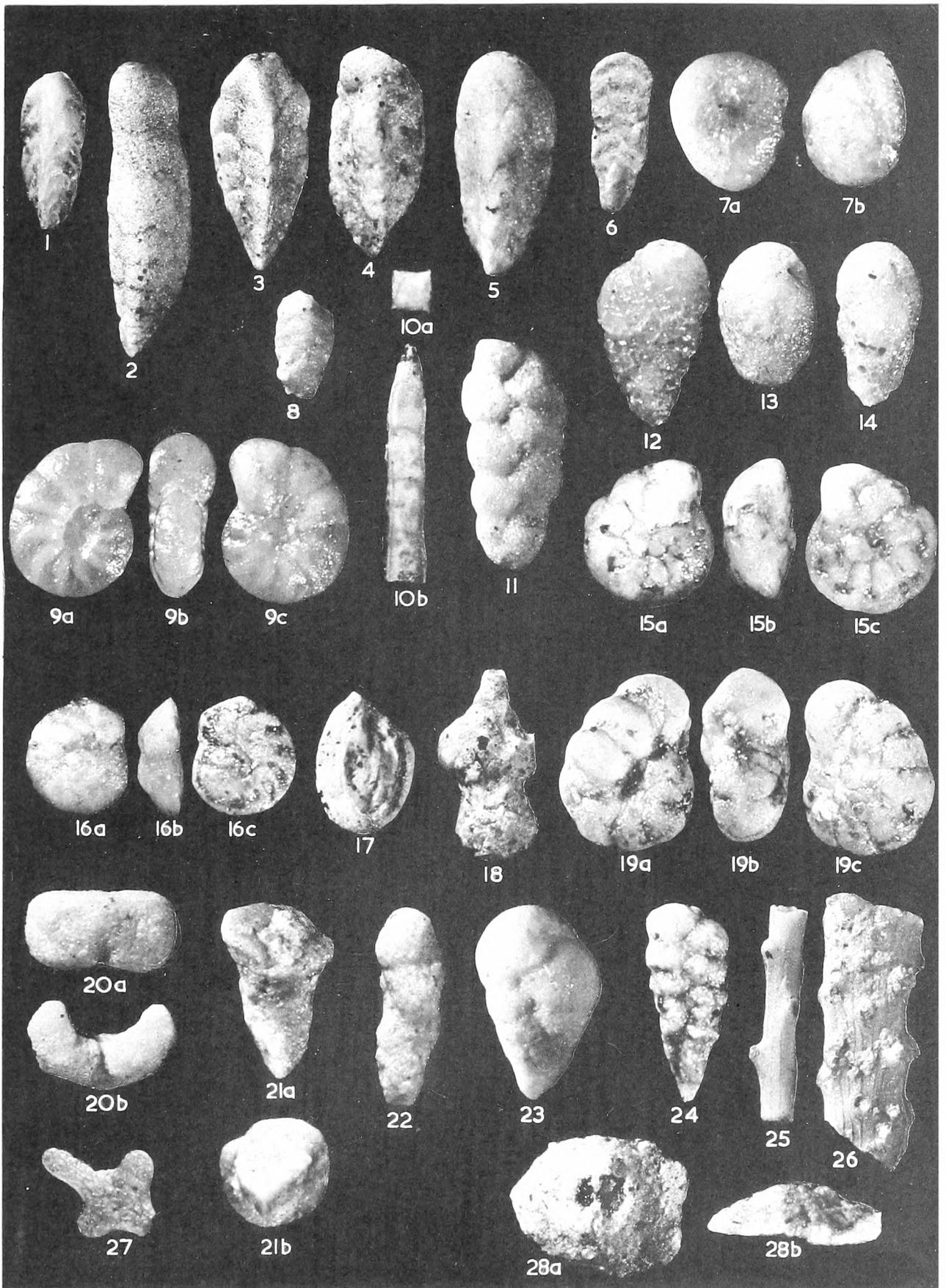
(Jefferies 1961) are the slightly phosphatized Cenomanian ammonites in Bed C at Hooken Cliff (Beer), the glauconitized ammonites at the base of the *labiatus* Zone at Haven Cliff, Seaton, the similar green-coated fossils at the base of the Turonian at Cap d'Antifer and Rouen and the phosphatized fossils at the base of the Turonian at Bellignies. There is also at least one case where pebble fossils occur in the standard succession (Bed 7, Eastbourne, loc. 2). In this instance the fossils are not glauconitized but covered with a patchy limonitic skin.

However, not all conglomerates of chalk pebbles associated with the *plenus* Subzone contain aragonitic pebble fossils. Thus there seem to be few or no such fossils in the conglomerate at the base of Bed 1 at any of the sections examined, or in the pebble bed (Bed 1) above the sub-*plenus* erosion surface at South Ferriby.

Factors controlling Pebble preservation. Turbulence and length of exposure prevented the preservation of normal aragonitic fossils in southern Norfolk and Cambridgeshire

EXPLANATION OF PLATE 78

- Figs. 1–15. Cold-water group; forms commonest in, and usually confined to, Bed 1 and the *subglobosus* Zone. 1, *Tristix excavatus* (Reuss), lateral aspect, $\times 40$; Pitstone, 0–3 in. below top *subglobosus* Zone. 2, *Tritaxia tricarinata* (Reuss) var. *plummerae* Cushman; one variety of a very variable species, lateral aspect, $\times 20$; Eastbourne (locality 4), Bed 1, 36 in. above base. 3, *T. tricarinata* (Reuss) var. *pyramidata* Reuss, lateral aspect, $\times 20$; Eastbourne (locality 4), Bed 1, 36 in. above base. 4, *T. tricarinata* (Reuss) var. *macfadyeni* Cushman, lateral aspect, $\times 40$; Eastbourne (locality 2), Bed 4, 34 in. above base. 5, *T. tricarinata* (Reuss) var. *macfadyeni* Cushman, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 6, *Spiroplectinata* cf. *complanata* (Reuss), $\times 40$; form intermediate between *S. complanata* (Reuss) and *S. jaekeli* Franke; Eastbourne (locality 3), Bed 1, 0–3 in. above base. 7, *Pernerina* sp., *a* apertural aspect, *b* lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 8, *Spiroplectammia* sp., lateral aspect, $\times 40$; Eastbourne (locality 3), 0–6 in. below top *subglobosus* Zone. 9, *Gavelinella baltica* Brotzen, *a* umbilical, *b* apertural, *c* spiral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 10, *Nodosaria prismatica* Reuss, *a* apertural, *b* lateral aspect, $\times 40$; Merstham, Bed 1, 0–3 in. above base. 11, *Dorothia gradata* (Berthelin), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 12, *Plectina ruthenica* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 13, *Hagenowella advena* Cushman, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 12 in. above base. 14, *Verneuilina polystropha* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 15, *Pseudovalvulinaria* sp., *a* umbilical, *b* apertural, *c* spiral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base.
- Figs. 16–28. Warm-water group; forms which enter or increase at the base of Bed 2 in the area of standard succession. 16, *Cibicides* cf. *turonica* Brotzen, *a* spiral, *b* apertural, *c* umbilical aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 17, *Quinqueloculina antiqua* (Franke), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 18, *Reophax* sp., lateral aspect, $\times 20$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 19, *Anomalinoidea globosa* Brotzen, *a* umbilical, *b* apertural, *c* spiral aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 20, asteroid terminal plate, *a* external aspect, *b* aspect showing slit for tube-foot, $\times 40$; Eastbourne (locality 1), Bed 2, 17–20 in. above base Bed 1. 21, *Siphogaudryina* sp., *a* lateral aspect, *b* apical aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 22, *Gaudryina* sp., lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 23, *Textularia chapmani* Lalicker, lateral aspect, $\times 40$; Eastbourne (locality 1), Bed 2, 12–14 in. above base 1. 24, *Textularia* cf. *washitensis* Carsey, lateral aspect; the chambers are somewhat more inflated than in *T. washitensis*, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 25, *Siphoniotyphlus tenuis* (Hagenow), thin branch, $\times 20$; Eastbourne (locality 1), Bed 2, 34–36 in. above base Bed 1. 26, Thick branch of same $\times 20$. Same locality. 27, Star plate. Probably from the abactinal surface of *Calliderma smithiae* (Forbes), $\times 40$; Eastbourne (locality 1), Bed 2, 17–20 in. above base Bed 1. 28, *Marssonella* sp., *a* apical, *b* lateral aspect, $\times 40$; Eastbourne (locality 1), Bed 2, 35–36 in. above base Bed 1.



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where a somewhat reduced version of the standard succession is present. In Devon and the west Paris Basin, however, where the water was probably shallower, and where length of exposure and turbulence, as judged by net deposition, were greater, aragonitic shells were not destroyed but were preserved as pebble fossils. Obviously some factor other than turbulence must distinguish the two cases.

Rate of lithification was probably the factor involved and in the case of some pebble fossils at least, lithification seems to have happened fairly early. Thus *Metoicoceras* at the base of the Turonian at Haven Cliff, Seaton, is sometimes preserved as an almost perfect 'Steinkern'. This indicates that when the fossil was disinterred by erosion it retained its shape (though the shell had been broken away) because of the hardness of the chalk inside it. In other words, whereas a normal aragonitic fossil progressively weakened after death so that its chance of preservation was inversely proportional to length of exposure, a pebble fossil was strengthened shortly after death by the hardening of the chalk inside it. After this it would be almost indestructible, since, with further rolling on the sea floor, it would be hardened still further by phosphatization. Apart from being less strongly phosphatized, the pebble fossils of the *plenus* Subzone are thus very like the phosphate nodules of the Cambridge Greensand or of the Rouen Horizon which Cayeux (1939, p. 167, 184) regarded as phosphatized, reworked pebbles of chalk.

When pebble fossils are absent from conglomerates of chalk pebbles they were probably destroyed by solution, chemical changes, or mechanical action before they had a chance to be incorporated in the conglomerate. The occurrence in Bed 7 at Eastbourne probably points to the presence of a small erosion surface. The rapid lithification of shallow-water chalks may indicate the presence in the parent ooze of aragonite which, because of the high temperature of the bottom water, was converted to calcite cement instead of being dissolved (Black 1953, p. lxxv in discussion).

The author's views on the preservation of aragonitic fossils in the Chalk have been deeply influenced by those of Mr. M. Black, of Cambridge, as propounded in lectures and discussion. The author would like to express his gratitude to Mr. Black, though the opinions expressed are naturally his own responsibility.

METHODS USED IN STUDYING FAUNAL DISTRIBUTION

The study of the palaeoecology of the *plenus* Subzone and the top of the *subglobosus* Zone was based partly on the macro- and partly on the microfauna and partly on general considerations such as the gross lithology of the rocks, their position in the Anglo-Paris Basin, the presence of erosion surfaces and whether or not aragonitic fossils were preserved. The distribution of the macrofossils was studied by bed-by-bed collecting at some forty localities in the Anglo-Paris Basin (Jefferies 1961). The microfossils, on the other hand, were studied by extracting them from the rock and counting them. The results of counting are shown in the form of distribution graphs in text-figs. 4-11.

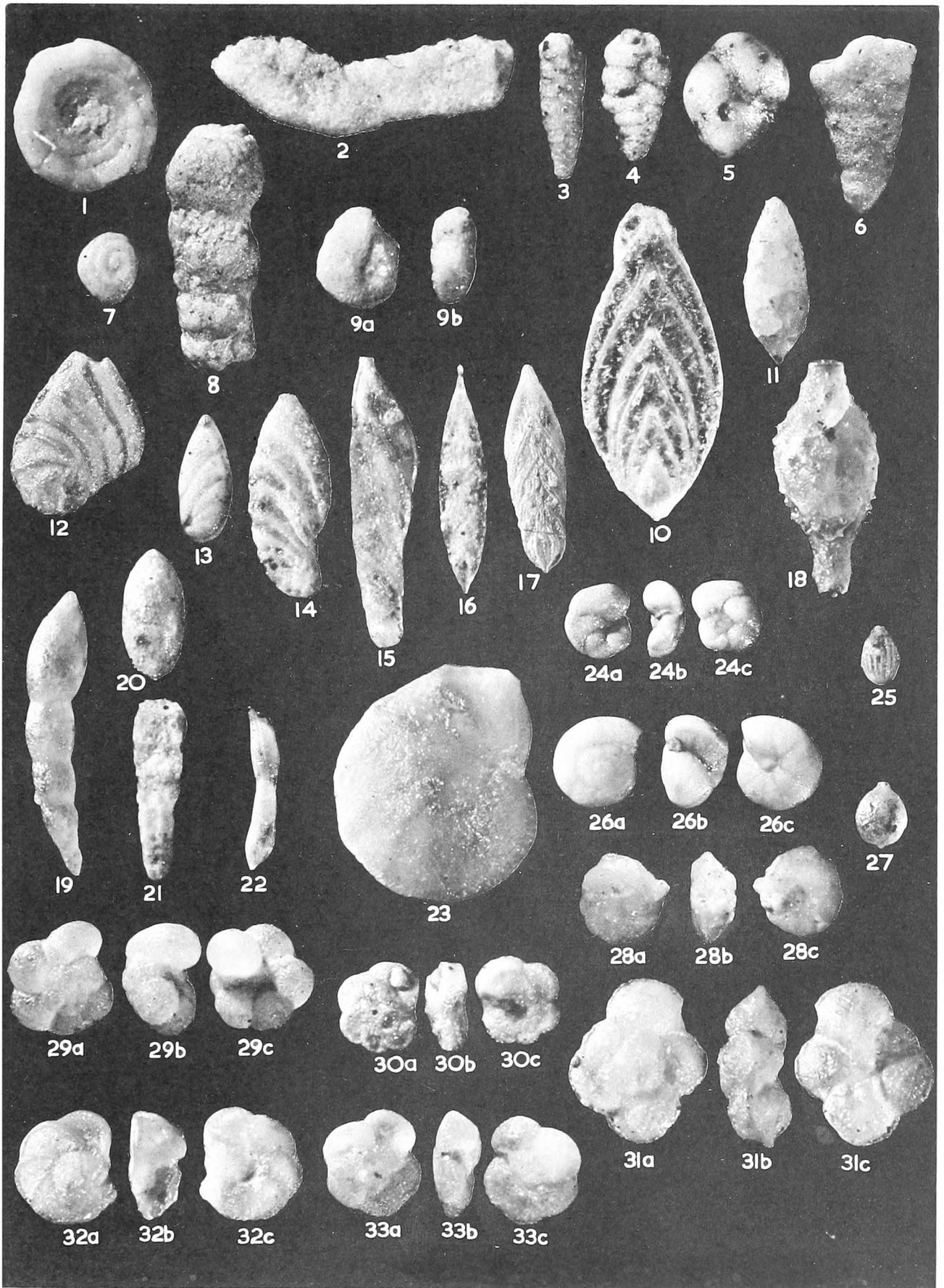
The method used for extracting the microfauna was as follows: the sample was broken into pieces about $\frac{1}{2}$ in. across and prominent burrows were removed. A known volume (up to 200 c.c.) of these pieces was then immersed in water in a jam jar and broken down by repeated freezing and thawing. Any pieces which would not pass a 5-mm. sieve after this treatment were crushed with a pestle and mortar and returned to the sample. This was then placed in a 3-lb. Kilner jar, topped up to 750 c.c. with water and shaken on a shaking machine for three to four hours at about 70 cycles/min. The resulting sludge

was thinned out by wet-sieving through a 200-mesh sieve and the portion retained by the sieve was returned to the Kilner, topped up to 750 c.c. again and shaken for a further three to four hours to clean the microfossils. Sometimes, when the rock was hard, two to four 1- or 1½-inch rubber bungs were placed in the Kilner during the shakings to act as mill balls. After a second shaking the sample was wet-sieved again through a 200-mesh sieve, dried on the sieve over a radiator, and dry-sieved through an 80-mesh sieve. The fractions passed and retained by the 80-mesh sieve were then ready for storage unless the coarse fraction contained many large fragments, in which case it was dry-sieved through a 30-mesh sieve and any microfossils in the 30-mesh fraction were picked out and added to the 80-mesh fraction before the latter was stored.

EXPLANATION OF PLATE 79

Figs. 1–28. Miscellaneous group; benthonic Foraminifera which do not belong to either the cold- or the warm-water behaviour groups. 1, *Ammodiscus cretaceus* Reuss, lateral aspect, $\times 40$; Eastbourne (locality 1), Bed 3, 34–36 in. above base Bed 1. 2, ?*Rhizammina algaeformis* Brady; a rare species included with *Ramulina aculeata* in the counts, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 3, *Gaudryina foeda* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 4, *G. serrata* Franke, lateral aspect, $\times 40$; Bellignies, Bed iv, 0–2 in. above base. 5, *Eggerellina sp.*, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 6, *Marssonella trochus* (d'Orbigny), lateral aspect, $\times 40$; Eastbourne (locality 2), Bed 1, 1–20 in. above base. 7, *Glomospira charoides* (Parker and Jones) var. *corona* Cushman and Jarvis, $\times 40$; Bellignies, Bed ii, 2–6 in. above base. 8, *Bulbophragmium sp.*, fragment of uniserial portion, $\times 20$; Eastbourne (locality 4), Bed 1, 12 in. above base. 9, *Haplophragmoides latidorsatum* (Bornemann), *a* lateral, *b* apertural aspect, $\times 40$; Merstham, Bed 4, 0–4 in. above base. 10, *Frondicularia bicornis* Reuss, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 11, *Globulina prisca* Reuss, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 12, *Palmula elliptica* (Nilsson), lateral aspect of juvenile specimen, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 13, *Vaginulina complanata* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 2), Bed 6. 14, *V. parallela* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 2), Bed 4, 17–20 in. above base. 15, *V. costulata* (Römer), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 16, *Frondicularia inversa* Reuss; not separated from *F. solea* in the counts, $\times 40$; Eastbourne (locality 2), Bed 4, 3–6 in. above base. 17, *F. solea* Reuss; not separated from *F. inversa* in the counts, $\times 40$; Eastbourne (locality 1), Bed 2, 17–20 in. above base Bed 1. 18, *Ramulina aculeata* Wright, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 19, *Dentalina sp.*, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 20, *Pseudoglandulina concinna* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 3), Bed 1, 0–2 in. above base. 21, *Nodosaria raphanus* (Linne) *obscura* Reuss, lateral aspect, $\times 40$; Eastbourne (locality 1), Bed 2, 17–20 in. above base Bed 1. 22, *Dentalina filiformis* (Reuss), lateral aspect, $\times 40$; Briollay, Sarthe, 'marnes à ostracées'. 23, *Lenticulina rotulata* Lamarck, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 24, *Discorbis allomorphinoides* (Reuss), *a* umbilical, *b* apertural, *c* spiral aspect, $\times 40$; Briollay, Sarthe, 'marnes à ostracées'. 25, *Lagena multistriata* Marsson; possibly an *Entosolenia*; lateral aspect, $\times 40$; Briollay, Sarthe, 'marnes à ostracées'. 26, *Gyroidinoides nitida* (Reuss), *a* spiral, *b* apertural, *c* umbilical aspects, $\times 40$; Pitstone, *subglobosus* Zone, 0–3 in. below top. 27, *Entosolenia sp.*, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 28, *Cibicides formosa* Brotzen, *a* spiral, *b* peripheral, *c* umbilical aspects, $\times 40$; Merstham, Bed 7a.

Figs. 29–33. Planktonic Foraminifera. 29, *Globigerina portsdownensis* Williams–Mitchell; commonest member of the Globigerinidae in the *plenus* Subzone; *a* spiral, *b* apertural, *c* umbilical aspects, $\times 40$; Eastbourne (locality 1), Bed 2, 17–20 in. above base Bed 1. 30, *Globotruncana lapparenti* Brotzen *lapparenti* Brotzen, *a* spiral, *b* apertural, *c* umbilical aspect, $\times 40$; Bellignies, 0–2 in. above base. 31, *Rotalipora turonica* (Brotzen), *a* spiral, *b* peripheral, *c* umbilical aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 32, *Thalmaninella deeckeii* (Franke), *a* spiral, *b* apertural, *c* umbilical aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 68 in. above base. 33, *Praeglobotruncana sp.*, *a* spiral, *b* apertural, *c* umbilical aspects, $\times 40$; Eastbourne (locality 2), Bed 4, 9–12 in. above base.



JEFFERIES, Turonian foraminifera

This method of extraction is based on a method used by Burnaby on the Chalk Marl (Burnaby 1961). The modification of Burnaby's method for use on the *plenus* Subzone (which includes harder rocks than the Chalk Marl) took several months so that the early extractions (at Eastbourne and Merstham) were less successful than the later ones (Pitstone and Crésantignes). This is shown by the average number of benthonic foraminifera large enough to be retained by an 80-mesh sieve which were extracted per c.c. of rock (Merstham 32.2, Eastbourne 40.8, Pitstone 71.6, Crésantignes 78.5). However, ecological interpretation is based mainly on the percentage composition of the microbenthos so that destruction is only important in so far as it affects some species more than others. The good agreement in the distribution graphs of Merstham (text-fig. 6) with Pitstone (text-fig. 7), on the one hand, and of Eastbourne (text-fig. 8) with Crésantignes (text-fig. 10) on the other, suggests that percentage destruction was largely uniform as between the different species of microbenthos and can therefore be disregarded.

Taxonomic examination was carried out on a half of each prepared sample from Eastbourne, the samples having been halved on a Burnaby rotary sample splitter. Any new species which appeared during the counting of later samples were transferred to a special miscellaneous taxonomic slide for later study. The foraminifera encountered are figured in Plates 78–79.

Counting was by a two-order procedure also developed by Burnaby; only the material large enough to be retained by an 80-mesh sieve (0.2 mm.) was counted. For the first-order count this was divided on a Burnaby sample splitter into fractions guessed to contain less than about 100 microfossils. Using a squared microfossil slide as a counting tray and a previously prepared tally sheet for recording, enough of these fractions were then counted completely for a total of more than 300 microfossils to be reached. The material which had been scanned was then weighed and the tally sheet examined to see which species had reached a total of eight or more. These constituted the first-order species. The second-order count proceeded like the first-order count except that specimens of first-order species were not recorded. Counting continued until the number of specimens of second-order species (those which had reached seven or less in the first-order count) also exceeded 300. When the second-order count was complete all the material which had been scanned (both orders) was weighed. The number of specimens of a first-order species which would have been counted if counting had continued can be estimated from the equation:

$$N = \frac{nW_2}{W_1}$$

Where N is the estimate, n the recorded number in the first-order count, W_1 the weight of the first-order material, and W_2 the weight of first- and second-order material. From the observed and estimated frequencies the per mil. frequencies of the different species can easily be calculated. The advantage of a multi-order counting method is that a reasonable number of specimens of a rare species can be counted without counting an enormous number of a common one. This is particularly useful for counting mixed plankton and benthos since the plankton is normally much commoner and has fewer species than the benthos.

The distribution diagrams are constructed on the following basis: Benthonic

foraminifera + bryozoa + asteroid ossicles = $B = 1,000$. Ostracods (one group only) and *Roveacrinus* ossicles are plotted on the basis $B = 1,000$. Planktonic foraminifera = $P = 1,000$. The justification for this method of plotting the results is that plankton is more abundant than benthos so that numerical variation in the plankton would obscure per mil. variation in the benthos, and that plankton and benthos represent separate communities which for ecological purposes should be treated separately.

THE UPPER PART OF THE SUBGLOBOSUS ZONE

The macrofauna of the upper *subglobosus* Zone is rather meagre in the area of standard succession, but many of the groups which are rare or absent in this area can be found nearer the edges of the Anglo-Paris Basin in Norfolk, Yorkshire, and Lincolnshire, or at Cap d'Antifer.

The fauna of the area of standard succession includes *Scapanorhynchus subulatus*, small turreted gastropods (as oyster casts only), *Schloenbachia* sp. (limonitized specimen at Crésantignes), *Plicatula inflata*, *P. barroisi*, *Entolium orbiculare*, *Aequipecten beaveri*, *Neitheia quinquecostata* (c), *Inoceramus pictus* (c), *Ostrea vesicularis* (small form) (c), *Lingula* sp. (c), *Terebratulina striatula* (c), *T.* cf. *nodulosa*, *Holaster trecensis* (c), 'problematicum' (c). Serpulids, Rhynchonellids, Terebratulids (except *Terebratulina*), asteroids, Cidarids, bryozoa, and the group of small *Discoidea* (represented at this level by *D. subuculus*) are possibly absent and certainly very rare. In this and subsequent lists (c) indicates common.

Westwards, however, at Cap d'Antifer, the top of the *subglobosus* Zone contains the Rhynchonellids *Orbirhynchia multicostata*, *O. compta*, and *O.* cf. *cuvieri* (the first of these being the commonest macrofossil), *Discoidea subuculus* and fragments of large bryozoa. Northwards the Terebratulid *Ornatothyris sulcifera* and also spines of *Cidaris hirudo* are common in a nodular band 20 feet below the top of the *subglobosus* Zone at Cherry Hinton. Furthermore, in northern Norfolk and Lincolnshire the Terebratulids *Concinnithyris burhamensis* and *C. subundata*, perhaps the same species (at Heacham, Hillington, and South Ferriby) and also *Discoidea subuculus* (at Heacham) and *Cidaris perornata* (at Heacham) occur in the top of the *subglobosus* Zone.

In explaining this faunal variation possible chronological differences cannot be left out of account. The *plenus* Subzone is condensed or absent in northern Norfolk, Lincolnshire, and Cap d'Antifer suggesting that some feet of chalk at the top of the *subglobosus* Zone may also be missing. It seems unlikely, however, that this possible age difference entirely accounts for the faunal differences, since the Rouen Horizon (early *subglobosus* Zone) is 35 feet below the top of the Zone at Cap d'Antifer and the Lower Chalk of Norfolk seems condensed rather than incomplete (Jukes-Browne and Hill 1903, fig. 2, p. 23). Much the most likely explanation of the peripheral distribution of these groups, therefore, is that Norfolk and Lincolnshire on the one hand, and Cap d'Antifer, on the other, were shallow-water areas on either side of the Weald and Central Paris Basin. Shallow water at Cap d'Antifer is suggested by the presence in the Cenomanian of numerous erosion surfaces and glauconitic bands and in Norfolk by the thinness of the Cenomanian and its lack of mud.

The softness of the bottom in the area of standard succession was probably responsible for the absence there of Rhynchonellids and most Terebratulids. This is suggested by the

fact that the two types of brachiopods which do occur probably did not require hard bottom. Thus *Lingula sp.* probably lived in a burrow, held in place by the weight and mucous covering of its pedicle (Craig 1952, p. 112), and *Terebratulina*, by analogy with its Recent relative *Clidonophora* (cf. Elliott 1938, p. 129), may well have been able to anchor itself in soft ooze by means of a tuft of rootlet-like fibres on the end of its pedicle.

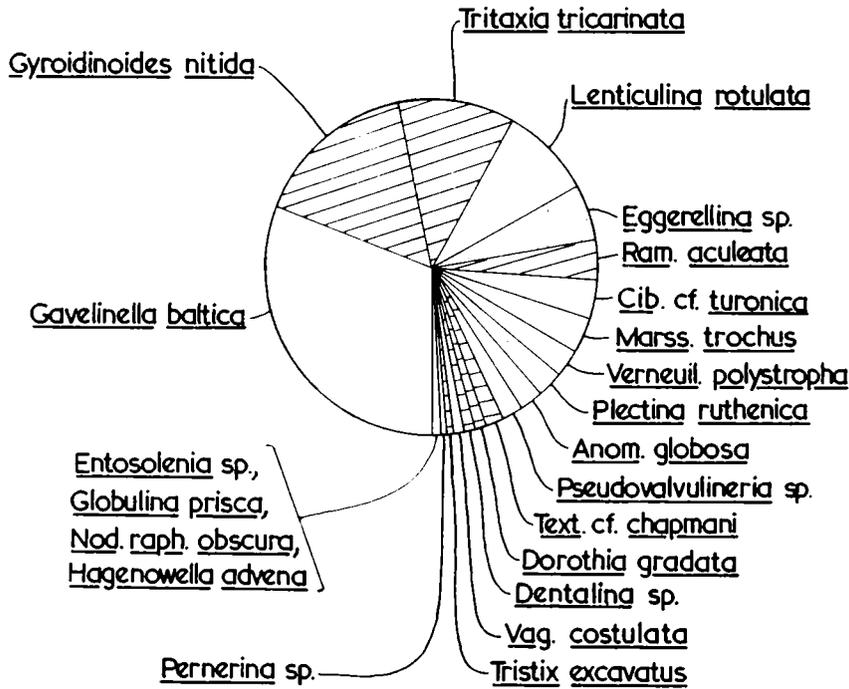
The microfauna confirms that the water at Cap d'Antifer was shallower than that of the area of standard succession. The composition of the benthonic microfauna of the latter is represented in text-fig. 4 by the pie-chart of sample 112 (top *subglobosus* Zone, Pitstone). It is very different from the benthonic fauna of sample 108 (top *subglobosus* Zone, Cap d'Antifer) and these differences are illuminating when compared with results from the *varians* Zone (from Burnaby 1961):

<i>Name of species</i>	<i>Burnaby's nearest species</i>	<i>Depth preferred in varians Zone</i>
Species commoner at Pitstone than at Cap d'Antifer		
<i>Gavelinella baltica</i>	<i>G. baltica</i>	neutral
<i>Gyroidinoides nitida</i>	<i>G. nitida</i>	deep
<i>Tritaxia tricarinata</i>	<i>T. pyramidata</i>	deep
<i>Ramulina aculeata</i>	<i>Ramulina sp. A</i>	deep
<i>Verneuilina polystropha</i>	—	—
<i>Textularia chapmani</i>	<i>T. chapmani</i>	deep
<i>Dorothia gradata</i>	<i>D. gradata</i>	deep
<i>Dentalina sp.</i>	<i>Dentalina sp.</i>	deep
<i>Vaginulina costulata</i>	<i>Vaginulina sp.</i>	? neutral
<i>Tristix excavatus</i>	<i>T. excavatus</i>	deep
<i>Pernerina sp.</i>	—	—
Species commoner at Cap d'Antifer than at Pitstone		
<i>Plectina ruthenica</i>	<i>P. ruthenica</i>	shallow
<i>Cibicides cf. turonica</i>	<i>C. cf. sandidgei</i>	neutral
<i>Eggerellina sp.</i>	<i>Ataxophragmium compactum</i>	shallow
<i>Marssonella trochus</i>	<i>M. oxycona</i>	neutral
<i>Anomalinoides globosa</i>	—	—
<i>Hagenowella advena</i>	<i>H. anglica</i>	shallow
Species equally common at both localities		
<i>Lenticulina rotulata</i>	<i>L. rotulata</i>	neutral

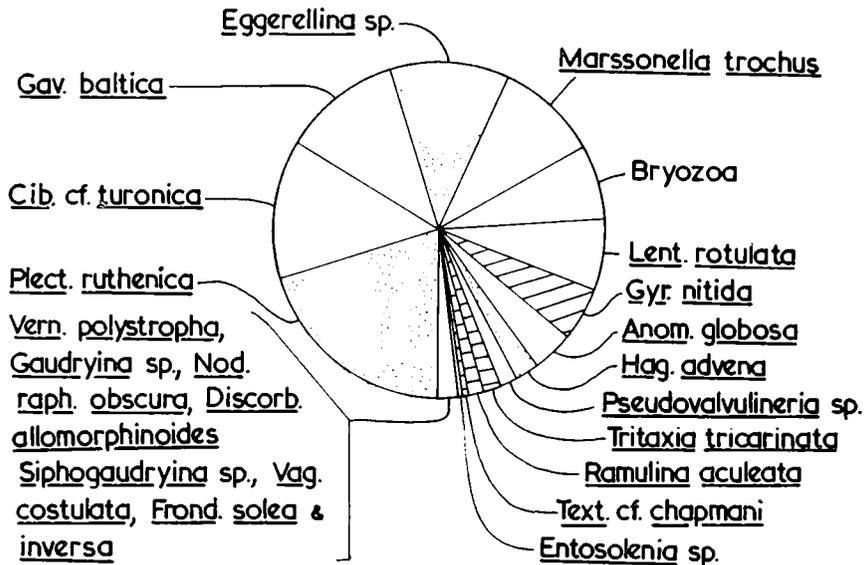
In drawing up the above table it has been assumed that species with their maximum in the middle of the *varians* Zone preferred deep water, that those with maxima at top and bottom preferred shallow water and that other species were neutral (Burnaby 1961). It is clear that species with deep-water relatives in the *varians* Zone were commoner at Pitstone than Cap d'Antifer and species with shallow-water relatives were commoner at Cap d'Antifer than at Pitstone.

Among the rarest species in the Cap d'Antifer pie-chart are two, *Gaudryina sp.* and *Siphogaudryina sp.*, which became abundant in the standard succession at the base of Bed 2. These species are so rare in sample 108, however, that they might have been brought down by burrows from the *plenus* Subzone. But if indigenous to the *subglobosus* Zone they would suggest that the populations of these species in the *plenus* Subzone were descended, at least in part, from ancestors that lived in the area of Cap d'Antifer.

Sample 112, Pitstone, 0-3 ins. below top *subglobosus* Zone.



Sample 108, Cap d'Antifer, 9-12 ins. below top *subglobosus* Zone.



TEXT-FIG. 4. The constitution of the microbenthos in the topmost *subglobosus* Zone at Pitstone and Cap d'Antifer. Cross-hatched species have deep-water relatives and stippled species have shallow-water relatives in the *varians* Zone at Barrington (cf. Burnaby 1961).

The bryozoa at Cap d'Antifer are ill-preserved but probably do not include *Siphonotyphlus tenuis* which is the main species of the standard succession (in which it only occurs above Bed 1). Nevertheless, the fact that bryozoa were present in shallow water in late *subglobosus* times but not in deep water suggests that the bryozoa of the *plenus*

Subzone of the area of standard succession had ancestors living in areas of shallow water in *subglobosus* times.

THE PLENUS SUBZONE

Bed 1. The fauna of Bed 1 is very like that at the top of the *subglobosus* Zone. Such changes as do occur can partly be explained by shallowing and increase in mud content; they seem, however, significantly small in view of great lithological signs of shallowing (erosion and increased mud content) at the base of the bed.

The following species of macrofossils have been found in Bed 1: *Ctenothrissa* sp. (c), *Scapanorhynchus raphiodon*, *S. subulatus* (c), *Ptychodus decurrens*, *Calycoceras* sp., *Metoicoceras geslinianum* (as oyster casts), *Spondylus latus*, *Plicatula barroisi*, *Entolium membranaceum* (near top only), *E. orbiculare*, *Aequipecten beaveri*, *Neithea quinquecostata*, *Lima globosa*, *Teredo amphisbaena*, *Inoceramus pictus* (c), *Ostrea vesicularis* (large grypheat form) (c), *Lingula* sp. (c), '*Rhynchonella*' *lineolata carteri*, *Orbirhynchia multicostata* (c), *Terebratulina striatula*, *T.* cf. *nodulosa*, *Cretiscalpellum glabrum*, *Enoploclytia* sp., ophiuroid, *Calliderma smithiae*, *Crateraster quinqueloba*, *Staurasteraster* sp., *Trachyaster* cf. *rugosus*, *Holaster trecensis*, *Micrabacia coronula* (? derived), 'problematicum' (c).

The changes at the base of Bed 1 may thus be summarized as follows: (i) *Plicatula inflata* and *Discoidea cylindrica* seem to have become extinct; (ii) *Holaster trecensis* is much rarer; (iii) certain species which are very rare or perhaps completely absent in the top of the *subglobosus* Zone of the area of standard succession appear or become much commoner. These include *Orbirhynchia multicostata* (c), '*Rhynchonella*' *lineolata carteri* (rare), *Calliderma smithiae* (rare), *Trachyaster* cf. *rugosus*, *Metoicoceras geslinianum* (rare), and *Scapanorhynchus raphiodon*; (iv) two species which are definitely present in the *subglobosus* Zone become much commoner, *Ctenothrissa* sp. and *Scapanorhynchus subulatus*; (v) two species increase in average size, *Ostrea vesicularis* and *Neithea quinquecostata*.

The abundant *Orbirhynchia multicostata* in the area of standard succession in Bed 1 were probably in part descended from ancestors which lived in the Cap d'Antifer region in late *subglobosus* Zone times and their spread must almost certainly be due to shallowing. The same shallowing probably also accounts for the rare appearance in Bed 1 of certain species which become common at the base of Bed 2. This includes '*Rhynchonella*' *lineolata carteri* and the asteroids *Calliderma smithiae* and *Crateraster quinqueloba*. Another asteroid, *Trachyaster* cf. *rugosus*, may also owe its appearance to shallowing though it became extinct at the base of Bed 2.

Changes connected with increased muddiness probably included the decline of *Holaster trecensis* and extinction of *Discoidea cylindrica* (since echinoids tend to dislike mud), and the increase in size of *Ostrea vesicularis* and *Neithea quinquecostata* due to increased food supply.

Normal aragonitic fossils, as pointed out above, are as rare in Bed 1 as in the *subglobosus* Zone except at Lulworth (Jefferies 1961), though oyster casts occur. This suggests that the pre-Bed 1 shallowing, though it produced a great increase in turbulence of bottom water and mud supply, caused no great rise in temperature. The absence of such a rise would explain why the faunal changes are so small.

The changes in the benthonic foraminifera, which are also slight, are summarized in the following table, based on Pitstone and Merstham (text-figs. 6, 7).

<i>Name of species</i>	<i>Behaviour in top subglobosus Zone</i>	<i>Burnaby's nearest sp.</i>	<i>Behaviour in varians Zone</i>
Species which disappears at the base of Bed 1			
<i>Tristix excavatus</i>	deep	<i>T. excavatus</i>	deep
Species which decrease at the base of Bed 1			
<i>Verneuilina polystropha</i>	deep	—	—
<i>Gyroidinoides nitida</i>	deep	<i>G. nitida</i>	deep
<i>Marssonella trochus</i>	shallow	<i>M. oxycona</i>	shallow
<i>Lenticulina rotulata</i>	neutral	<i>L. rotulata</i>	neutral
<i>Entosolenia sp.</i>	?	<i>Lagena A</i>	?
Species which increase or appear at the base of Bed 1			
<i>Tritaxia tricarinata</i>	deep	<i>T. pyramidata</i>	deep
<i>Plectina ruthenica</i>	shallow	<i>P. ruthenica</i>	shallow
<i>Hagenowella advena</i>	shallow	<i>H. anglica</i>	shallow
<i>Pseudovalvulineria sp.</i>	shallow	—	—
<i>Spiroplectinata cf. complanata</i>	—	<i>S. complanata</i>	bottom half
<i>Textularia cf. washitensis</i>	—	<i>T. subconica</i>	deep
Spp. which do not change in abundance at the base of Bed 1 or behave inconsistently from place to place			
<i>Pernerina sp.</i>	deep	—	—
<i>Gavelinella baltica</i>	deep	<i>G. baltica</i>	neutral
<i>Ramulina aculeata</i>	deep	<i>Ramulina A</i>	deep
<i>Dentalina sp.</i>	deep	<i>Dentalina sp.</i>	deep
<i>Anomalinooides globosa</i>	shallow	—	—
<i>Cibicides cf. turonica</i>	shallow	<i>Cibicides cf. sandidgei</i>	neutral
<i>Eggerellina sp.</i>	shallow	<i>Ataxophragmium compactum</i>	shallow
<i>Textularia chapmani</i>	deep	<i>T. chapmani</i>	deep

Thus, among the species which show consistent change in abundance at both localities *T. excavatus* (extinction), *G. nitida* (decrease), *P. ruthenica* (increase), *Hagenowella advena* (increase), *Pseudovalvulineria* (increase) and *V. polystropha* (decrease) behave as would be expected from their distributions in the top *subglobosus* and *variens* Zones, assuming that the change at the base of Bed 1 was a simple shallowing. However, the deep-water *Tritaxia tricarinata* increased and the shallow-water *Marssonella trochus* decreased, and this perhaps suggests respectively a liking and a dislike for mud. Mud may also have influenced the size of the increase in *Pseudovalvulineria sp.* When this table is compared with the previous one it is clear that the change at the base of Bed 1 had less ecological effect than the difference between Pitstone and Cap d'Antifer in late *subglobosus* times.

Bed 2. Unlike the change at the base of Bed 1, the faunal change at the base of Bed 2 seems disproportionately large compared with any changes in lithology, which consist merely of an increase in mud content and certain signs of slower sedimentation or slight erosion (Jefferies 1961). In the macrofauna the changes are as follows: (i) A group of forms disappeared at least temporarily. These included *Ctenothrissa sp.*, *Scapanorhynchus subulatus* (except a single specimen in Bed 2-3 at Lulworth), *Neithea quinquecostata*,

Lima globosa, *Lingula* sp., *Orbirhynchia multicosata* (except for one specimen in Bed 2 at Steyning), *Cretiscalpellum glabrum*, *Trachyaster* cf. *rugosus*, 'problematicum', *Holaster trecensis* (except rare occurrences in Beds 5–7). This list includes nearly all the commonest species in Bed 1. (ii) Several macrofossils appear or become much commoner at the base of Bed 2: *Plicatula barroisi*, *Entolium membranaceum* (which occurs in Bed 1 only as a rarity near the top but which is the commonest fossil in Bed 2), *Cidaris perornata*, *C. hirudo*, *Discoidea minima*, *Calliderma smithiae* (c.), 'Rhynchonella' *lineolata carteri* (c.), *Scaphites equalis*, *Nucula* sp., *Solarium* sp., *Cerithium* sp., *Metoicoceras geslinianum*, *Protocardia hillana*, *Grammatodon* cf. *cenomanense*, *Aporrhais* sp., *Dentalium* sp. It is noteworthy that all the members of this group after '*R.*' *lineolata carteri* are aragonitic.

In the benthonic microfauna the changes can be expressed in tabular form (on the basis of text-figs. 6–10):

Name of species	Behaviour in subglobosus Zone	Burnaby's nearest species	Behaviour in varians Zone
Species which disappear at the base of Bed 2 and do not reappear in the rest of the Subzone			
<i>Verneuilina polystropha</i>	deep	—	—
<i>Plectina ruthenica</i>	shallow	<i>P. ruthenica</i>	shallow
<i>Pernerina</i> sp.	deep	—	—
<i>Dorothia gradata</i>	deep	<i>D. gradata</i>	deep
<i>Spiroplectinata</i> cf. <i>complanata</i>	—	<i>S. complanata</i>	bottom half
<i>Hagenowella advena</i>	shallow	<i>H. anglica</i>	shallow
<i>Gavelinella baltica</i>	deep	<i>G. baltica</i>	neutral
<i>Pseudovalvulineria</i> sp.	shallow	—	—
Species which disappears at the base of Bed 2 but which reappears in some places at the top of Bed 4			
<i>Tritaxia tricarinata</i>	deep	<i>T. pyramidata</i>	deep
Species which disappear or decline at the base of Bed 2 but which reappear or become common again in Bed 2 or the base of Bed 3			
<i>Gyroidinoides nitida</i>	deep	<i>G. nitida</i>	deep
<i>Marssonella trochus</i>	shallow	<i>M. oxycona</i>	neutral
<i>Ramulina aculeata</i>	deep	<i>Ramulina</i> sp. A	deep
<i>Ammodiscus cretaceus</i>	—	<i>Ammodiscus</i> sp.	deep
<i>Dentalina</i> sp.	deep	<i>Dentalina</i> sp. A	deep
<i>Lenticulina rotulata</i>	neutral	<i>L. rotulata</i>	neutral
Species present in Bed 1 which become much commoner in Bed 2			
<i>Anomalinoides globosa</i>	shallow	—	—
<i>Cibicides</i> cf. <i>turonica</i>	shallow	<i>C.</i> cf. <i>sandidgei</i>	neutral
<i>Eggerellina</i> sp.	shallow	<i>Ataxophragmium compactum</i>	shallow
<i>Textularia chapmani</i>	deep	<i>T. chapmani</i>	? deep
<i>Textularia</i> cf. <i>washitensis</i>	—	<i>T. subconica</i>	deep
Asteroid terminals	shallow	—	—
<i>Quinqueloculina antiqua</i>	—	<i>Quinqueloculina</i> sp.	bottom half
Species which are absent in Bed 1 and the top of the subglobosus Zone in area of standard succession and which first occur in Bed 2			
<i>Siphogaudryina</i> sp.	? shallow	<i>Siphogaudryina</i> sp.	bottom half
<i>Reophax</i> sp.	—	—	—

Name of species	Behaviour in subglobosus Zone	Burnaby's nearest species	Behaviour in varians Zone
<i>Siphoniotyphlus tenuis</i>	—	—	—
<i>Gaudryina sp.</i>	? shallow	—	—
<i>Marssonella sp.</i>	—	—	—
Star plates	—	—	—

Notes. (1) The occurrence of *Verneuilina polystropha* in Bed 4 at Pitstone (text-fig. 7) is based on one specimen and is probably due to sieve contamination. (2) *Eggerellina sp.* increases at the base of Bed 2 at Crésantignes and Eastbourne but at Pitstone and Merstham does not increase till later. (3) *Quinqueloculina antiqua* was found in Bed 2 at Eastbourne and Crésantignes but not at Merstham or Pitstone; it was found in Bed 1 only at Eastbourne during taxonomic examination, but not during counting, and therefore does not appear in the distribution charts in that bed.

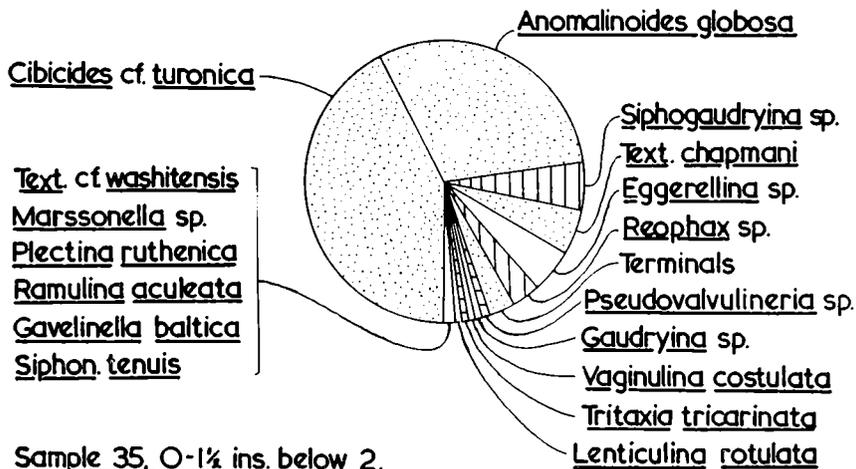
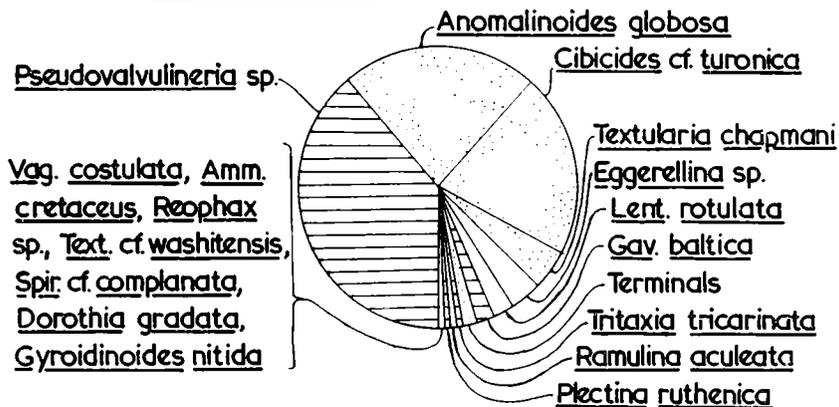
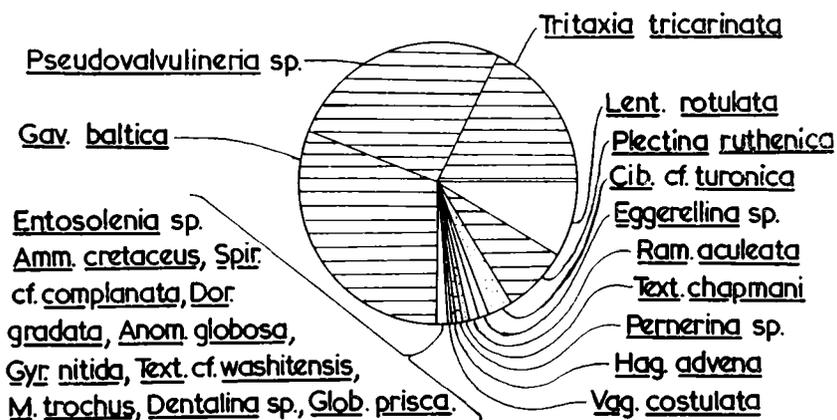
The main changes in the planktonic fauna are (again on the basis of text-figs. 6–10): (i) The extinction of *Thalmaninella deeckei*; (ii) An increase in *Praeglobotruncana sp.* This sometimes begins below the top of Bed 1 and sometimes the species declines for an interval shortly above the base of Bed 2 as at Crésantignes and Merstham. (iii) A decline in *Rotalipora turonica*. (iv) Generally an increase in Globigerinidae. (v) There also seems to have been an increase in the crinoid *Roveacrinus*.

The change at the base of Bed 2 seems to have started below the top of Bed 1. In the macrofauna this is indicated by a specimen of *Entolium membranaceum* just below the top of Bed 1 at Steyning. In the microbenthos the same thing shows more clearly in sample 35 (text-fig. 5) which came from just below the top of Bed 1 at Merstham. In general the species which were shortly to disappear completely had already much declined in this sample, *Tritaxia tricarinata*, *Spiroplectinata cf. complanata*, *Dorothia gradata*, *Plectina ruthenica*, *Hagenowella advena*, *Pernerina sp.* and *Gavelinella baltica* (though *Pseudovalvulineria sp.* had a brief maximum). Species which occur in Bed 1 but which are much commoner in Bed 2 have already much increased, e.g. *Textularia chapmani*, *Anomalinoides globosa*, and *Cibicides cf. turonica*. And Bed 2 immigrants were absent or still very scarce, e.g. *Reophax sp.*, *Siphogaudryina sp.*, and *Gaudryina sp.* The intermediate character of this sample was not due to contamination, for burrows carrying Bed 2 material were carefully removed before preparation. The relative scarcity of Bed 2 immigrants shows that contamination was in fact successfully avoided. Sample 114 at Pitstone from a corresponding stratigraphical position has the same intermediate character.

At this point it is worth recapitulating the main features of the change at the base of Bed 2. They are as follows: the appearance of normal aragonitic fossils, an increase in mud content, certain signs of erosion at the base of Bed 2, and an abrupt change in the non-aragonitic elements of the fauna towards a shallower-water type.

Firstly, as explained above, the appearance of aragonitic forms in the fauna is certainly preservational and probably indicates a decrease in the total CO₂ content of the bottom water which could well be due to a rise in temperature, possibly consequent on a shallowing. It corresponds to the appearance of aragonitic fossils in such shallow-water bands of the Chalk as the Chalk Marl, Chalk Rock, and Top Rock.

Secondly, the increase in mud content at the base of Bed 2 is very temporary and cannot itself be directly responsible for the main features of the faunal change. This is shown by the fact that a much greater increase at the base of Bed 1 was accompanied by a much smaller faunal change and also by the close resemblance between the faunas of Beds 2 and 3 despite the fact that Bed 3 is a chalk. However, as suggested elsewhere

Sample 36, 0-3 ins. above base 2.Sample 35, 0-1½ ins. below 2.Sample 34, 6-10 ins. below 2.

TEXT-FIG. 5. Premonitory changes in the microbenthos at the top of Bed 1 at Merstham. Species which increase or appear at the base of Bed 2 are stippled. Species which become extinct are cross-hatched.

(Jefferies 1961), it is likely that most Chalk marl bands are connected with a fall in erosion base and that this fall was connected with a shallowing of the sea.

Thirdly, the indications of erosion at the base of Bed 2 are not entirely conclusive but it is plausible to connect them with the increase in mud content at the base of Bed 2 and to regard them as due to shallowing.

Fourthly, the reasons for thinking that the change in the fauna at the base of Bed 2 was towards a shallower-water type are as follows:

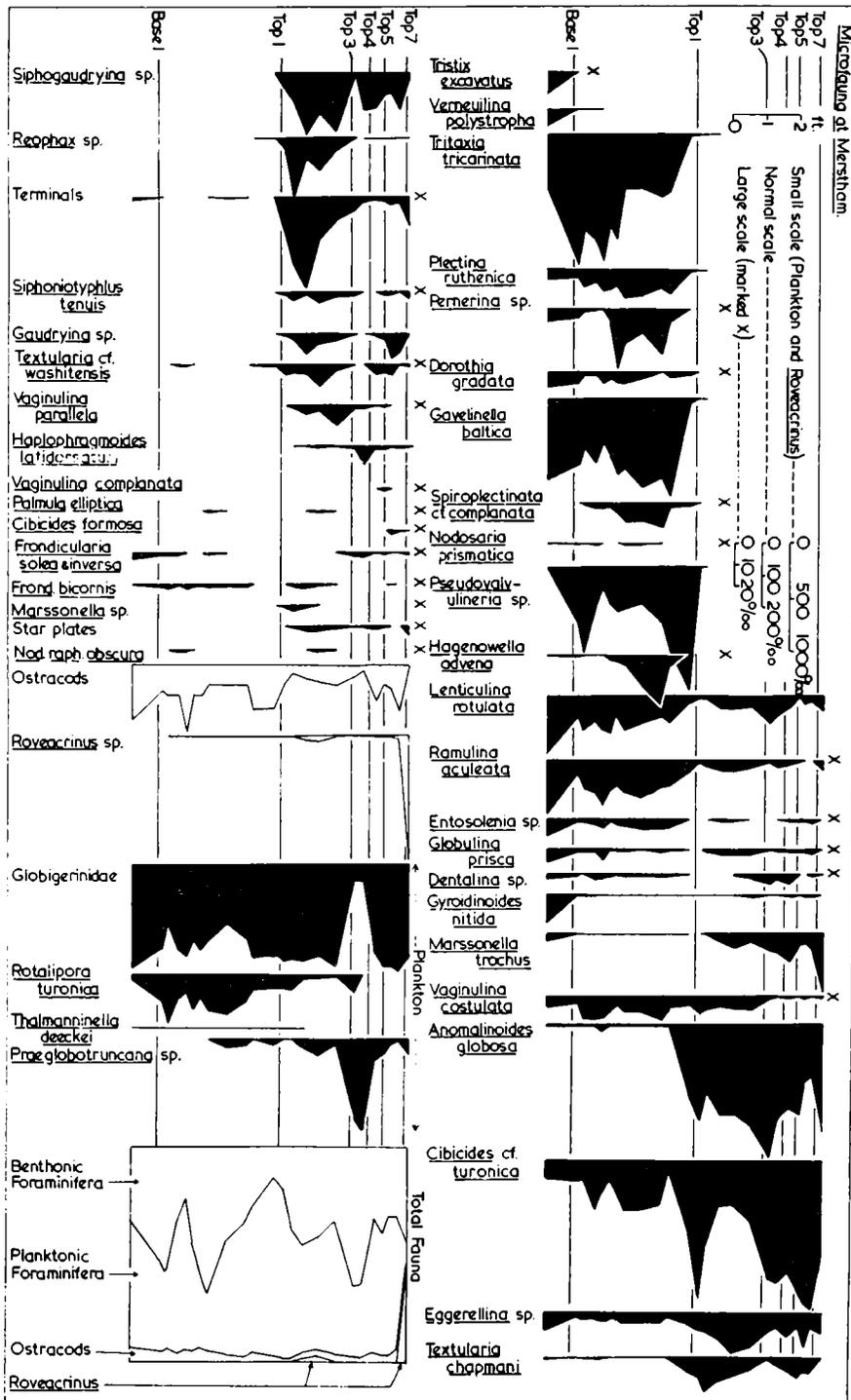
(i) There are a few macrofossils which appear at the base of Bed 2 in the area of standard succession and which had shallow-water distribution or shallow-water relatives in the upper *subglobosus* Zone; these include *Discoidea minima* (cf. *D. subuculus* in the *subglobosus* Zone), *Cidaris hirudo*, *C. perornata*, and bryozoa. However, *Orbirhynchia multicostata*, which had had shallow-water distribution in late *subglobosus* Zone times, died out at this level.

(ii) Examination of the table shows that species of microbenthos with shallow-water distribution or shallow-water relatives in late *subglobosus* times are apt to increase or appear in the area of standard succession at the base of Bed 2 while those with deep-water distribution or relatives in late *subglobosus* times are apt to disappear. There are, however, certain exceptions to this rule; thus *Plectina ruthenica*, *Hagenowella advena*, and *Pseudovalvulineria sp.*, which had had shallow-water distribution in late *subglobosus* times, nevertheless died out at the base of Bed 2.

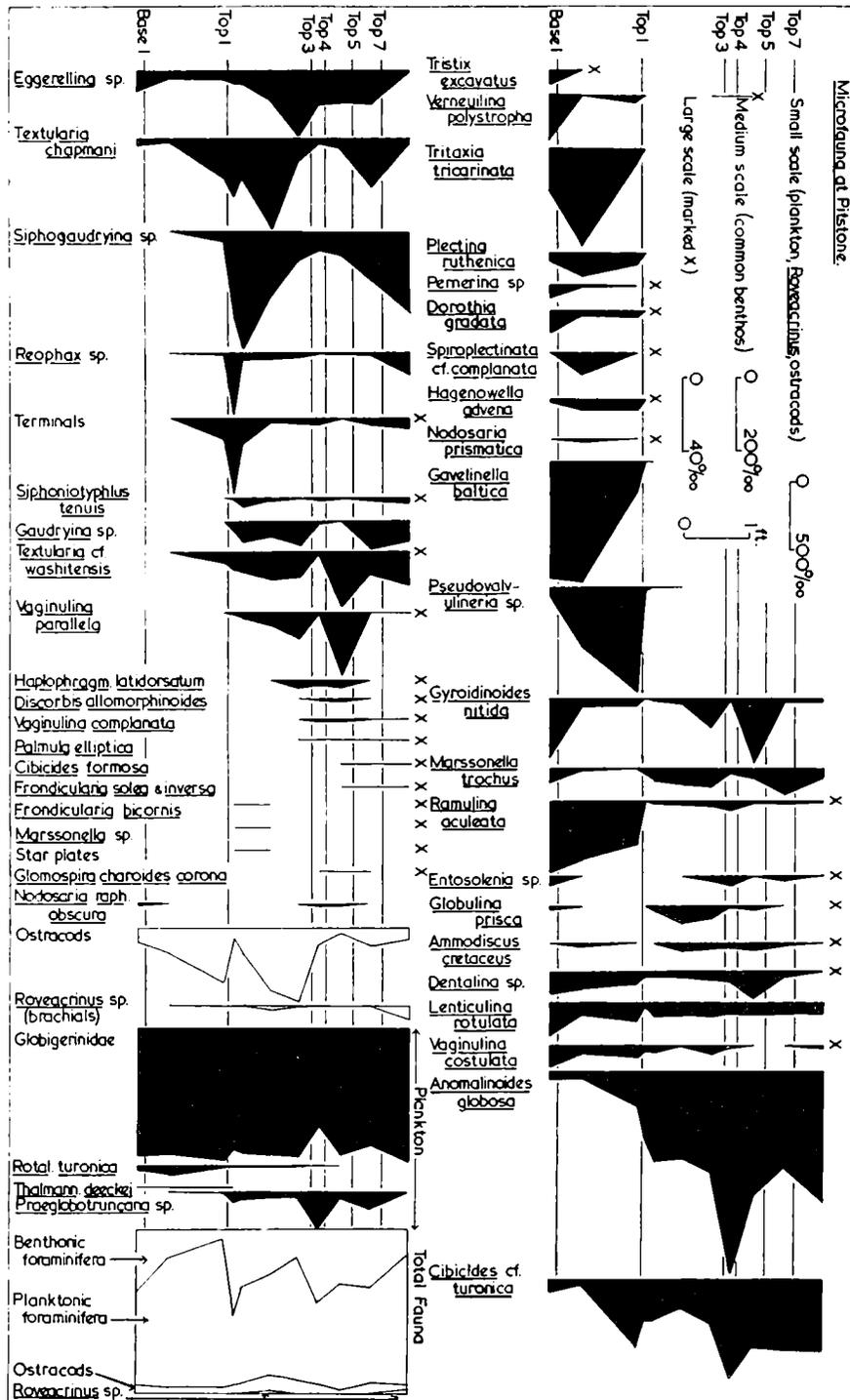
(iii) Some of the forms which appear in Bed 2 in the area of standard succession had relatives in the lower part of the *varians* Zone which was deposited in shallow water, viz. *Siphogaudryina sp.* (cf. *Siphogaudryina sp.* of Burnaby, fig. 1), *Quinqueloculina antiqua* (cf. *Quinqueloculina sp.* of Burnaby, loc. cit.), '*Rhynchonella*' *lineolata carteri* (also found in the Cambridge Greensand), and *Plicatula barroisi* (cf. *P. sigillina* of the Cambridge Greensand).

(iv) Some of the forms which increase at the base of Bed 2 have shallow-water relatives in Recent seas. Thus *Quinqueloculina* (represented by *Q. antiqua* in Bed 2 at Eastbourne and Crésantignes) is at present commonest at a depth of 30–40 metres (Curtis 1955, p. 268) and is usually regarded as characteristic of shallow water (Lowman 1949, Phleger and Parker 1951). Similarly *Cibicides* cf. *turonica* becomes much commoner at the base of Bed 2 and *Cibicides* in the Gulf of Mexico is commonest above a depth of 220 metres. Bryozoa and asteroidea (*Crateraster quinqueloba* and *Calliderma smithiae*), which respectively enter and become much commoner at the base of Bed 2, are also mainly of shallow-water distribution at the present day.

Shallow water is usually more turbulent and also warmer than deep water. From the point of view of lithology, in particular the deposition of mud and cutting of erosion surfaces, turbulence is more important than temperature. For ecology and the preservation of aragonite, however, temperature is more important than turbulence. Hutchins (1947) has emphasized the importance of temperature to modern marine animals and it has often been invoked to explain the distribution, and in particular the depth zonation, of benthonic foraminifera. For instance, Norton (1930, p. 332) in the West Indies and Natland (1933, p. 227) off California, defined their foraminiferal depth zones in both fathoms and degrees centigrade. Parker (1948, p. 231) used temperature and annual temperature range to explain the depth zonation of benthonic foraminifera south of Cape Cod and also the differences in the faunas north and south of the Cape. Phleger



TEXT-FIG. 6. The microfauna at Merstham.



TEXT-FIG. 7. The microfauna at Pitstone.

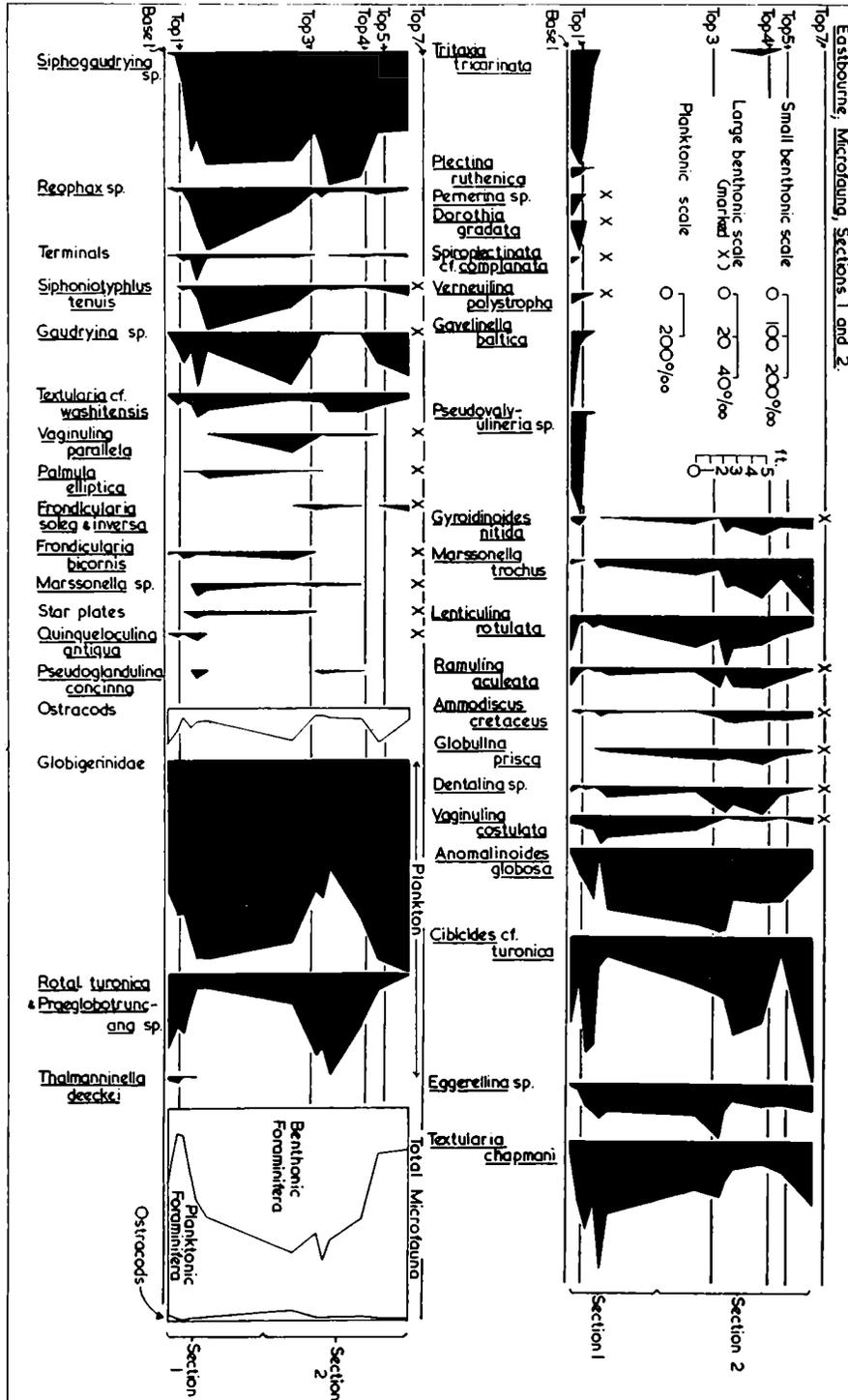
(Phleger and Parker 1951, pt. 1, p. 50) remarked that the top of the main thermocline in the Gulf of Mexico, at about 100 metres, coincided with a very great faunal change. He noted, however, that penetration of light, agitation of the bottom, and great annual temperature range also distinguished the depths above 100 metres from the depths below. Crouch (1952), when studying the distribution of foraminifera in submarine basins off the coast of California, concluded that the foraminiferal fauna at the bottom of a basin correlated better with sill-depth (i.e. temperature) than with true depth. And Resig (1958, p. 302) confirmed a change in the benthonic foraminifera at sill-depth in the Santa Cruz basin in the same general area. Bandy (1953), also working off California, agreed that temperature was an important factor, though not the only one, and he has also confirmed (1956, p. 189) Phleger's conclusion that temperature was important in the Gulf of Mexico. This does not mean that the pattern of distribution of foraminifera always depends on temperature as has been neatly demonstrated by Said (1950) in the strange hydrographical conditions of the Red Sea. In this sea something resembling the normal depth zonation is present (*Quinqueloculina* common in shallow water, *Uvigerina* at depth) but this cannot be due to temperature which has a total range of less than 2° C., with the lowest temperatures at middle depths, not at the bottom. Similarly Resig (1958) found zonation even in the isothermal parts of the Santa Cruz Basin. The results of these workers, however, do not show that temperature is unimportant in the cases where it has been invoked, but only that under rather unusual conditions it is not the main cause of faunal variation in benthonic foraminifera.

It is therefore likely that the change at the base of Bed 1, though it caused greatly increased turbulence resulting in erosion and muddiness, nevertheless caused little rise in temperature and therefore had little effect on the fauna or on the preservation of aragonitic fossils. The change at the base of Bed 2, on the other hand, caused little increase in turbulence but a strong rise in temperature of the bottom water which led to the preservation of aragonitic fossils and an abrupt change in the other elements of the fauna. The supposition that the change at the base of Bed 2 was largely due to a rise in temperature explains why it seems to have occurred at Bellignies (text-fig. 11) where the water was so turbulent throughout *plenus* times that the succession was condensed.

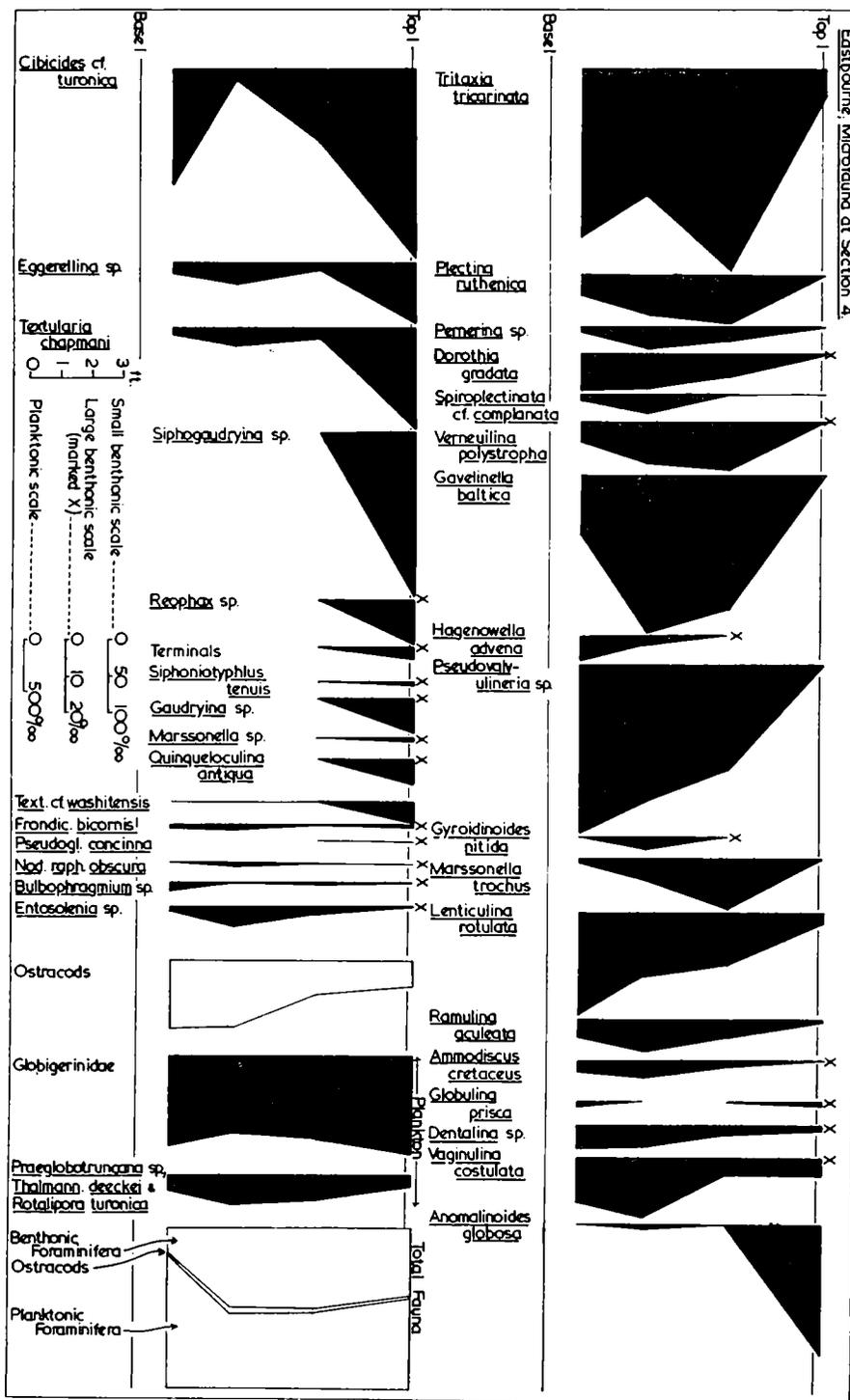
The change in temperature at the beginning of Bed 2 times was probably greater than the difference in temperature between Pitstone and Cap d'Antifer in late *subglobosus* times or the increase in temperature at the beginning of Bed 1 times. This would explain why some species with a shallow-water distribution in the top of the *subglobosus* Zone and which increase in the area of standard succession at the base of Bed 1 (viz. *Plectina ruthenica*, *Hagenowella advena*, *Pseudovalvulineria* sp., and *Orbirhynchia multicostata*) nevertheless disappear at the base of Bed 2.

The disappearance of *Lingula* sp. at the top of Bed 1 is also anomalous for this species belonged to a genus well known for its shallow-water habits in Recent sea. However, this particular species is present throughout the Lower Chalk up to this level, being especially common at the top of the *subglobosus* Zone, and shows no sign of shallow-water preferences. Its disappearance at the base of Bed 2, along with most other species common in Bed 1 and the *subglobosus* Zone, is therefore not surprising.

The actual values of bottom-water temperature for Bed 1 and the *subglobosus* Zone cannot be estimated with certainty. However, Bed 1, *ex hypothesi*, was laid down in water colder than the equilibrium temperature of aragonite which under modern



TEXT-FIG. 8. Eastbourne, microfauna, sections 1 and 2; exact localities given in Jefferies (1961).



TEXT-FIG. 9. Eastbourne, microfauna at section 4; exact locality given in Jefferies (1961).

conditions, at least in the laboratory, is 5–10° C. (see above). Bed 2 was laid down in water warmer than this equilibrium temperature, and, as will be argued below from the nature of the fauna, in water somewhat warmer than Beds 4–6. The latter, on the basis of O¹⁸ analyses of *Actinocamax plenus* which must almost certainly have come from them, may have been laid down at a temperature of about 16.9° C. (Lowenstam and Epstein 1954).

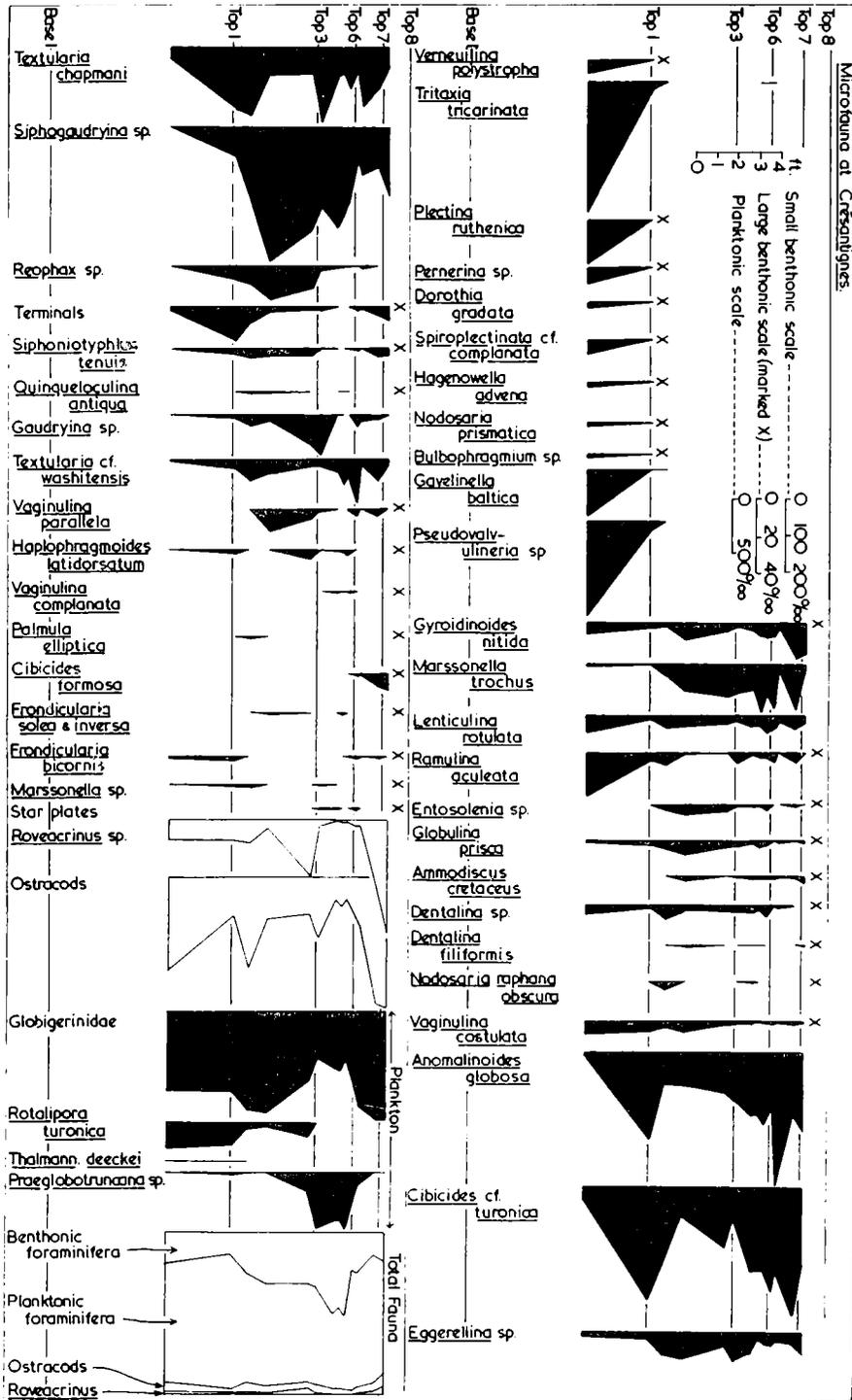
Finally it is interesting to note certain analogies between the change at the base of Bed 2 and the change at the top of the Ma division of the Dutch Maestrichtian. In Ma, Visser (1951) has recorded a fauna with abundant *Plectina ruthenica* and *Pseudovalvulineria lorneiana*. This gives place to a fauna in the stratigraphically higher Mb and Mc divisions which, in one locality, contains abundant *Quinqueloculina* and *Heterostomella*. The Ma fauna recalls Bed 1 (with *Plectina ruthenica* and *Pseudovalvulineria sp.*) whereas the Mb and Mc fauna recalls Bed 2 (with *Quinqueloculina antiqua* and *Siphogaudryina sp.* which resembles *Heterostomella*). This change in the Dutch Maestrichtian is usually taken to be a shallowing or a rise in temperature (which led to the invasion of Tethyan forms, including rudists).

The occurrence of *Ornatothyris sp.* in Bed 2 or the base of Bed 3 from Marham roughly as far south as Tring coincides with the area in which Bed 2 is very thin or absent and in which, therefore, the sub-Bed 2 erosion surface was for a long time exposed on the sea bed. This probably favoured *Ornatothyris sp.* by providing a suitable surface for pedicle attachment. The northern distribution of this species is connected with the fact that all through the Cenomanian the genus was almost confined to Yorkshire and Lincolnshire.

Beds 2–3 and 3. Most macrofossils are rarer in Beds 2–3 and 3 than in Bed 2 though they are easier to collect because Bed 2 is often very thin. The fossils which so decline include all the commoner calcitic species (except *Inoceramus pictus*) such as the large gryphteate form of *Ostrea vesicularis* (which seems never to occur higher than the top of Bed 2), '*Rhynchonella*' *lineolata carteri*, *Terebratulina striatula*, *T. cf. nodulosa*, *Entolium membranaceum*, *Calliderma smithiae*, and *Crateraster quinqueloba*. The aragonitic species *Grammatodon cf. cenomanense*, *Cerithium sp.*, and *Protocardia hillana* also seem to decline. On the other hand, *Metoicoceras geslinianum* does not decline so quickly as most other species, and *Solarium sp.* and *Aporrhais sp.* are commoner in Bed 3 than in Bed 2. The result is an increase in the ratio of aragonitic to calcitic forms but a decline in the absolute numbers of both groups. One other important change in the macrofauna is the appearance of *Actinocamax plenus* as a rarity at the top of Bed 3. This represents the start of the North Boreal invasion which is much more important in Bed 4. These changes coincide with a decline in mud content and probably, therefore, if the theory of origin of marl bands postulated in Jefferies (1961) is correct, with an increase in the rate of deposition. Most of the calcitic fossils which decline from Bed 2 to Bed 3 increase again in Bed 4 (which marks an increase in mud content and possibly a decrease in the rate of deposition). It therefore seems likely that the abundance (per unit volume of rock) of these species was controlled either by a liking for mud, or else tended to be merely inversely proportional to the rate of deposition.

In the microfauna there are local inconsistencies but the main changes are as follows:

(i) *Anomalinoidea globosa* and *Cibicides cf. turonica* reach a peak in, or occasionally



TEXT-FIG. 10. Microfauna at Crésantignes.

just below, Bed 2 (Crésantignes, Eastbourne, Pitstone, and Merstham), tend to decline in Bed 2–3, and then often increase again up to the top of Bed 3 (Pitstone, Eastbourne, Merstham, but not Crésantignes).

(ii) *Reophax sp.*, *Textularia chapmani*, *Siphogaudryina sp.*, and *Siphoniotyphlus tenuis* commonly increase to a peak in Beds 2–3 (at a somewhat higher level than *A. globosa* and *C. cf. turonica*) and then decline again towards the top of Bed 3. Exceptions to this generalization are at Pitstone (text-fig. 7) where *Reophax sp.* reaches a peak in Bed 2 instead of in Beds 2–3 and at Eastbourne (text-fig. 7) where *Siphogaudryina sp.* does not show a definite peak in Beds 2, 2–3, or 3.

(iii) *Quinqueloculina antiqua* and *Marssonella sp.* die out at the top of Bed 2.

(iv) The group of temporary absentees or rarities in Bed 2 increase above that Bed, i.e. *Lenticulina rotulata*, *Dentalina sp.*, *Ammodiscus cretaseus*, *Marssonella trochus*.

These changes can be interpreted in terms of change in temperature and mud content. Temperature probably increased to a maximum during the deposition of Beds 2–3 and then decreased again. This is suggested by the fact that three Bed 2 immigrants, which should be thermophile, have a maximum at about that level, viz. *Siphoniotyphlus tenuis*, *Siphogaudryina sp.*, and *Reophax sp.* The decline in temperature at the top of Bed 3 is confirmed by the occasional presence at that level of the 'North Boreal' *Actinocamax plenus*. The effect of fall in mud content can probably be seen in the disappearance of *Quinqueloculina antiqua* which was probably a mud-lover as shown by its abundance at Bellignies.

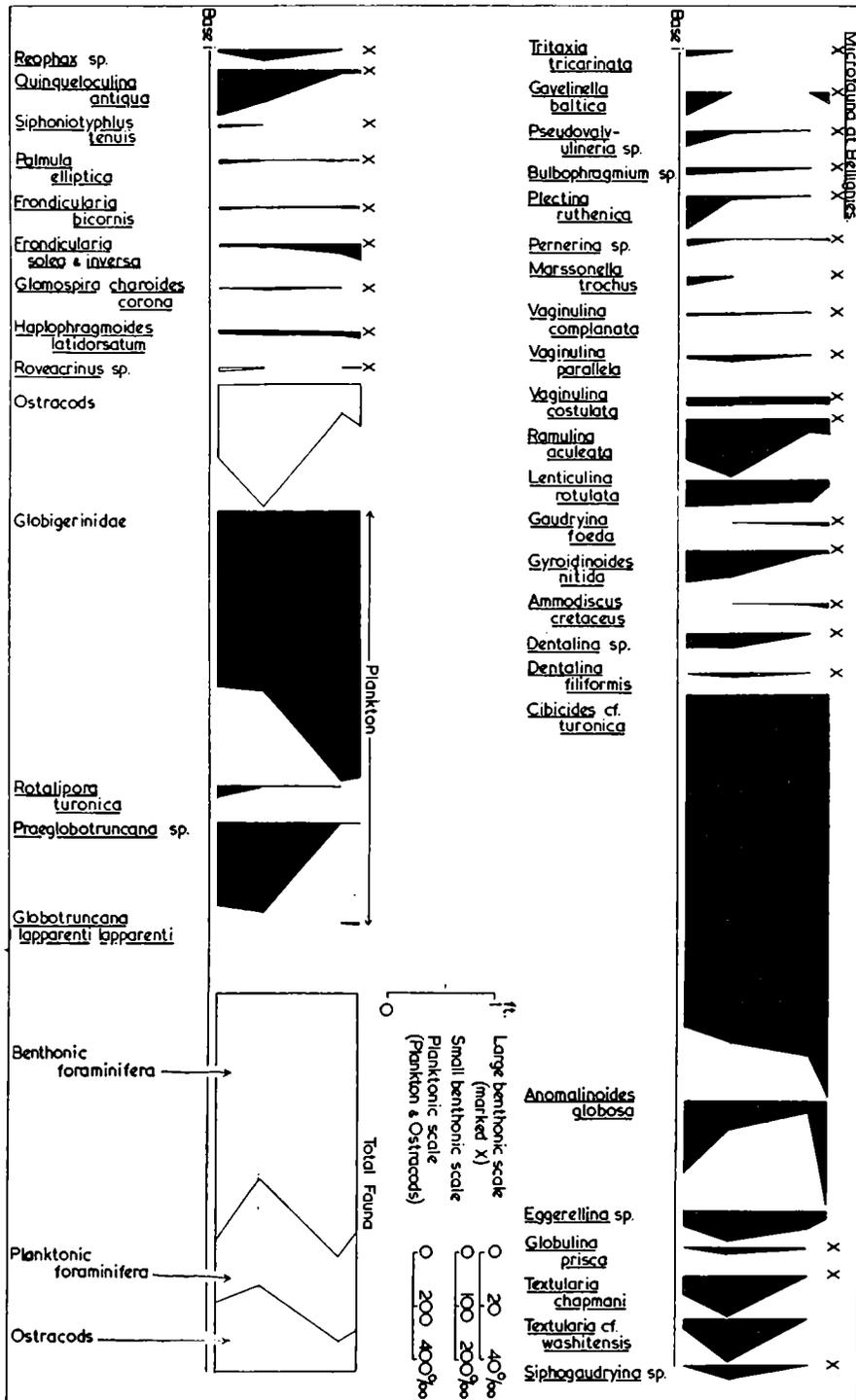
Beds 4, 5, and 6. The macrofauna of Beds 4, 5, and 6 is very like that of Beds 2 and 3 but there are certain differences which suggest a lower temperature of deposition. It can be divided into the following distributional groups:

(i) '*Rhynchonella*' *lineolata carteri*, *Entolium membranaceum*, *Crateraster quinqueloba*, *Terebratulina striatula*, *T. cf. nodulosa* are significantly commoner in Beds 4 and 6 than in Beds 5 or 3 (and had also tended to be commoner in Bed 2 than in Bed 3). It seems likely that the abundance of this group was controlled either by muddiness or by rate of deposition, or by both.

(ii) Some macrofossils are found almost exclusively in Beds 4–6, viz. *Oxytoma seminudum* (also found rarely in Bed 2, however), *Ditrupa difformis* (mainly in the South Downs), *Actinocamax plenus* (also rarely in the top of Bed 3), and *Aequipecten arlesiensis*. *Plicatula barroisi* is much commoner in Bed 4 than above or below. The abundance of *Actinocamax plenus* in these beds is particularly striking, for belemnites of any sort are very rare in the English Chalk for hundreds of feet above and below.

(iii) Aragonitic fossils are common in Beds 4–6 only where the Subzone is more than about 10 feet thick (possibly in connexion with decreased temperature and increased turbulence) and the ammonites belong to the *gourdoni*, not to the *geslinianum* fauna.

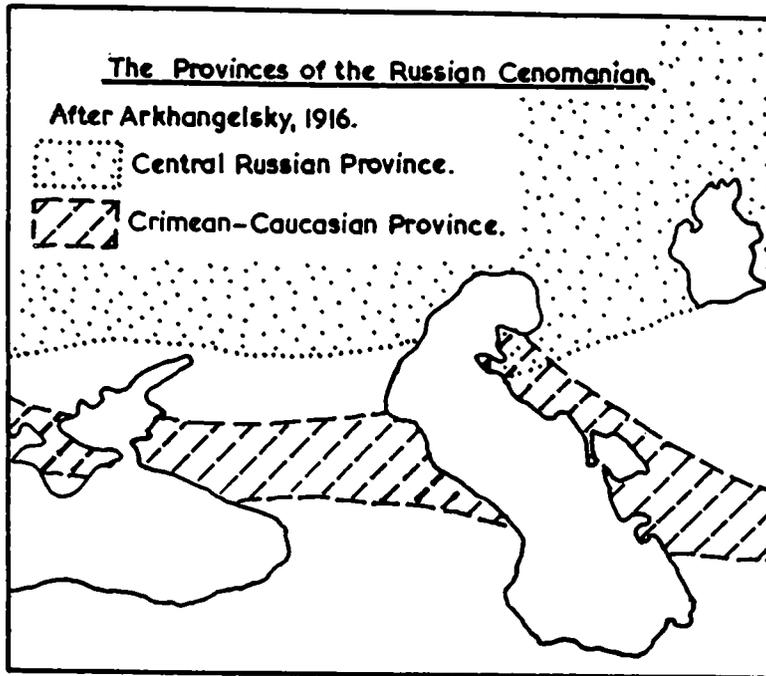
In trying to explain the faunal peculiarities of Beds 4–6 the work of Arkhangelsky (1916) is important. This author recognized two main types of Cenomanian in European Russia (text-fig. 12). In the north and as far south as the southern Ukraine occurred the 'Central Russian' (or more strictly the Central European Russian) Type. This was characterized by the abundance of forms which Arkhangelsky identified as *Actinocamax primus* Arkhangelsky, *Pteria pectinata* (Sowerby), *Pecten robinaldinus* d'Orbigny, and



TEXT-FIG. 11. Microfauna at Bellignies.

Exogyra conica (Lamarck). Ammonites, particularly *Acanthoceras*, were rare, but species of *Schloenbachia* occurred. South of this area was the Crimean-Caucasian Type in which *A. primus*, *P. pectinata*, *Pecten robinaldinus*, and *E. conica* were rare or absent, but in which ammonites were commoner and included *Acanthoceras*, *Turrilites*, and *Scaphites* as well as *Schloenbachia*. The difference between the two areas was largely one of temperature (Arkhangelsky 1916, p. 95).

The interest of Arkhangelsky's work, from the present point of view, is that two, and possibly three, of the index species of the 'Central Russian' Province had close relatives



TEXT-FIG. 12. The provinces of the Russian Cenomanian.

among the forms characteristic of Beds 4–6. Thus *Actinocamax primus* was very similar to *A. plenus* and possibly a direct ancestor (Jeletzky 1948). *Pteria* (*Oxytoma*) *pectinata* (Sowerby), as described by Woods (1905, p. 59), is very like *Oxytoma seminudum* (Dames) and the form mentioned by Arkhangelsky may really have been *O. seminudum* for the type of the latter came from the Cenomanian of north Germany, whereas the type of *P. pectinata* came from the Lower Albian Folkestone Sands. Also Arkhangelsky's *Pecten robinaldinus* d'Orbigny may possibly be related to *Aequipecten arlesiensis* for both species have the same type of imbricate ribbing (Woods 1902, p. 181). It therefore seems reasonable to suppose that the occurrence, certainly of *Actinocamax plenus* and *Oxytoma seminudum*, and possibly of *Aequipecten arlesiensis*, in Beds 4–6, indicates a fall in temperature by analogy with the distribution of their close relatives in the Russian Cenomanian.

There is other evidence besides Arkhangelsky's that *Oxytoma seminudum* and *Actinocamax plenus* had northern affinities. Thus *O. seminudum*, even in the Cenomanian of western Europe, is commoner in the north than the south; it is, firstly, one of the characteristic fossils of the *subglobosus* Zone of Yorkshire (= *varians* Zone of southern England) (Wright and Wright 1942, p. 115) but is certainly rare in the *varians* Zone of

southern England; secondly it is often abundant in the Cenomanian pebbles of north Germany (Noetling 1885, table p. 48); and thirdly it is common in the Cenomanian of Northern Ireland (J. M. Hancock, personal communication). In addition to this *Oxytoma seminudum* is very nearly identical to *O. tenuicostatum* (Römer) (Cox 1939, p. 18) and *O. tenuicostatum*, according to Naidin (1959, p. 129), is a 'typical boreal form' in the Upper Cretaceous of the Russian platform. With regard to *Actinocamax plenus* it is worth noting that Jeletzky (1950, p. 22) has postulated that *Actinocamax* in the Turonian Favel Formation of Manitoba had spread into that area from permanently cold, more northerly waters. Also the genus *Actinocamax* is regarded by Naidin (1959, p. 129) as characterizing the north-eastern and colder parts of the Russian Platform in the Upper Cretaceous whereas the warmer, south-western parts had either almost no belemnites, or else, in the Senonian, had mainly *Goniot euthis*. A particular case of this is the distribution of *Actinocamax intermedius* Arkhangelsky which is a characteristic fossil of the Upper Turonian in the north-eastern part of the Russian Platform (Naidin 1960, p. 47) at which horizon belemnites are virtually unknown in England or northern France.

The resemblance of the index species of Beds 4–6 to the index species of Arkhangelsky's 'Central Russian' area does not prove that the population of these species in Beds 4–6 of the Anglo-Paris Basin had actually descended from immediate Central European Russian ancestors. In fact, even if this were true, it could never be demonstrated. This is because the Upper Cenomanian, except in the Lvov-Lublin Basin, is everywhere missing in the 'Central Russian' area (Naidin 1960, p. 45) and Upper Turonian rests directly on Lower Cenomanian. Besides this the Cenomanian belemnite of the 'Central Russian' area is *A. primus* and only farther south and west, in extra-Russian Europe, Moldavia and the Ukraine does *A. plenus* occur (Naidin 1954, fig. 2, p. 20). Naidin has suggested (loc. cit.) that this was a case of contemporaneous geographical subspeciation with *A. primus* adapted to colder and *A. plenus* to warmer water. If this were true the *A. plenus* in Beds 4–6 in the Anglo-Paris Basin could clearly not have had immediate ancestors in the 'Central Russian' area where only *A. primus* occurred. However, Naidin's interpretation is probably over-simplified since, according to Jeletzky (1948, p. 341), far from being contemporaneous, *A. primus* characterizes Lower and *A. plenus* Upper Cenomanian. The mutually exclusive areas of distribution of the two species shown in Naidin's map (1954, fig. 2) seem to reflect the interaction of four facts, viz. the commonness of *A. primus* in the Lower Cenomanian of Arkhangelsky's 'Central Russian' area; the absence of Upper Cenomanian and Lower Turonian from that area; the presence in extra-Russian Europe of Lower Turonian deposits with abundant *A. plenus*; and the very great rarity of all *Actinocamax* in the Cenomanian of extra-Russian Europe. In view of this the *A. plenus* in Beds 4–6 of the Anglo-Paris Basin could well have had immediate Central European Russian ancestors all trace of which has been lost because of the non-preservation of Upper Cenomanian rocks in that area. However this may be, the important point is that *Actinocamax plenus* and *Oxytoma seminudum* (almost certainly) and *Aequipecten arlesiensis* (quite possibly) spread into the Anglo-Paris Basin during the deposition of Beds 4–6 from somewhere where the water was cooler. Whether they came from Central European Russia or Greenland (from which Swinnerton (1943) has recorded a probably Senonian fauna of *Actinocamax*) or any other northern area is much less important.

None of the North Boreal index species were found above Bed 6 except for a juvenile *Actinocamax* at the base of Bed 7 at Crésantignes (where the correlation of these few inches of succession is not entirely satisfactory) and another *A. plenus* possibly from Bed 8 at Merstham. This suggests that the cool period which allowed these species to spread into the Anglo-Paris Basin during the time of deposition of Beds 4–6 was followed by an increase in temperature at the beginning of Bed 7 times.

The serpulid *Ditrupa difformis* is in some respects puzzling in its distribution in Beds 4–6. Outside the area of standard succession it seems to have preferred shallow water; it is abundant, for instance, just above the sub-*plenus* erosion surface at Bellignies, in Bed C in Devon, just above the sub-*labiatus* surface near le Mans, and in the shallow-water Cenomanian of Northern Ireland and Cap d'Antifer. Further, Avnimelech (1941) noted that the related *Hamulus octocostatus* was restricted to shallow water in the Campanian of Israel. In view of this liking for shallow water it is surprising that in Bed 4 the species is commonest where the Bed is thick (mainly in Sussex) and the water was presumably deep. This may possibly mean that some of the larvae produced by the prosperous populations round the Ardennes Massif, of which the population at Bellignies was part, settled on the sea bottom in deep water in nearby Sussex but were unable, or not easily able, to reproduce there.

The abundance of *Plicatula barroisi* in Bed 4 is perhaps related to the abundance of *Actinocamax plenus*. The guards of the latter seem to have provided particularly suitable attachment surfaces for the spat for they are often covered with *P. barroisi* which is seldom fixed to anything else.

The benthonic microfauna of Beds 4–6 shows much variation and cannot be interpreted except by comparison with the beds above and beneath. Because of this it will be discussed place by place without confining the discussion to Beds 4–6 alone. At Pitstone (text-fig. 7), which was the northernmost section where the microfauna was studied statistically, the behaviour of *Textularia chapmani*, *Siphogaudryina* sp., *Reophax* sp., asteroid terminals, *Siphoniotyphlus tenuis*, and *Gaudryina* sp. is significant. All these species show a minimum in Beds 4–6 with maxima above and beneath. This is interesting because all except *T. chapmani* and asteroid terminals were Bed 2 immigrants into the area of standard succession, and even the two exceptions greatly increased at the base of Bed 2. This suggests, if the change at the base of Bed 2 was due to a rise in temperature, that all these species were thermophile. Their minima in Beds 4–6 would, therefore, suggest that the water when these beds were deposited was colder than when higher and lower beds were being deposited and this agrees with the occurrence of North Boreal species in the macrofauna. The behaviour of *Cibicides* cf. *turonica* and *Anomalinoides globosa* in Beds 4–6 at Pitstone is roughly converse to the species just mentioned in that they have maxima in Bed 4 and minima above and beneath. This suggests that Bed 4 was deposited at roughly their optimum temperature, in agreement with their occurrence in Bed 1 (where, however, *A. globosa* is rare) and with the fact that in Beds 2–3 and 3 they usually reach a maximum slightly earlier than the Bed 2 immigrants. The occurrence of *Verneuilina polystropha* in Bed 4 at Pitstone might be thought to confirm the cooling at that level for the species otherwise dies out at the top of Bed 1. The record, however, is based on one specimen and may well be due to sieve contamination. The presence of *Discorbis allomorphinoides* in Beds 4 and 5 at Pitstone is interesting since this species is the commonest benthonic foraminiferan in the 'marnes

à ostracées' of the south-west Paris Basin (area of le Mans) and was not found elsewhere in the area of standard succession. The reasons for its presence at Pitstone are unknown.

At Merstham (text-fig. 6) the benthonic microfauna behaves much as at Pitstone. *Cibicides* cf. *turonica* and *Anomalinoidea globosa* reach a maximum in Bed 4 and *Textularia chapmani*, asteroid terminals, *Gaudryina* sp., and *Siphonotyphlus tenuis*, as at Pitstone, are rarer in Beds 4–6 than above or beneath. However, the counting did not extend high enough to show whether *Reophax* sp. becomes common again at the base of the Melbourn Rock as at Pitstone. There are also some differences from Pitstone. Thus *Siphogaudryina* sp. at Merstham, though it has a minimum at the base of Bed 4, has a maximum at the top of that bed; *Textularia* cf. *washitensis* is definitely rarer in Beds 4–6 than above or beneath, agreeing with the fact that it greatly increases at the base of Bed 2, but differing from the situation at Pitstone; *Gyrogoninoides nitida* is definitely rarer in Beds 3 and 4–6 than at Pitstone; and *Discorbis allomorphinoides* was not found at Merstham. Some of these differences between the two sections may represent a southward decline in the cold-water current of Beds 4–6 (though the behaviour of *T.* cf. *washitensis* is anomalous). One must also take into account, however, the fact that the extraction at Merstham was on average only half as successful as at Pitstone.

At Eastbourne (text-fig. 8) the behaviour of the benthonic microfauna in Beds 4–6 is rather different from Merstham or Pitstone. The most striking fact is the occurrence of *Tritaxia tricarinata* at the top of Bed 4 (23 specimens counted). This species had temporarily disappeared at the beginning of Bed 2 times in the area of standard succession and was consequently probably thermophobe. Its reappearance would therefore suggest cooling. Why the species did not reappear at the two more northern localities is not clear but the ecological control of a rare species may be even more subtle than that of a common one. At both Eastbourne and Crésantignes there are maxima in *Textularia chapmani*, *Eggerellina* sp., and *Gaudryina* sp. immediately above the base of Bed 4. These maxima do not occur at Merstham or Pitstone where Bed 4 is thinner and this suggests that at the two more northern localities the lowest parts of Bed 4 have wedged out against the sub-Bed 4 erosion surface. Excluding these short-lived maxima, however, the thermophile species *Gaudryina* sp., *Siphonotyphlus tenuis*, perhaps *Textularia chapmani*, and asteroid terminals are generally rarer at Eastbourne in Beds 4–6 than above or beneath. On the other hand, *Siphogaudryina* sp. has a definite maximum in Bed 4 and in this respect the signs of cooling in Beds 4–6 at Eastbourne are less clear than at Pitstone. Counting did not extend high enough at Eastbourne to show whether *Reophax* sp. becomes common again at the base of the Melbourn Rock.

At Crésantignes the thermophobe *Tritaxia tricarinata* also recurs, probably in Bed 5. The thermophile *Siphonotyphlus tenuis* and asteroid terminals, and also, in a general way, *Gaudryina* sp. are rarer in Beds 4–6 than above or beneath (except for the maximum of *Gaudryina* sp. at the base of Bed 4) and, again, counting did not extend high enough to show whether *Reophax* sp. increases again at the base of the Melbourn Rock. *Siphogaudryina* sp. behaves much as at Eastbourne.

Thus the benthonic microfauna of Beds 4–6 shows signs of the cooling deduced from the macrofauna in two ways: (i) The rarity of thermophile species, most of which had immigrated into the area of standard succession at the beginning of Bed 2 times, as compared with the beds above and beneath. This phenomenon is clearer at Pitstone

than at Merstham and clearer at Merstham than at Eastbourne or Crésantignes; it thus seems to weaken southwards. (ii) At Eastbourne and Crésantignes, but not in the two more northern sections, *Tritaxia tricarinata* recurs in the top of Bed 4 or Bed 5.

The southward weakening in the oscillation in thermophile species suggests an influence spreading from the north and this agrees with conclusions derived from the macrofauna. On the other hand, the southern distribution of the recurrence of *Tritaxia tricarinata* points in the opposite direction, but this is a phenomenon on a very much smaller scale.

Among the planktonic foraminifera the most striking features of the distribution in Beds 4–6 are as follows: (i) *Rotalipora turonica* dies out in Bed 4. (ii) *Praeglobotruncana* sp. has a maximum in Bed 4. (iii) Globigerinidae have a minimum in Bed 4 which is almost exactly converse to the maximum in *Praeglobotruncana* sp.

Because there are so few species involved, and because none of them are parallel in behaviour to any benthonic species, it is not possible to interpret these changes ecologically with any confidence. It seems possible, however, that the extinction of *Rotalipora turonica* may have been due to the maximum of *Praeglobotruncana* sp., for the two species are rather similar and may therefore have been competitors.

The fauna of Beds 4–6 is more like that of Beds 2 and 3 than like that of Bed 1. In particular only one of the species (*Tritaxia tricarinata*) which disappeared as a result of the warming at the beginning of Bed 2 times attempted to return during the deposition of Beds 4–6 and even it was much less common than in Bed 1. These facts suggest that, although Beds 4–6 were deposited in colder water than Beds 2 and 3, Bed 1 was deposited in much colder water still. In view of this, however, it is difficult to explain why the index species of the cooling during the deposition of Beds 4–6 (*Actinocamax plenus*, *Oxytoma seminudum*, and *Aequipeecten arlesiensis*) had not already appeared in the area of standard succession during the deposition of Bed 1. Evidently if the temperature of deposition of Bed 1 was suitable for these species (which may, however, have been stenothermal rather than thermophobe) then some other factor must have been unsuitable. Further work would be needed to discover what it was.

Beds 7 and 8. The macrofauna of these beds is very like that below except that: (i) The North Boreal index species have died out. (ii) *Orbirhynchia wiesti* is common in Bed 7 and rare above or beneath. The microfauna has already been dealt with under Beds 4–6.

The ecology of the condensed succession at Bellignies. The vertical distribution of the fauna at Bellignies (text-fig. 11) is interesting because it suggests that the faunal change which occurred at the beginning of Bed 2 times in the area of standard succession also occurred at a locality where the succession was condensed. It also seems to show the ecological effect of high mud content for the matrix is a plastic green clay.

With regard to the first point the actual age of the 'tourtia de Mons' (Bed i) at Bellignies, as judged by the macrofauna (Jefferies 1961), is probably the same as Beds 4–6 of the standard succession and the greater part of the benthonic microfauna is certainly younger than Bed 1. Especially in the lowest sample shown in text-fig. 11, however, a number of species occur which must be of Bed 1 age or earlier, viz. *Tritaxia tricarinata*, *Gavelinella baltica*, *Pseudovalvulineria* sp., *Plectina ruthenica*, *Pernerina* sp. The preservation of these species is no different from the rest of the microfauna, suggesting that they

are not earlier than Bed 1 or late *subglobosus* Zone in age. Even if they are derived from the Middle Cenomanian 'sarrasin' beneath the 'tourtia', it is evident that a change analogous to the change at the beginning of Bed 2 times also occurred at Bellignies, although it may have happened much earlier. An attempt to extract a microfauna from the hard sugary 'sarrasin' was unsuccessful.

The effect of the muddiness of the matrix can probably be seen in the extreme abundance of *Entolium membranaceum* in the macrofauna for, as explained above, the distribution of this species in the standard succession suggests a liking for mud. Also, in the microfauna, the effect of muddiness may perhaps be seen in the large size of *Quinqueloculina antiqua* (agreeing with its disappearance at the top of Bed 2), the rarity of *Marssonella trochus* (agreeing with its decrease at the base of Bed 1), the absence of *Gaudryina* sp. and the absence of bryozoa, which, as a phylum, prefer clear water (Buge, in Piveteau 1952, p. 738).

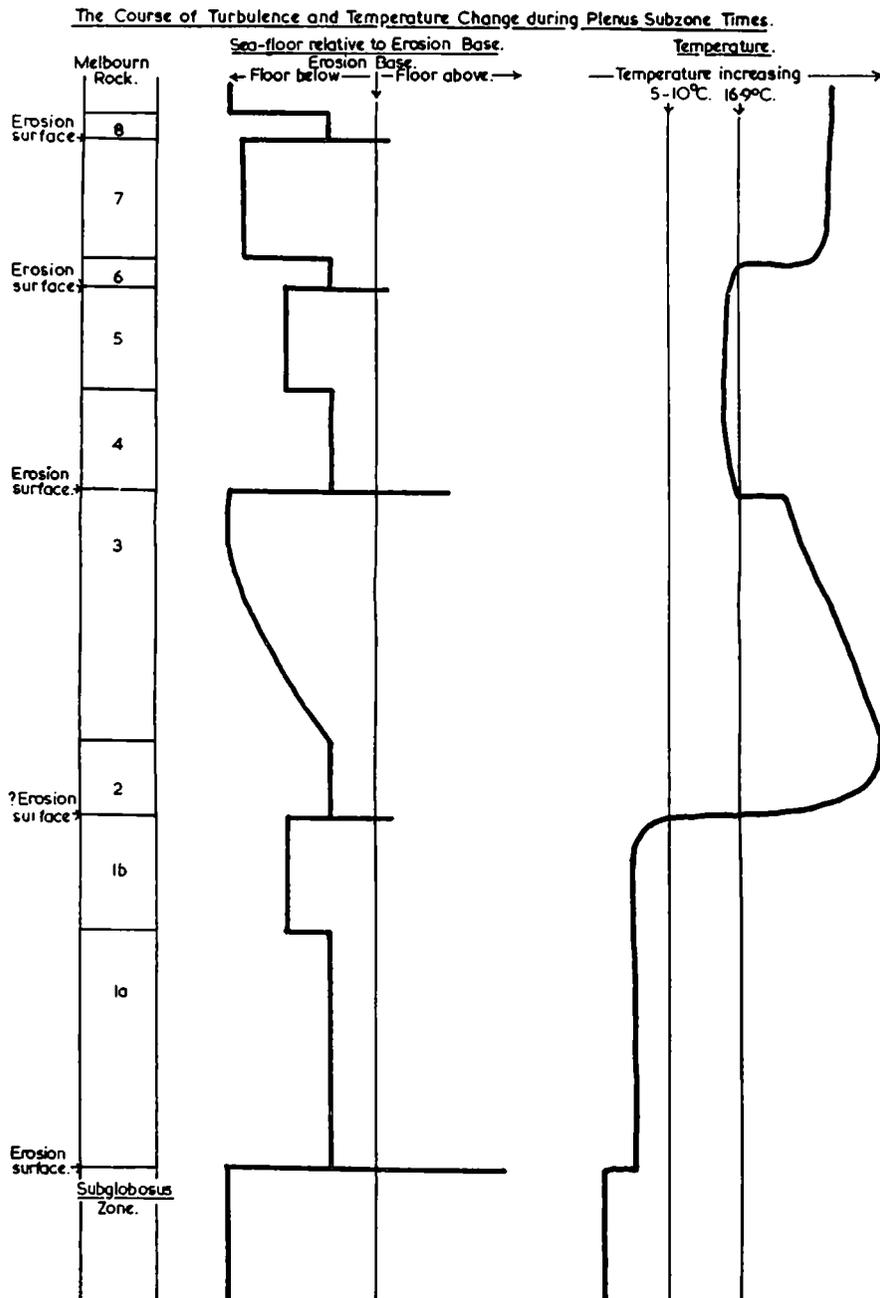
CONCLUSIONS

In a general way it is therefore possible to reconstruct temperature changes from the end of *subglobosus* times to the time of deposition of the base of the Melbourn Rock. The temperature of Bed 1 times was higher than that of *subglobosus* Zone times but not much higher or there would have been more faunal change. Both Bed 1 and the upper *subglobosus* Zone were laid down below the equilibrium temperature of aragonite which may have been about 5–10° C. The temperature of deposition of Bed 2 was very much higher than that of Bed 1 and higher than the equilibrium temperature of aragonite or the temperature of deposition of Beds 4–6 and the increase in temperature at the beginning of Bed 2 times took place during the deposition of only a few inches of rock. It is likely, however, that deposition was rather slow at this time. Temperature rose to a maximum at the start of deposition of Bed 3 and then declined again. Eventually it fell so low that 'North Boreal' macrofaunal species of central European Russian affinities spread into the Anglo-Paris Basin during the deposition of Beds 4–6. The temperature of deposition of these beds, however, as judged by the nature of the fauna, was still higher than that of Bed 1, and, on the evidence of O¹⁸ analysis of belemnites probably from this level, it may have been about 16.9° C. After the deposition of Beds 4–6 the temperature rose again and the North Boreal species disappeared. This pattern of temperature change is summarized in text-fig. 13.

It is also possible to sketch the position of erosion base relative to the sea bed during the deposition of the *plenus* Subzone (text-fig. 13) on the assumption that an increase in mud content, or the presence of an erosion surface, indicate a fall in erosion base, and a decrease in mud content indicates a rise. There is no clear correlation between changes in the level of erosion base and changes in temperature.

The following distributional groups can be recognized in the fauna of the *plenus* Subzone:

(i) *Cold-water Group*. This includes forms characteristic of Bed 1 and the top of the *subglobosus* Zone which either do not occur higher in the *plenus* Subzone or else occur only very sporadically; they liked a temperature below equilibrium for aragonite. This group contains the macrofossils *Scapanorhynchus subulatus*, *Ctenothrissa* sp., *Plicatula inflata* (not in Bed 1), *Entolium orbiculare*, *Aequipecten beaveri*, *Neitheia quinquecostata*,



TEXT-FIG. 13. Temperature and turbulence changes in the *plenus* Subzone.

Lima globosa, *Lingula* sp., *Cretiscalpellum glabrum*, *Holaster trecensis*, *Discoidea cylindrica* (not in Bed 1), 'problematicum'; the benthonic foraminifera *Verneuilina poly-stropha*, *Tritaxia tricarinata*, *Dorothia gradata*, *Plectina ruthenica*, *Hagenowella advena*, *Pernerina* sp., *Nodosaria prismatica*, *Tristix excavatus* (not in Bed 1), *Gavelinella baltica*, *Pseudovalvulineria* sp.; and the planktonic foraminiferan *Thalmaninella deeckeii*.

(ii) *Warm-water Group*. This includes forms which occur more or less abundantly in the beds above Bed 1 but which are rare or absent in that bed or in the *subglobosus* Zone in the area of standard succession and which liked a temperature at which aragonite

was not dissolved. It contains the macrofossils *Plicatula barroisi*, *Entolium membranaceum*, *Lima elongata*, '*Rhynchonella*' *lineolata carteri*, *Calliderma smithiae*, *Crateraster quinqueloba*, *Cidaris perornata*, *C. hirudo*, *Discoidea minima*, *Hemiaster nasutus*; and the benthonic microfossils *Reophax sp.*, *Textularia chapmani*, *T. cf. washitensis*, *Gaudryina sp.*, *Siphogaudryina sp.*, *Cibicides cf. turonica*, and *Anomalinoidea globosa*, star plates and *Siphonotyphlus tenuis*. Some of these forms were present or had relatives in shallow water in late *subglobosus* Zone times, while being absent or rarer in deep water during that period, e.g. *Discoidea minima* (related to *D. subuculus* of the *subglobosus* Zone), *Cidaris perornata*, *C. hirudo*, probably *Gaudryina sp.* and *Siphogaudryina sp.*, *Cibicides cf. turonica*, and *Anomalinoidea globosa*.

All of the macrofossils of this group were commoner in muddy beds than in pure ones which may partly be due to a liking for mud and partly due to slower deposition of the muddier beds. The situation at Bellignies suggests that *Quinqueloculina antiqua* and *Entolium membranaceum* liked mud and that *Siphonotyphlus tenuis* and *Gaudryina sp.* probably disliked it.

(iii) *North Boreal Group*. This includes forms which are common in Beds 4–6 and which had relatives in the Central Russian Cenomanian of Arkhangelsky, viz. *Actinocamax plenus*, *Oxytoma seminudum*, and probably *Aequipecten arlesiensis*. These species probably liked cooler water than most of the warm-water group but not so cold as the cold-water group.

(iv) *Aragonitic Group*. Unlike the other groups the distribution of the aragonitic group (gastropods, scaphopods, aragonitic lamellibranchs, nautiloids, and ammonites) was controlled more by preservation than ecology. It is much to be hoped that other workers will look for groups comparable to these at other levels in the Chalk. It seems likely, for instance, that changes similar to the one at the base of Bed 2 will be found at the base of most bands in which aragonitic fossils are preserved (such as the Chalk Rock and Top Rock), and even at the base of any bands which are considerably harder than the beds beneath, suggesting the original presence of aragonite. To be useful such studies will have to be as quantitative as possible.

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