CORALLIAN (UPPER JURASSIC) MARINE BENTHIC ASSOCIATIONS FROM ENGLAND AND NORMANDY

by F. T. FÜRSICH

ABSTRACT. Using the trophic group approach, seventeen macroinvertebrate and one trace-fossil association have been described quantitatively, using 170 bulk collections, from the Middle and Upper Oxfordian of Normandy, Dorset, Oxfordshire, and Yorkshire. Most associations are dominated by bivalves and gastropods, whilst echinoderms and brachiopods are less important. Sedimentary and biostratinomic evidence indicate that, with few exceptions, the associations are the autochthonous or parautochthonous relics of ancient communities. The taphonomy and environments of each association have been discussed and comparisons have been drawn with other Mesozoic benthic associations. The highly abundant oyster *Nanogyra nana* is interpreted as an opportunistic species and the abundance of the pectinid *Chlamys* is regarded as a feature typical of Corallian faunas. The scarcity of brachiopods, which are also uncommon elements in many other Jurassic and Cretaceous benthic faunas, is thought to be related to the short dispersal time of their larvae, combined with competition by bivalves and changing environments.

PALAEOECOLOGY, and especially studies of ancient communities triggered off by research in modern ecology have increasingly gained popularity amongst palaeontologists. Besides the classic work of Petersen (1913) on the fauna of the North Sea and that of Thorson (e.g. 1933, 1957) it is on studies of Russian workers like Turpaeva (1948, 1949, 1957; see also Neyman 1967) that methods and approach in palaeosynecological studies are based. Studies of communities include the description of their composition and structure and their relationship to the environment. Generally, these aspects can best be studied on Recent communities whilst another aspect, that of community evolution, represents the main contribution of the palaeontologist to the field of synecology. The aim of this paper is to contribute to this last aspect of community studies, although it can serve only as a small contribution to a framework of data which will eventually enable us to test concepts now in vogue. Studies of ancient communities or associations (the latter term is preferred for reasons given below) have been mainly on the Palaeozoic (e.g. Boucot 1975; Bretsky 1969, 1970; Hurst 1975; Walker and Laporte 1970; Ziegler *et al.* 1968) and on the Cretaceous (e.g. Kauffman 1967; Rhoads *et al.* 1972; Scott 1974). For the Jurassic, invertebrate associations have been described quantitatively only recently (Wright 1973, 1974; Duff 1975), the bulk of palaeosynecological work being only semi-quantitative (e.g. Hallam 1960, 1967; Sellwood 1972).

The purpose of the paper is to give a quantitative description and environmental interpretation of the seventeen macroinvertebrate and one trace-fossil association which have been recognized. Sedimentary and biostratinomic evidence has been used to establish the taphonomy and general environment of each association. Using this basic information, facies and substrate relationships of the fauna have been investigated and the results published separately (Fürsich 1976*a*, *b*).

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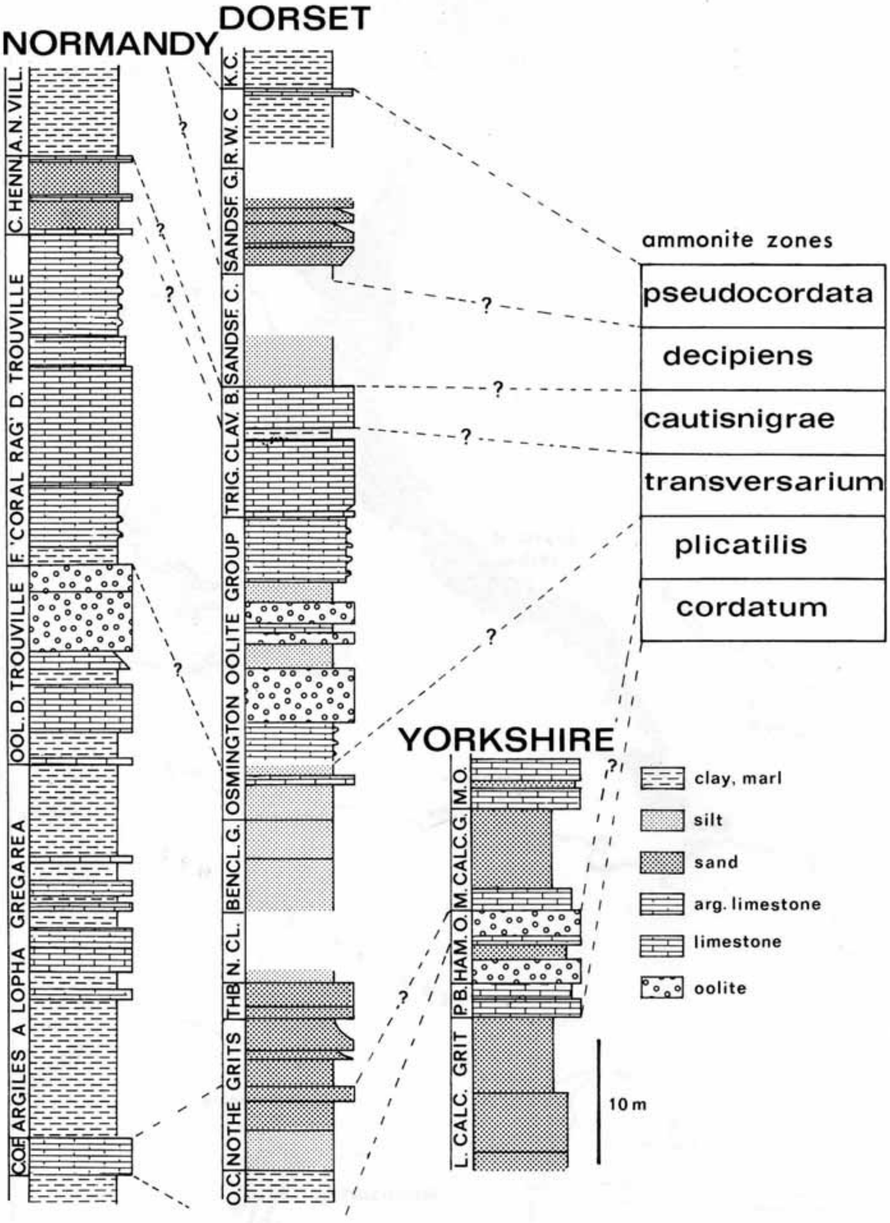
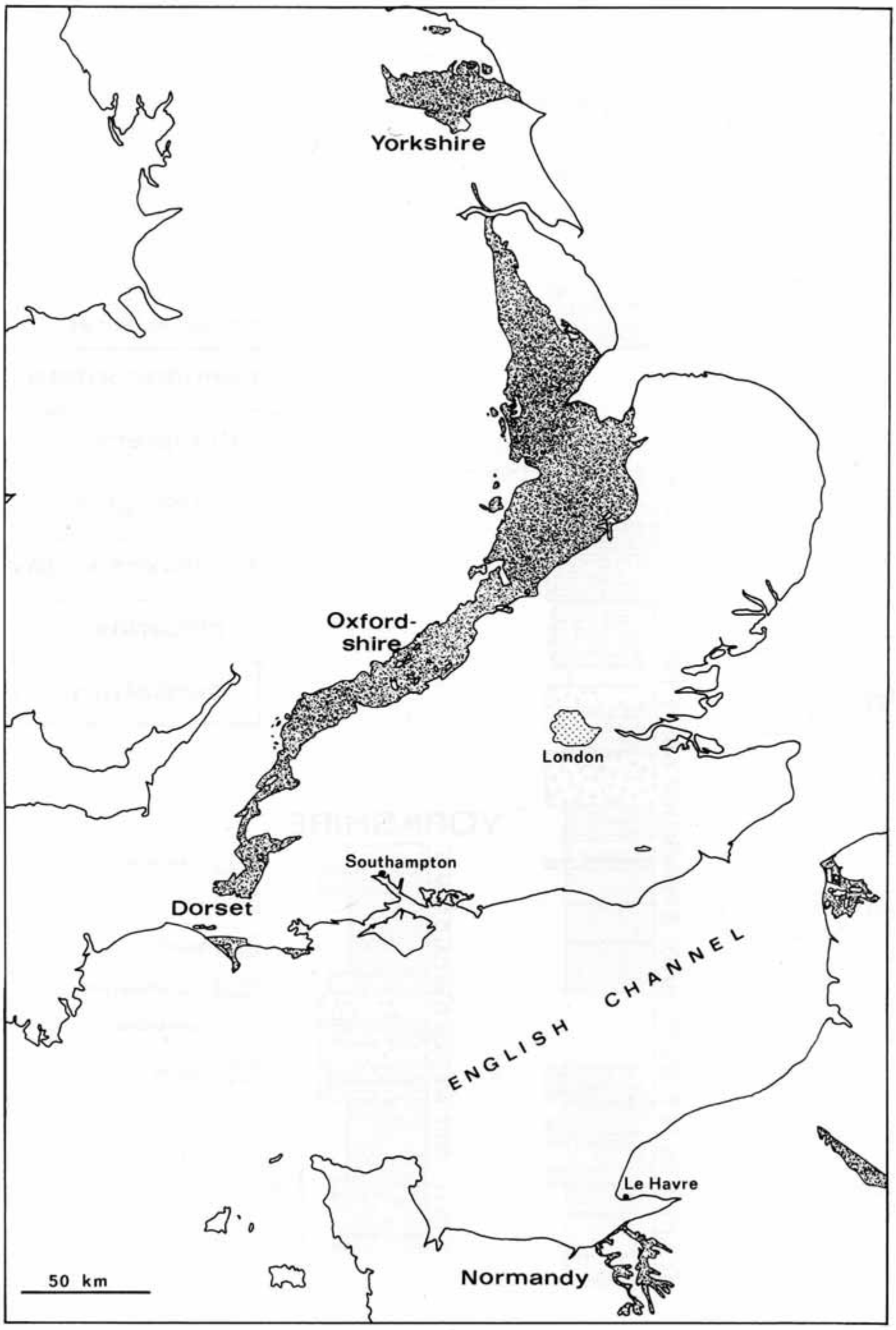
Geological setting. The Corallian (Middle and Upper Oxfordian; text-fig. 1) stretches from Yorkshire down to Dorset in England and also in Normandy, France (text-fig. 2). The main sections under study were provided by cliffs in Yorkshire (Filey Brigg), Dorset (Bowleaze Cove, Osmington Mills to Ringstead Bay, Shortlake to Black Head, Sandsfoot Castle, East Fleet), and Normandy (Houlgate to Villerville). Additional information, especially on the reef facies, was gained in quarries in the Vale of Pickering, Yorkshire, in Oxfordshire, and in Berkshire (for a list of the localities see appendix).

In Dorset, the Corallian consists of four limestone-clay-sand cycles (Talbot 1973), separated partly by erosion surfaces. These cycles correspond to regressing sequences, the erosion surfaces marking renewed transgressions. The sediments were laid down in a shallow sea, probably in the upper shelf region, and the main facies types comprise offshore calcareous sands and carbonates, oolite banks, nearshore muds, subtidal sand bars, lagoonal muds, intertidal sands, estuarine sands and muds, and nearshore ferruginous oolitic muds. The sediments of the Corallian of Yorkshire (sands, mixed limestones, oolites, and patch reefs) and Normandy (similar in lithology to Dorset) have received less attention, and one purpose of the study was to apply the palaeoecological evidence, tested in the well-known Dorset section, to these two areas (Fürsich 1976*b*).

Previous work. There are several prerequisites to a palaeosynecological study: stratigraphical studies to facilitate correlations; sedimentological studies to define environments; and taxonomic studies to interpret the autecology of the faunal elements. For the Corallian, these prerequisites have been largely fulfilled. Blake and Hudleston (1877), Hudleston (1878), Arkell (e.g. 1927, 1933, 1935–1948, 1936), Wilson (1933, 1949), Callomon (1960), and Wright (1972) have dealt with the stratigraphy, whilst Twombley (1964), Wilson (1968*a*, *b*), Lee (1971), Brookfield (1973*a*), and Talbot (1973, 1974) have developed various sedimentological models for the Yorkshire and Hampshire Basins. The bivalves, the bulk of the fauna, have been described by Arkell (1929–1937), and the trace fossils by Fürsich (1974). Microfaunal studies have been carried out by Whatley (1965), Gordon (1965), and Guyader (1968). (For an extensive bibliography see Brookfield 1973*a*.) First attempts to distinguish faunal assemblages have been made by Arkell (1929–1937) who recognized, for example, a bivalve assemblage typical of the reef environment. Arkell (1928, 1935) also dealt with the ecology of the Corallian patch reefs in a more general way. The trace-fossil fauna has been interpreted in terms of distribution patterns and environmental significance by Fürsich (1975). Otherwise, no ecological studies have been undertaken.

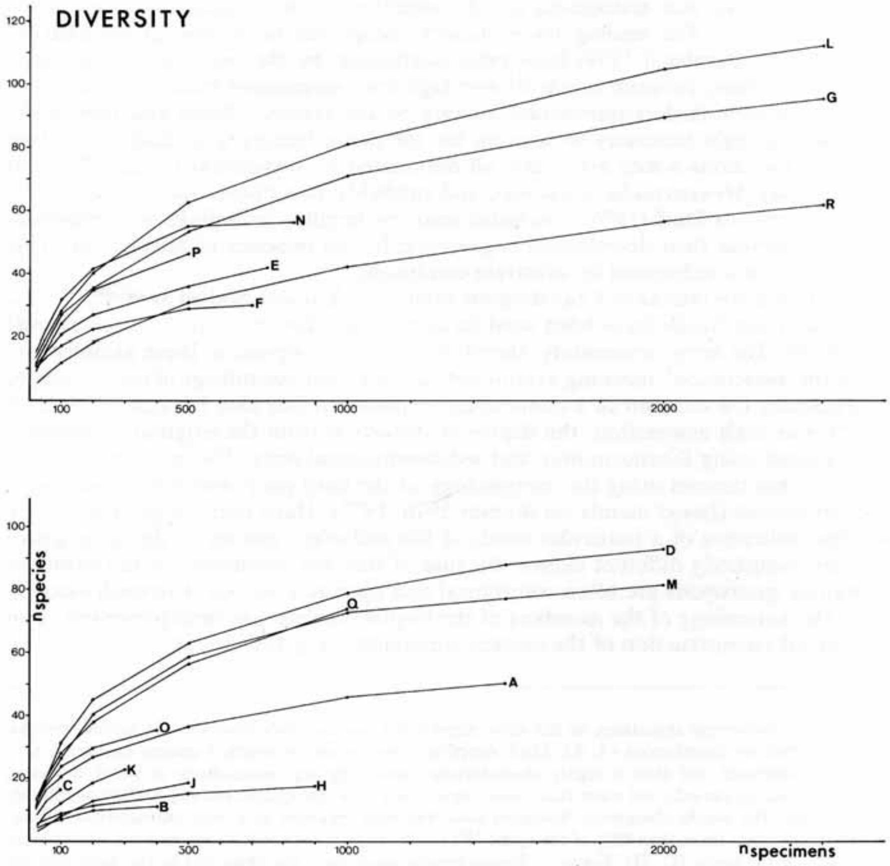
TEXT-FIG. 1. Composite sections of the Corallian of the main areas under study; adapted from Fürsich (1975). C.O.F. = Calcaire à oolithes ferrugineuses; OOL. D. TROUVILLE = Oolithe de Trouville à *Nucleolites scutatus*; F. 'CORAL RAG' D. TROUVILLE = Facies 'Coral Rag' de Trouville; C. HENN. = Calcaire de Hennequeville; A.N. VILL. = Argiles Noires de Villerville; O.C. = Oxford Clay; THB = '*Trigonia*' *hudlestoni* Bed; BENCL. G. = Bencliff Grit; TRIG. CLAV. B. = '*Trigonia*' *clavellata* Beds; SANDSF. C. = Sandsfoot Clay; SANDSF. G. = Sandsfoot Grit; R.W.C. = Ringstead Waxy Clay; K.C. = Kimmeridge Clay; L. CALC. GRIT = Lower Calcareous Grit; P.B. = Passage Beds; HAM. O. = Hambleton Oolite; M. CALC. GRIT = Middle Calcareous Grit; M.O. Malton Oolite.


NORMANDY
A.N.VILL.
C.HENN.
F. 'CORAL RAG' D. TROUVILLE
OOL. D. TROUVILLE
ARGILES A LOPHA GREGAREA
C.O.F.
DORSET
K.C.
R.W.C.
SANDSF. G.
SANDSF. C.
SANDSF. B.
TRIG. CLAV. B.
OSMINGTON OOLITE GROUP
BENCL. G.
N. CL.
THB
NOTHE GRITS
O.C.
YORKSHIRE
M.O.
M. CALC. G.
HAM. O.
P.B.
L. CALC. GRIT
ammonite zones
pseudocordata
decipiens
cautisnigrae
transversarium
plicatilis
cordatum
?
clay, marl
silt
sand
arg. limestone
limestone
oolite
10 m



TEXT-FIG. 2. Outcrop of Upper Jurassic rocks in England and Normandy.

Material and methods. One hundred and seventy bulk collections with more than 30 000 fossils were used for this study. The collections were broken up partly in the field, partly in the laboratory and all macrofossils were saved. For bivalved animals, the fauna has been totalled by counting only the most numerous valve together with the articulated specimens. Preservation, fragmentation, encrusters and borers, size sorting, and relationship between right and left valves in bivalved animals were noted. Orientation of shells, especially with respect to life position was recorded as were the trace-fossil fauna, sedimentary structures, and diagenetic features. The diversity of the samples has been measured using Sanders's (1968) rarefaction method (text-fig. 3). For grouping the collections into associations the trophic group approach



TEXT-FIG. 3. Diversity of Corallian benthic associations expressed by rarefaction curves (Sanders 1968).

has been selected. Firstly, for each collection the trophic nucleus consisting of the numerically dominant species which make up 80% of the fauna (Neyman 1967) was constructed. Then collections with an identical or similar trophic nucleus were grouped into associations. Each of these associations is characterized by one or more species which reach here the peak of their distribution (text-fig. 4). In addition, the associations differ in their trophic nucleus, and in most cases exhibit a distinct ecological composition (e.g. text-fig. 6). The trophic group analysis, developed in Russia by Turpaeva (1948), has been discussed by Walker (1972) and applied to fossil material, for instance by Rhoads *et al.* (1972) and by Duff (1975). Rhoads *et al.* (1972) also discuss the drawbacks of this method when applied to fossil faunas, as biomass and original composition of the fauna have been lost. Walker (1972) suggested substituting biovolume for biomass when working with fossil samples and for this purpose, size histograms for the members of the trophic nuclei are given (e.g. text-fig. 7). The feeding levels usually recognized in trophic group analysis (Walker and Bambach 1974) have been augmented by the introduction, in intermediate position, between low-level and high-level suspension feeders, of medium-level suspension-feeders represented mainly by the bivalves *Pinna* and *Gervillella*. This was thought necessary to account for the dense feeding stratification realized in the associations which are nearly all dominated by suspension-feeders. Pendent bivalves like *Meleagrinella*, *Oxytoma*, and probably also *Pteroperna pygmaea* were —in contrast to Duff (1975)—included into the benthos as high-level suspension-feeders, because their distribution is governed by the presence of seaweed or algae which in turn is influenced by substrate conditions.

The Corallian faunas lack (as do most fossil samples) soft-bodied animals. Where possible, trace fossils have been used to compensate for this but they are no real substitute. The term 'community' therefore cannot be applied to these samples and the term 'association', meaning a non-random, recurrent assemblage of fossils usually representing the remnant of a community, is preferred (see also Fürsich 1975; Duff 1975). For each association, the degree of distortion from the original community is discussed using biostratinomic and sedimentological data. The *autecology* of the bivalves was derived using the morphology of the hard parts and comparison with Recent species (based mainly on Stanley 1970, 1972). Hard parts of gastropods are far less indicative of a particular mode of life and often species of the same genus occupy completely different niches. Because of this, the reconstructed life habits of Corallian gastropods are often conjectural and open to criticism. For each association, the autecology of the members of the trophic nucleus has been presented in an attempted reconstruction of the ancient community (e.g. text-fig. 5).

TEXT-FIG. 4. Numerical abundance of the most important Corallian body fossils in the various benthic macroinvertebrate associations (A–R). Dark stippling: association for which a species exhibits a pronounced preference and thus is highly characteristic; light stippling: associations in which a species preferredly occurs (usually not more than two); these species are less specific but still useful for defining associations. The nearly ubiquitous *Nanogyra nana* has been regarded as a very characteristic species where it represents more than 80% of the fauna (R) and as an accessory species where it represents more than 50% of the fauna (G, H). Torqu. = *Torquirhynchia inconstans*; the other bar in the same column represents *Thurmanella*.

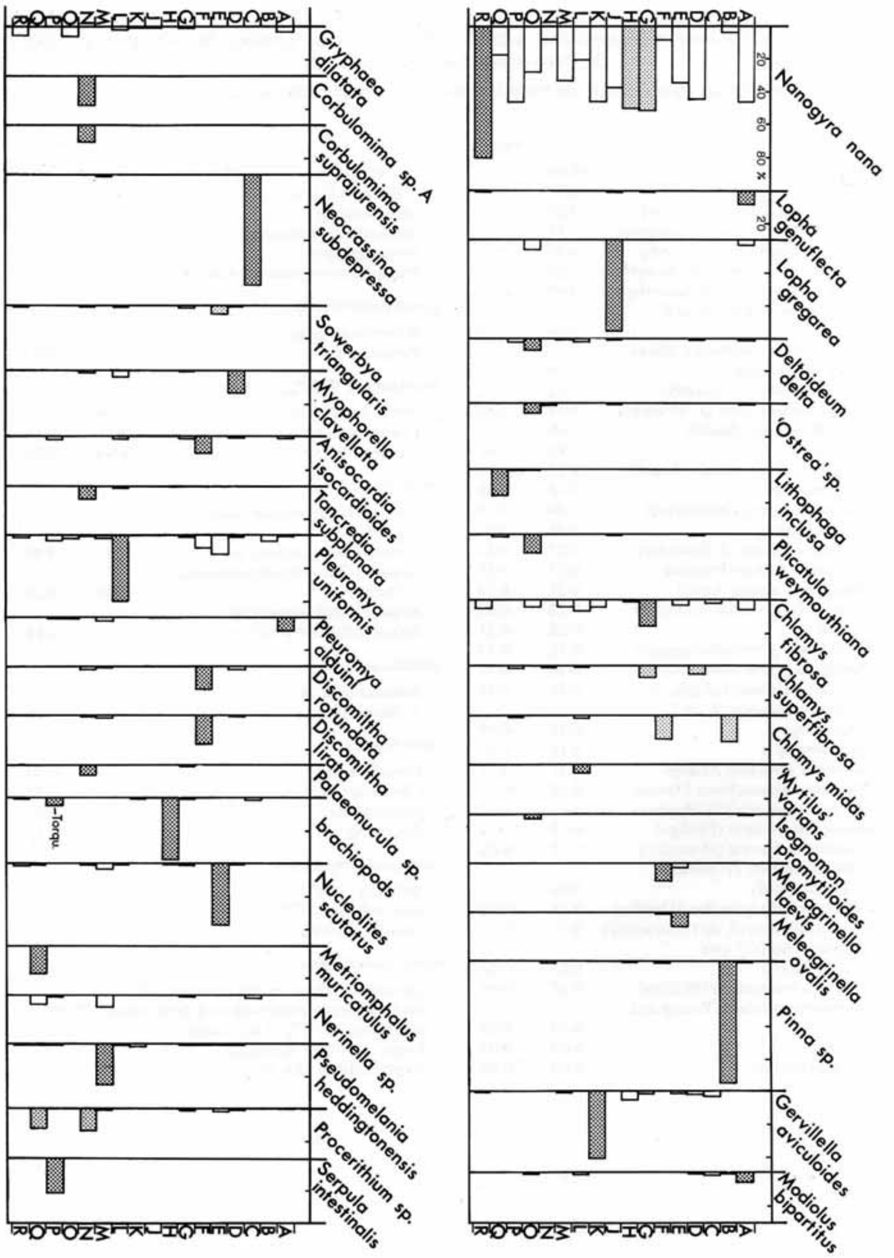

A B C D E F G H I K L M N O P Q R
Gryphaea dilatata
Corbulomima sp. A
Corbulomima suprajurensis
Neocrassina subdepressa
Sowerbya triangularis
Myophorella clavellata
Anisocardia isocardioides
Tancredia subplanata
Pleuromya uniformis
Pleuromya alduini
Discomiltha rotundata
Discomiltha lirata
Palaeonucula sp.
Torqu.
brachiopods
Nucleolites scutatus
Metriomphalus muricatulus
Nerinella sp.
Pseudomelania heddingtonensis
Procerithium sp.
Serpula intestinalis
20 40 60 80 %
Nanogyra nana
20
Lopha genuflecta
Lopha gregarea
Deltoideum delta
'Ostrea' sp.
Lithophaga inclusa
Plicatula weymouthiana
Chlamys fibrosa
Chlamys superfibrosa
Chlamys midas
'Mytilus' varians
Isognomon promytiloides
Meleagrinella laevis
Meleagrinella ovalis
Pinna sp.
Gervillella aviculoides
Modiolus bipartitus

TABLE 1. *Modiolus bipartitus*/*Pleuromya alduini* association (A). (Similar tables of data for the remaining sixteen associations have been deposited with the British National Library, deposition SUP 14007.) Eighteen collections. 1798 specimens.

Composition of fauna (members of the trophic nucleus are marked with an asterisk):

	%	Pres. %
bivalves (98·94%):		
*_Nanogyra nana_ (J. Sowerby)	48·66	0·83
*_Lopha_ (_A._) _genuflecta_ Arkell	8·17	0·55
*_Pleuromya alduini_ (Brongniart)	7·89	0·83
*_Chlamys_ (_R._) _fibrosa_ (J. Sowerby)	7·17	0·66
*_Modiolus bipartitus_ J. Sowerby	6·50	0·83
*_Gryphaea_ (_B._) _dilatata_ (J. Sowerby)	3·50	0·83
Lopha (*A.*) *gregarea* (J. Sowerby)	3·05	0·78
Pholadomya aequalis J. de C. Sowerby	2·66	0·50
Anisocardia isocardioides (Blake and Hudleston)	1·39	0·28
Pinna lanceolata J. Sowerby	1·22	0·22
Pleuromya uniformis (J. Sowerby)	1·11	0·44
Deltoideum delta (Smith)	1·05	0·11
Homomya sp.	0·88	0·33
Isognomon promytiloides Arkell	0·83	0·17
Isognomon sp.	0·44	0·39
Limatula elliptica (Whiteaves)	0·44	0·28
Myophorella sp.	0·38	0·22
Goniomya literata (J. Sowerby)	0·27	0·28
Oxytoma expansa (Phillips)	0·22	0·55
Quenstedtia daviesi Arkell	0·22	0·55
Protocardia dyonisea (Buvignier)	0·22	0·55
'*Ostrea*' sp.	0·22	0·11
Pholadomya protei (Brongniart)	0·16	0·17
Parallelodon aemulum (Phillips)	0·16	0·11
Meleagrinella ovalis (Phillips)	0·16	0·11
Cercomya undulata (J. de C. Sowerby)	0·16	0·05
Isocyprina sp.	0·16	0·11
Cucullaea contracta Phillips	0·11	0·11
Plicatula weymouthiana Damon	0·11	0·11
Mactromya aceste (d'Orbigny)	0·11	0·11
Placunopsis radiata (Phillips)	0·11	0·11
Protocardia intexta (Muenster)	0·11	0·05
Trautscholdia cf. *Tr. cordata* (Trautschold)	0·11	0·11
Chlamys (*Chl.*) *splendens* (Dollfus)	0·11	0·11
Thracia depressa (J. de C. Sowerby)	0·11	0·11
Camptonectes (*C.*) *lens* (J. Sowerby)	0·05	0·05
Sowerbya triangularis (Phillips)	0·05	0·05
Entolium corneolum (Young and Bird)	0·05	0·05
Pteria sp.	0·05	0·05
Corbulomima sp.	0·05	0·05
Placunopsis duriuscula (Phillips)	0·05	0·05
Nuculana (*N.*) sp.	0·05	0·05
Myopholas sp.	0·05	0·05
Arcomytilus pectinatus (J. Sowerby)	0·05	0·05
Praeexogyra sp.	0·05	0·05
Plagiostoma rigidum (J. Sowerby)	0·05	0·05
gastropods (0·16%):		
Bathrotomaria sp.	0·11	0·05
Purpurina sp.	0·05	0·05
brachiopods (0·32%):		
'*Rhynchonella*' sp.	0·16	0·05
Thurmanella sp.	0·11	0·11
'*Terebratula*' sp.	0·05	0·05
serpulids (0·55%):		
Serpula (*Dorsoserpula*) *sulcata* J. Sowerby		0·11
Serpula (*Dorsoserpula*) sp.		0·44
Serpula (*Cycloserpula*) *intestinalis* Phillips	0·55	0·16
Serpula (*Cycloserpula*) sp.		0·16
Serpula (*Pentaserpula*) sp.		0·11
miscellanea:		
Nubeculinella sp.		0·94
'*Cidaris*' spines		0·05
trace fossils:		
Planolites sp.		0·50
Chondrites sp.		0·55
pyritic tubes		0·61
Talpina sp.		0·11

ecological composition:

epifauna: 75·87%
semi-infauna: 7·73%
infauna: 16·34%

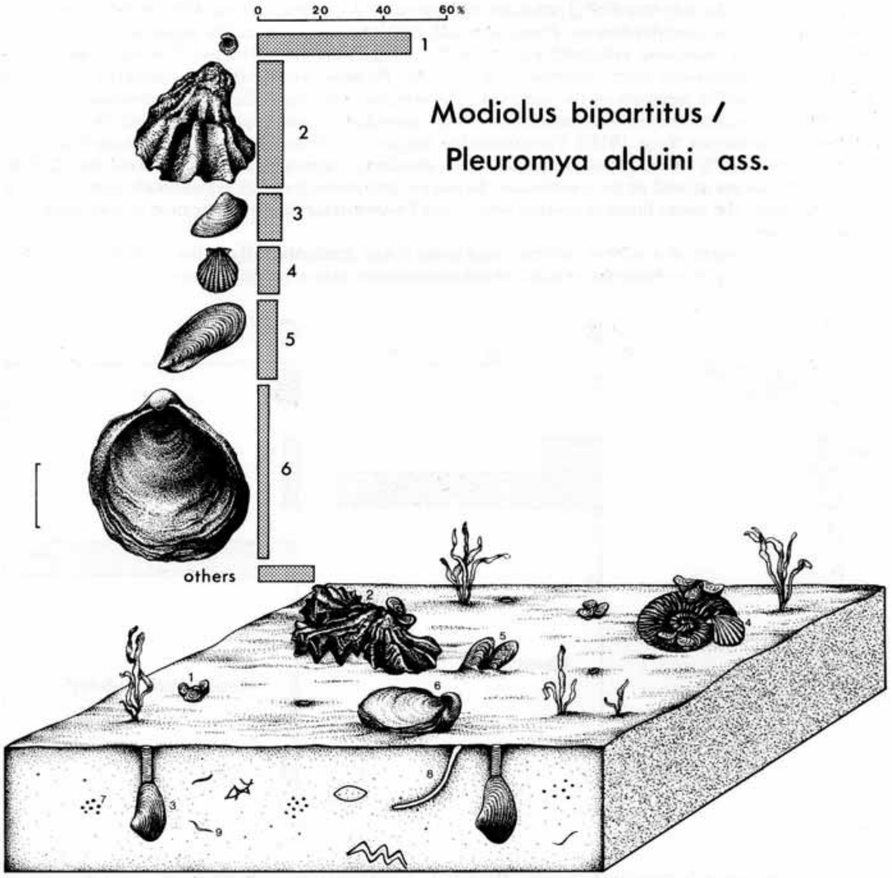
biostratinomic data:

uncemented fauna in life position: 4·63%
bivalved fauna preserved with both valves: 22·85%
encrusted: 19·35% of the fauna
bored: 1·11% of the fauna
fragmentation: 50–95%

CORALLIAN MACROINVERTEBRATE ASSOCIATIONS

A. *Modiolus bipartitus*/*Pleuromya alduini* association

Description. Eighteen collections with altogether 1798 specimens can be attributed to this association (Table 1). Six bivalves (text-fig. 5) form the trophic nucleus with *Nanogyra nana* making up nearly 50% of the fauna whilst *Lopha genuflecta*, *Pleuromya alduini*, *Chlamys* (*R.*) *fibrosa*, *Modiolus bipartitus*, and *Gryphaea dilatata* comprise the rest. Three species (*P. alduini*, *L. genuflecta*, *M. bipartitus*) are characteristic of this association (i.e. they reach in it by far the peak of their distribution). Bivalves account for 98·9%

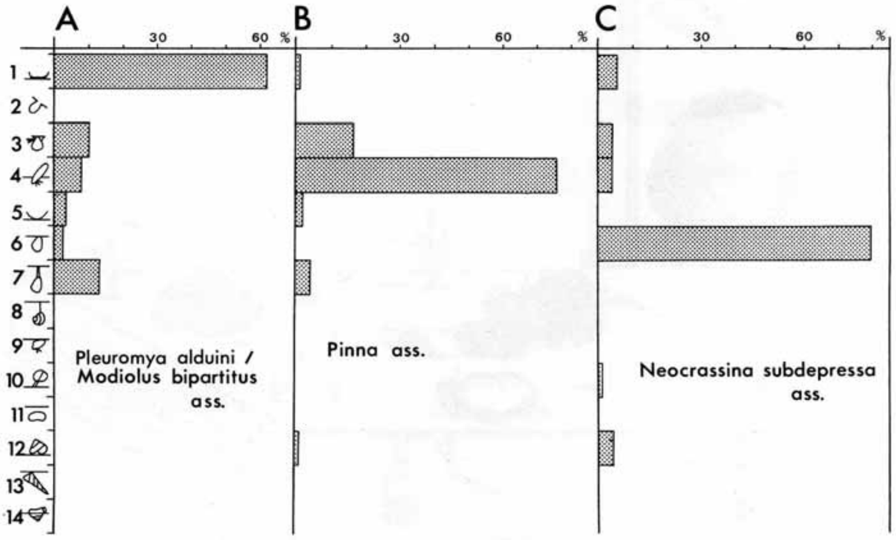


TEXT-FIG. 5. Trophic nucleus and attempted reconstruction of the *Modiolus bipartitus*/*Pleuromya alduini* association (A). Percentage figures give numerical abundances of the various faunal elements. Length of bar: 4 cm. 1, *Nanogyra nana*; 2, *Lopha genuflecta*; 3, *Pleuromya alduini*; 4, *Chlamys fibrosa*; 5, *Modiolus bipartitus*; 6, *Gryphaea dilatata*; 7, *Chondrites* sp.; 8, *Planolites* sp.; 9, pyritic tubes; benthic algae hypothetical.

of the fauna; the remaining groups are gastropods (0·2%), brachiopods (0·3%), and serpulids (0·5%). Echinoderms are only represented by some cidarid spines. Ammonites (mainly *Cardioceras s.l.* and *Aspidoceras*) are common, belemnites rare. Both these groups have not been included in the statistics as they do not belong to the benthos. The trace-fossil fauna (present in fourteen collections) is unvaried, the abundance is medium, the diversity low. Only three ichnospecies were found, all of them having been created by deposit-feeders: *Chondrites*, *Planolites*, and pyritic tubes. The over-all diversity of the benthos is medium (text-fig. 3).

Text-fig. 6 shows that more than 60% of the body fauna are epifaunal cemented forms, especially *Nanogyra* and *Lopha*. Deep-burrowing bivalves, mainly *Pleuromya* and *Pholadomya*, account for 13·6% whilst the semi-infaunal *Pinna lanceolata* and *M. bipartitus* form 7·7%. The percentage of epifaunal byssally attached forms is relatively low (9·9%); its main representative is *Chlamys fibrosa*. 4·6% of the uncemented fauna, especially the deep-burrowing *Pleuromya* and *Pholadomya*, occur in life position. 22·8% of the bivalved fauna are preserved with both valves; 19·3% of the fauna are encrusted. The epizoans are the foraminifera *Nubeculinella* (very common), the bivalves *Plicatula weymouthiana*, *Nanogyra nana*, and *L. gregarea*, as well as serpulids of the subgenera *Cycloserpula*, *Dorsoserpula*, and *Pentaserpula*. 1·1% of the fauna are bored by the bivalve *Lithophaga inclusa*, polychaetes, and a phoronid (represented by the ichnogenus *Talpina* (see Voigt 1972)). Fragmentation ranges from 50 to 95%, most collections being near the lower limit. 11·7% of the fauna are preserved as steinkerns, especially aragonitic forms like shallow and deep burrowers as well as the ammonites. *Gryphaea* and *Deltoideum* are occasionally very worn. In some collections, the oyster fauna is covered with a thin Fe-hydroxide film, an indication of long exposure on the sea floor.

Association A occurs in a narrow substrate and facies range, predominantly in the condensed ferruginous facies consisting of argillaceous micrites or calcareous clays with a varying amount of Fe-ooliths.

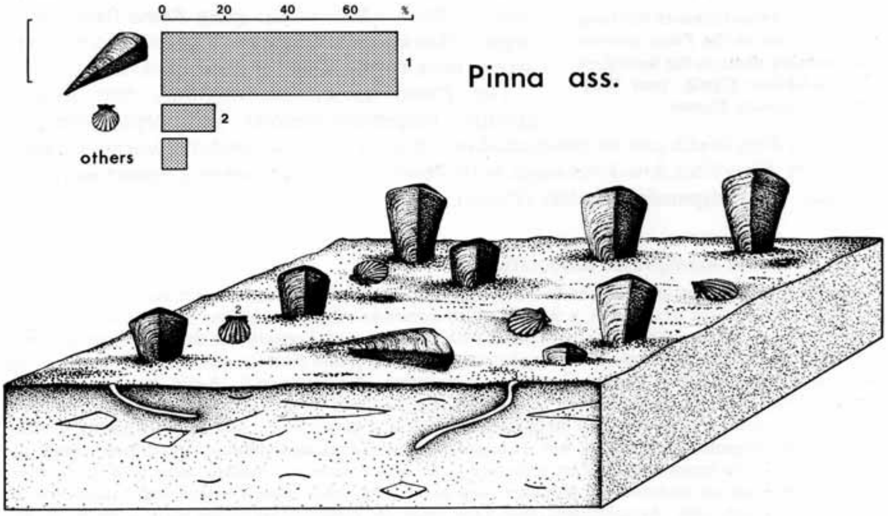


TEXT-FIG. 6. Ecological composition of associations A–C. 1, epifaunal cemented bivalves; 2, boring bivalves; 3, epifaunal byssally attached bivalves; 4, semi-infaunal bivalves; 5, free-resting bivalves; 6, shallow burrowing suspension-feeding bivalves; 7, deep burrowing suspension-feeding bivalves; 8, infaunal bivalves deposit-feeding at the depositional interface; 9, infaunal deposit-feeding bivalves; 10, epifaunal brachiopods; 11, infaunal deposit-feeding echinoids; 12, epifaunal gastropods; 13, infaunal and semi-infaunal gastropods; 14, free-living serpulids.

Discussion. The presence of fauna in life position and the preservation of nearly one-fourth of the fauna with both valves indicate that transport played an insignificant role in the formation of this association. Preservational bias can be ruled out as the aragonitic fauna is still preserved as steinkerns, so that association A can be regarded as the autochthonous part of a true community whose soft parts were removed. Facies, high fossil density, and biostratigraphic evidence point to a very slow accumulation of the sediment under predominantly quiet conditions. This, however, did not lead to a mixing of different superimposed communities as is the case with some collections (described below) but the same communities must have persisted for long periods of time. Slow sedimentation rate probably resulted in a slightly consolidated substrate; this might have been responsible for the absence of any deposit-feeders except in the trace-fossil fauna. Shells lying on the surface provided suitable substrate for initial settlement of the oysters which occur usually in clusters, often several generations settling on top of each other. Three feeding levels may be recognized: infaunal deposit-feeders, represented by the trace fossils, low-level suspension-feeders, e.g. shallow and deep burrowers, and *Chlamys*; and medium-level suspension-feeders, e.g. *Pinna*.

B. *Pinna* association

Description. Six collections with 453 specimens represent this association. *P. sandsfootensis* is by far the dominant species (75·5%) and, together with *Chlamys* (*R.*) *midas*, forms the trophic nucleus (text-fig. 7). *P. sandsfootensis* is confined to this association (see also Arkell 1929–1937) and thus serves as its most characteristic species. *C. midas* is somewhat less specific as it reaches a second peak in its distribution in

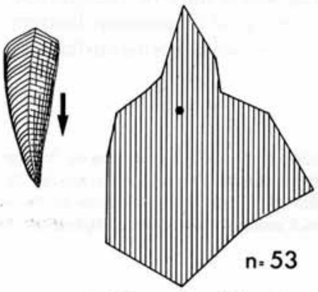


TEXT-FIG. 7. Trophic nucleus and attempted reconstruction of the *Pinna* association (B). Length of bar, 8 cm. 1, *Pinna sandsfootensis*; 2, *Chlamys midas*; 3, *Planolites* sp.

the *Discomiltha* association (F). 99·3% of the fauna are bivalves, the rest gastropods. The only, although abundant, trace fossil occurring with the association is *Planolites*. The over-all diversity is very low (text-fig. 3). Semi-infaunal bivalves (75·9%; i.e. *Pinna*, *Modiolus bipartitus*) dominate the ecological spectrum (text-fig. 6) leaving only 16·8% for the byssally attached epifauna (*Chlamys*). Burrowing forms are rare except *Pleuromya uniformis* (3·9%) which is the only representative of the deep-burrowing bivalves. The virtual absence of the cemented epifauna so abundant in other associations is also striking. 3·3% of the uncemented fauna (mainly *Pinna*) are in life position. The number of bivalved animals with both valves preserved is very high: 73·1%. The fauna is neither bored nor encrusted. Fragmentation varies between 75·0 and 85·0%. Except for most burrowing forms (mainly *Pleuromya*) specimens are preserved with their shell.

All six collections come from medium-grained sandstones of the Sandsfoot Grit (Dorset coast) thus showing a clear relationship between substrate/facies and association.

Discussion. The six collections have been obtained from different horizons within a massive sandstone body. The close similarity of the samples indicate that the *Pinna* association persisted for some time during the formation of the sandstone body. Lack of encrusters and borers indicates that shells did not remain exposed on the sea floor for long and that the rate of sedimentation was thus fairly continuous. The *Pinna* association is the autochthonous relic of a former community which is illustrated by the high percentage of still bivalved specimens and the presence of shells in life position. Numerous flat-lying bivalved *Pinna* evidence short periods of stronger currents or wave movements which led to their excavation *in situ* without further transport. Orientation studies on these flat-lying *Pinna* (text-fig. 8) suggest that either tidal currents or oscillatory wave action were responsible for their excavation.



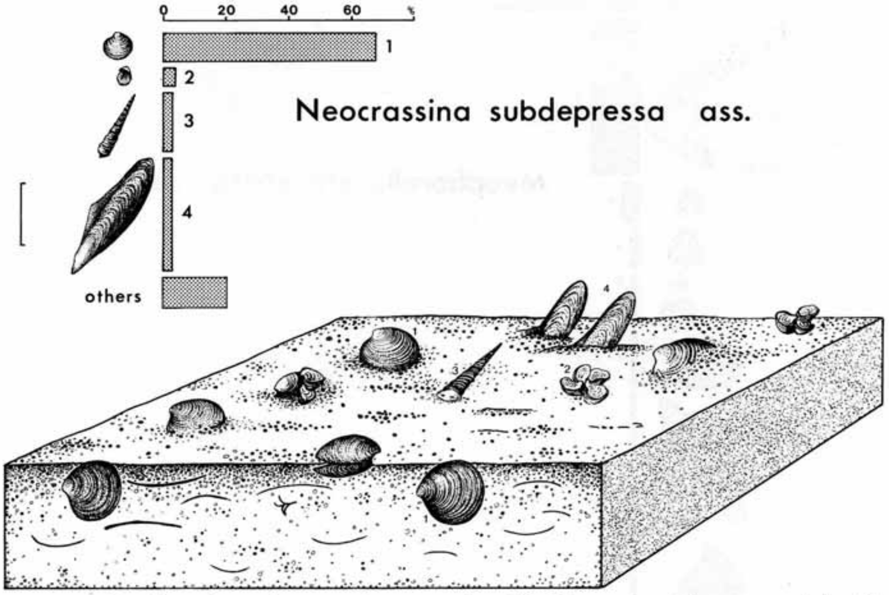
TEXT-FIG. 8. Orientation of flat-lying bivalved *Pinna* in the *Pinna* association. Bedding plane in the Sandsfoot Grit, Sandsfoot Castle, near Weymouth, Dorset.

The *Pinna* association contains two trophic groups: suspension-feeders and deposit-feeders. Three feeding-levels can be distinguished: infaunal deposit-feeders (worms?) represented by *Planolites*, low-level suspension-feeders (e.g. *Pleuromya*, *Ctenostreon*), and medium-level suspension-feeders (*Pinna*).

C. *Neocrassina subdepressa* association

Description. This association has been found in only one collection with ninety specimens. It is dominated by *N.* (*N.*) *subdepressa* (text-fig. 9), a species which occurs in other associations only sporadically. The bivalves *Nanogyra nana*, *Gervillella aviculoides*, and the gastropod *Nerinella* are the remaining members of the trophic nucleus. The bivalves *Perampliata ampliata* (2·2%) and *Fimbria umbonata* (2·2%) occur only rarely in other associations and are thus also characteristic of association C. Again, bivalves dominate the fauna (94·4%) and brachiopods (1·1%) form the rest. No trace fossils are present. Shallow-burrowing bivalves (*Neocrassina*) are the most important ecological group (79·8%; text-fig. 6) whereas byssally attached and cemented epifauna, as well as semi-infaunal bivalves and epifaunal gastropods, share the remaining 20%. No faunal elements are preserved in life position and no bivalves occur with both valves. 11·1% of the fauna are encrusted by *Nanogyra nana* and *Cycloserpula*; borers are missing. Fragmentation is 95%, quite a high value. All specimens, even gastropods, are preserved with their shell; a preservational bias of the fauna can thus be excluded.

The *Neocrassina* association occurs in rubbly, somewhat argillaceous oomicrite.

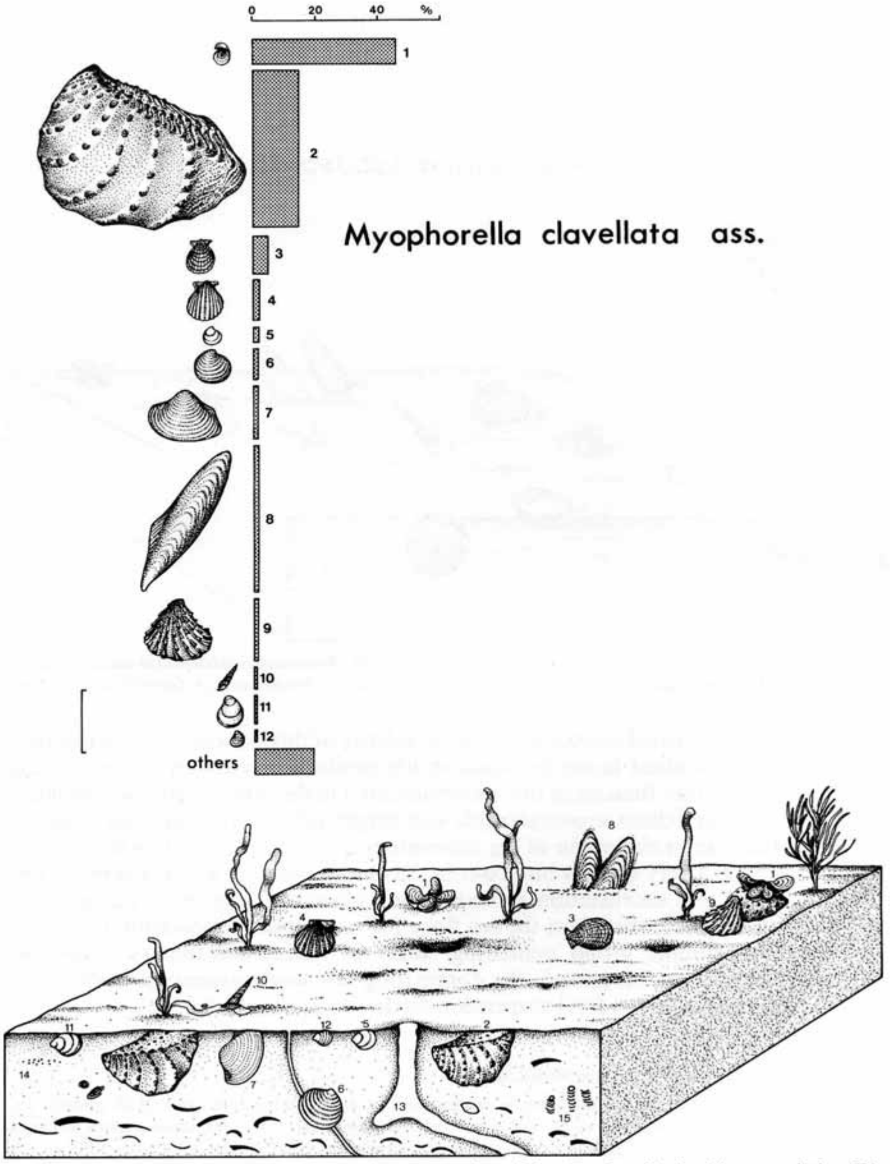


TEXT-FIG. 9. Trophic nucleus and attempted reconstruction of the *Neocrassina subdepressa* association (C). Length of bar, 6 cm. 1, *Neocrassina subdepressa*; 2, *Nanogyra nana*; 3, *Nerinella* sp.; 4, *Gervillella aviculoides*.

Discussion. There existed some doubts on the validity of this association. For instance, the absence of bivalved fauna or fauna in life position favours an origin through transportation rather than an *in situ* accumulation. On the other hand, the specimens of *N. subdepressa* exhibit a considerable size range and no signs of wear could be detected. Thus, an *in situ* origin of the association is favoured, assuming that *N. subdepressa* lived as a very shallow burrower in the muddy oolite in which it is preserved. Disarticulation and encrustation probably took place after currents excavated the infauna and the shells rested on the sea floor for some time. Association C forms a homogeneous trophic group consisting solely of suspension-feeders. Only two feeding levels can be recognized: the dominating low level suspension-feeders (e.g. *Neocrassina*) and medium level suspension-feeders (e.g. *Gervillella*).

D. *Myophorella clavellata* association

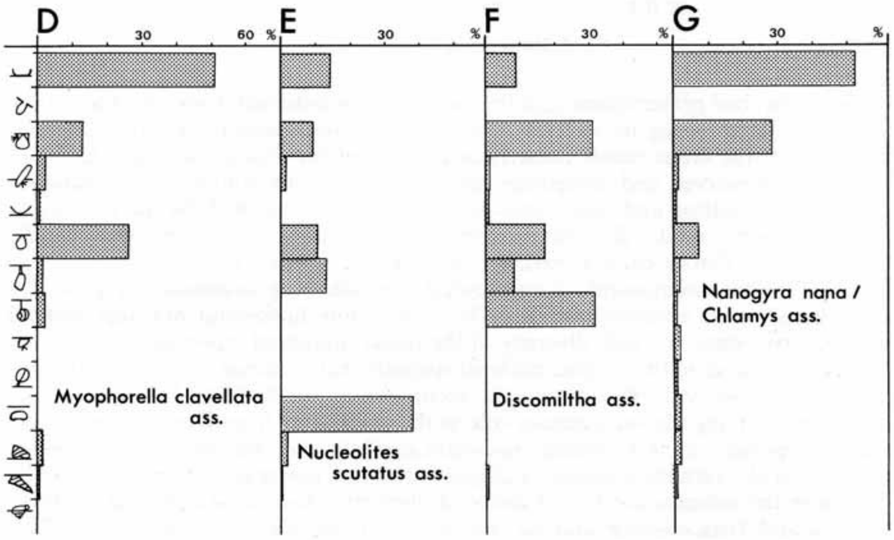
Description. The *M. clavellata* association is represented by eleven collections with 2120 species. The trophic nucleus (text-fig. 10) consists of twelve species: *Nanogyra nana* is the dominant species, followed by the shallow burrower *M. clavellata*, the epifaunal byssally attached *Chlamys* (*R.*) *superfibrosa* and *C.* (*Chl.*) *qualicosta*. The remainder is taken up by *Trautscholdia morini*, *Discomiltha rotundata*, *Cucullaea contracta*, *Gervillella aviculoides*, *Plicatula weymouthiana*, *Procerithium* sp., *Trautscholdia* cf. *curvirostra*, and *T. contejeani*. The association is characterized by the occurrence of several species of *Trautscholdia*, the presence of *C. contracta* and the abundance of *M. clavellata* and *Chlamys* (*R.*) *superfibrosa*. The latter has a second peak in its distribution in association G, but occurs there with a different set of species.



TEXT-FIG. 10. Trophic nucleus and attempted reconstruction of the *Myophorella clavellata* association (D). Length of bar, 4 cm. 1, *Nanogyra nana*; 2, *Myophorella clavellata*; 3, *Chlamys superfibrosa*; 4, *Chlamys qualicosta*; 5, *Trautscholdia morini*; 6, *Discomiltha rotundata*; 7, *Cucullaea contracta*; 8, *Gervillella aviculoides*; 9, *Plicatula weymouthiana*; 10, *Procerithium* sp.; 11, *Trautscholdia curvirostra*; 12, *Trautscholdia contejeani*; 13, *Spongeliomorpha suevica*; 14, *Chondrites* sp.; 15, *Teichichnus rectus*; benthic algae hypothetical.

Bivalves form 96·9% of the fauna, followed by gastropods (2·7%), and echinoderms (0·4%). Trace fossils show a relatively high diversity (six species) and a medium abundance. The dominant forms are decapod crustacean burrows (*Spongeliomorpha suevica* var. B), and burrows of various worm-shaped animals (*Chondrites*, *Teichichnus rectus*, and *Planolites*). The over-all diversity is high (text-fig. 3).

In the *M. clavellata* association epifaunal cemented bivalves (50·8%; mainly *Nanogyra*), byssally attached epifaunal bivalves (11·4%; e.g. *Chlamys*), and shallow burrowers (29·0%; e.g. the bivalves *Myophorella*, *Trautscholdia*) form the dominant ecological groups, whilst mucus-tube feeders (*Discomiltha*), semi-infaunal bivalves (*Gervillella*), and deep-burrowing bivalves (*Pholadomya*, *Pleuromya*) are of only little importance (text-fig. 11). No specimens occur in life position, but 6·6% of the bivalved fauna are preserved with both valves. 8·5% of the fauna have been encrusted by *Nanogyra*, *Plicatula*, *Serpula* (*Cycloserpula*), *S.* (*Pentaserpula*) and the foraminifera *Nubeculinella*. 0·8% of the shells have been bored by cirripeds, polychaetes, and phoronids. Fairly common are browsing traces of echinoderms on *Chlamys* and other shells. Fragmentation ranges from 50 to 95%, with a mean value of 90%. Shell orientation has been measured in seven collections (Table 2). All but one sample showed a clear dominance of shells in the convex-up position. In two cases imbrication could be found. 15·4% of the fauna (mainly shallow- and deep-burrowing bivalves as well as many gastropods) are preserved as steinkerns. In some collections a large number of the specimens are worn or exhibit algal envelopes.



TEXT-FIG. 11. Ecological composition of associations D–G. Legend in text-fig. 6.

The *M. clavellata* association occurs in Normandy and Dorset, especially in condensed sandy and/or intraclastic sideritic limestones as well as in sandy limestones and marls, thus showing a clear substrate preference.

Discussion. The *M. clavellata* association occurs in two modifications: the collections from Normandy are of low diversity, show considerably better preservation, are less encrusted and bored, and less fragmented, whilst the Dorset collections exhibit a high diversity, often a bad preservation (algal envelopes, signs of wear), and a higher percentage of the fauna is fragmented and bored. In Dorset, high density

TABLE 2. Shell orientation in the *Myophorella clavellata* association (D).

Collection	Convex-up	Convex-down	Oblique
BR 44	100	15	19
BR 47	100	33	47
BH 24	100	25	33
BH 28 top	100	38	21
SC 16	100	28	79*
HV I 15	18	54	58*
HV II 5	71	11	8

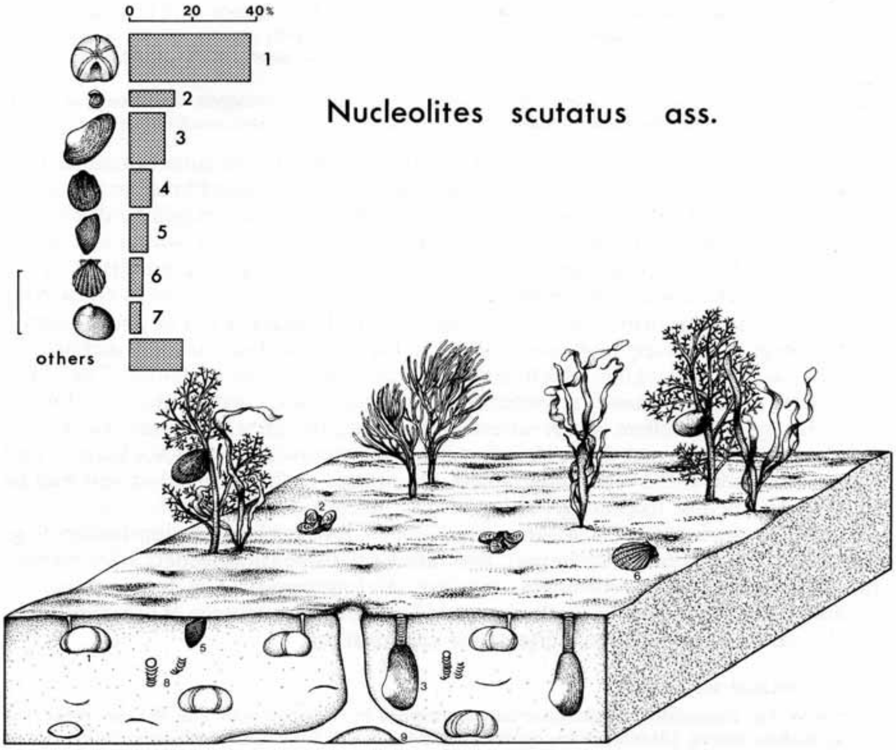
* Shells partially imbricated.

of the fauna, bad preservation, and the mixed and sideritic substrate point to a slow accumulation resulting in, at least partially, condensed deposits. Extensive lateral transport of the fauna seems unlikely as no size sorting exists and some shells are excellently preserved and sometimes bivalved. A parautochthonous accumulation caused by excavation and short, small-scale transport of the shells by currents seems a more feasible model for the formation of this association. The *Myophorella* association of Dorset cannot therefore be regarded as the remnant of one ancient community but components from several neighbouring communities probably contributed to its composition. Very likely not only horizontal but also vertical mixing took place: the high diversity of the fauna (indicated especially by the large number of species in the trophic nucleus) suggests that a change in community took place once or several times during the accumulation of the beds. Despite the fact that faunal mixing played a certain role in the collections from Dorset, they nevertheless represent a very distinct association. Only the *Neocrassina subdepressa* association (C) exhibits a similar ecological structure (compare text-figs. 6 and 11), but there the infauna consists of different elements (*Neocrassina* instead of *Myophorella* and *Trautscholdia*) and the cemented epifauna plays a far lesser role. That a *Myophorella* community existed at some time in the Upper Jurassic of north-west Europe, can also be demonstrated with most of the collections from Normandy which also show signs of short-stage transport but occur in beds which indicate normal or even rapid sedimentation.

Two trophic groups are present in the *Myophorella* association: 96·7% of the fauna are suspension-feeders, whilst 3·3% are deposit-feeders (mucus-tube-feeding *Discomiltha* and *Procerithium*). Four feeding levels can be distinguished: the very rare *Palaeonucula* as well as the trace fossils *Teichichnus*, *Cylindrichnus*, and *Chondrites* representing the infaunal deposit-feeders, *Discomiltha* and *Procerithium* deposit-feeders at the depositional interface, the common *Myophorella* and *Trautscholdia* the low level suspension-feeders, and *Gervillella* the medium level suspension-feeders.

E. *Nucleolites scutatus* association

Description. Seven hundred and eighty-six specimens in six collections represent this association. The trophic nucleus consists of seven species (text-fig. 12), the most important being the echinoid *N. scutatus*, followed by *Nanogyra nana*, *Pleuromya uniformis*, *Meleagrinella ovalis*, *Sowerbya triangularis*, *Chlamys*



TEXT-FIG. 12. Trophic nucleus and attempted reconstruction of the *Nucleolites scutatus* association (E). Length of bar, 4 cm. 1, *Nucleolites scutatus*; 2, *Nanogyra nana*; 3, *Pleuromya uniformis*; 4, *Meleagrinella ovalis*; 5, *Sowerbya triangularis*; 6, *Chlamys fibrosa*; 7, *Meleagrinella laevis*; 8, *Teichichnus rectus*; 9, *Spongeliomorpha suevica*; benthic algae and hydrozoan/anthozoan coelenterate hypothetical.

(*R.*) *fibrosa*, and *M. laevis*. The association is characterized by *Nucleolites scutatus* and *M. ovalis*; in addition, *S. triangularis* reaches here the peak of its distribution. Bivalves (58·9%) no longer form the only important group of the fauna, but echinoderms (38·5%) are of nearly equal importance. Gastropods (2·5%) only play a minor role. The *N. scutatus* association is dominated by infaunal elements (text-fig. 11); the echinoids *Nucleolites*, *Clypeus*, and *Holectypus*, shallow-burrowing bivalves like *Sowerbya* and *Anisocardia*, deep-burrowing *Pleuromya*, and infaunal gastropods like *Pseudomelania* constitute 62·8% of the fauna. Byssally attached epifaunal elements (34·3%) are not so much represented by the genus *Chlamys* (as is the case in most other associations) but by the free-swinging pendant *Meleagrinella*. The number of epifaunal cemented forms is relatively low (14·4%). Trace fossils are of medium abundance and diversity; the ichnospecies present are: *Spongeliomorpha suevica* var. B, *Teichichnus rectus*, *Skolithos* sp., and the resting trace of an anthotoan (*Bergaueria* sp.), i.e. a mixture between deposit-feeders, suspension-feeders, domichnia, fodinichnia, and cubichnia. The over-all diversity is medium (text-fig. 3). Only 0·6% of the uncemented fauna occur in life position (mainly *Homomya*, *Pleuromya*), but 22·5% of the bivalved fauna are preserved with both valves (amongst them epifaunal forms like *Meleagrinella*). *Dorsoserpula*, *Cycloserpula*, *Nanogyra*, and the bryozoan *Berenicea* encrust 3·7% of the fauna; boring elements are not present.

Fragmentation ranges from 0 to 95%, the mean value is around 60%. Except for 9·9% (mainly deep-burrowing bivalves and some gastropods which occur as steinkerns) the specimens are preserved with their shell. In two collections, a part of the epifauna exhibits algal envelopes; otherwise no signs of wear have been found.

The *Nucleolites scutatus* association shows a substrate preference for limestones which may, however, range from pure micritic limestones to oolites. Sandy, somewhat shelly limestones dominate.

Discussion. The *N. scutatus* association can be regarded as the autochthonous relic of an ancient community. This is stressed by the high percentage of bivalves preserved with both valves. That no fauna in life position has been found might be due to the fact that in the case of the burrowing echinoderm *Nucleolites* life position and stable position are identical (thus quite a few of the *Nucleolites* might be preserved in life position). The two collections, in which part of the epifauna is encrusted by calcareous algae and other organisms, have been found in shelly limestone and poorly sorted oolite. There, a relatively high energy level probably led to discontinuous sedimentation and *in situ* reworking which remained restricted to the epifauna. The other collections represent quieter environments with continuous sedimentation which is indicated by the excellent preservation of the fauna (in addition, many *Nucleolites* are filled with calcite and not with sediment). Both, deposit-feeders (*Nucleolites*) and suspension-feeders (the remaining fauna), are present in the association and lead to an inhomogeneous trophic grouping. Four feeding levels may be recognized: infaunal deposit-feeders (*Nucleolites*, *Teichichnus*), low-level suspension-feeders (e.g. *Pleuromya*, *Anisocardia*, *Nanogyra*), medium-level suspension-feeders (*Gervillella*), and high-level suspension-feeders (pendent *Meleagrinella*). The low number of epifaunal encrusting bivalves is clearly related to the low percentage of other epifauna which restricted the substrate suitable for colonization.

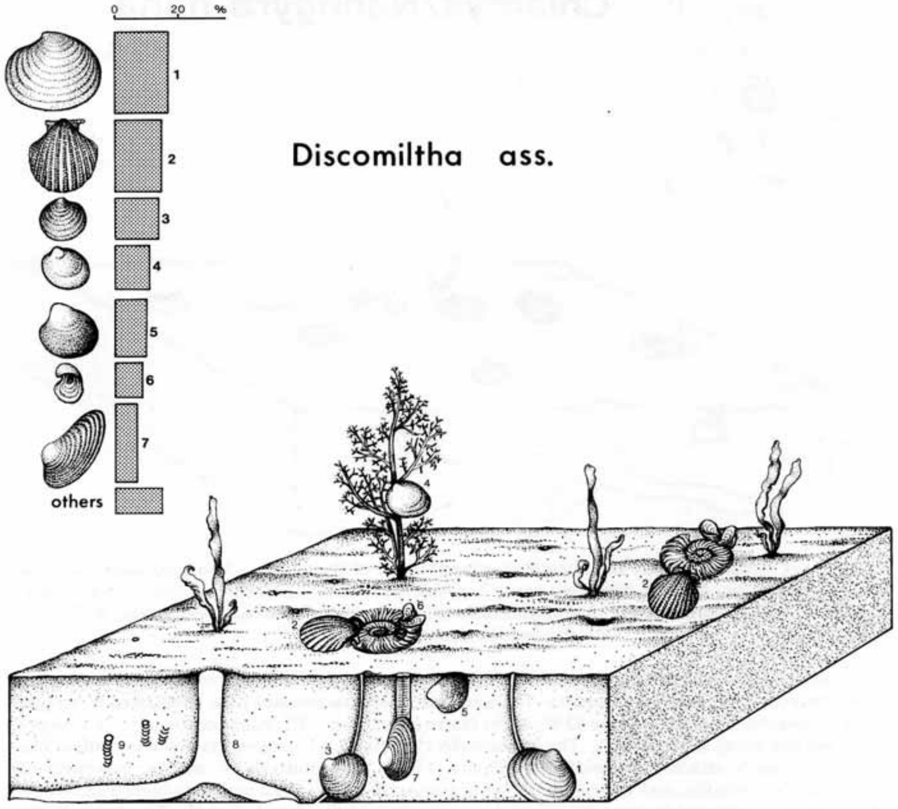
F. *Discomiltha* association

Description. The *Discomiltha* association is only represented by two collections with 702 specimens. The trophic nucleus (text-fig. 13) contains two species of *Discomiltha*, *D. lirata*, and *D. rotundata*, the remaining species being *Chlamys* (*R.*) *midas*, *Meleagrinella laevis*, *Anisocardia isocardioides*, *Nanogyra nana*, and *Pleuromya uniformis*. Four of these species are characteristic of the association: *D. lirata*, *D. rotundata*, *A. isocardioides*, and *M. laevis*. *C. midas* reaches a second peak in its distribution in the *Pinna* association and is thus less specific. As usual, bivalves dominate the fauna (99·6%) with gastropods forming the rest. Ammonites (not discussed here) are a very common faunal element. Trace fossils are of low diversity but high abundance and consist of the crustacean burrows *Spongeliomorpha suevica* var. B, *Sp. paradoxica*, and of *Teichichnus*. The over-all diversity is relatively low (text-fig. 3). Ecologically, mucus-tube feeders (*Discomiltha*) and epifaunal byssally attached bivalves (e.g. *Chlamys*, *Meleagrinella*) are of equal importance (31·8% and 31·0% respectively; see text-fig. 11). Shallow burrowers (8·1%; e.g. *Pleuromya*) and epifaunal cemented forms (9·2%; *Nanogyra*) comprise the rest. No specimens were found in life position, but 25·5% of the bivalves (predominantly *Discomiltha* and *Pleuromya*) are preserved with both valves. 1·4% of the fauna are encrusted by *Cycloserpula*; no specimens are bored. Fragmentation is in both collections about 50%. Nearly four-fifths of the specimens, mainly the burrowing bivalve fauna and the ammonites, are preserved as steinkerns.

Both collections are from medium-grained sandstone which indicates the narrow facies and substrate range of association F.

Discussion. The *Discomiltha* association is the relic of an ancient community which is indicated by the high percentage of specimens preserved with both valves and the low percentage of fragmented forms. The extensive burrow systems of crustaceans (*Spongeliomorpha*) point to fairly stable conditions at least for part of the time.

Their producers (deposit-/suspension-feeders or scavengers?) constituted an important part of the community. The absence of infaunal deposit-feeding bivalves is probably due to the relatively coarse substrate, whilst the encrusting fauna lacked substrate suitable for colonization and is thus far below its usual significance. No other association possesses a similar ecological structure. The occurrence of two species of *Discomiltha* among three most common representatives of the trophic nucleus indicates that interspecific competition must have been low, or else, that small differences in the feeding habit existed. Five feeding levels can be distinguished: infaunal deposit-feeders (represented by *Teichichnus*), deposit-feeders at the depositional interface (*Discomiltha*), low-level suspension-feeders (e.g. *Chlamys*, *Pleuromya*, *Anisocardia*), medium-level suspension-feeders, represented by some *Pinna* and

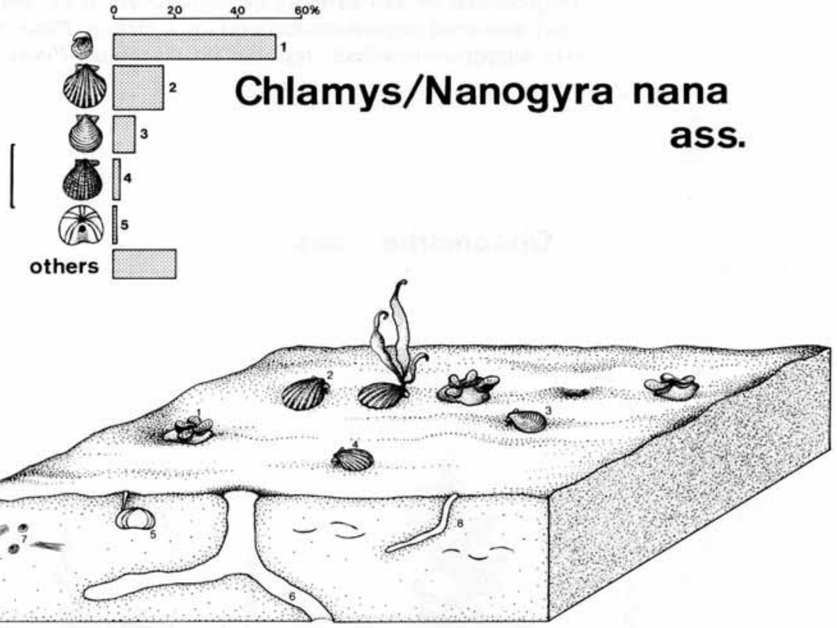


TEXT-FIG. 13. Trophic nucleus and attempted reconstruction of the *Discomiltha* association (F). Length of bar, 3 cm. 1, *Discomiltha lirata*; 2, *Chlamys midas*; 3, *Discomiltha rotundata*; 4, *Meleagrinella laevis*; 5, *Anisocardia isocardioides*; 6, *Nanogyra nana*; 7, *Pleuromya uniformis*; 8, *Spongeliomorpha suevica*; 9, *Teichichnus rectus*; benthic algae and hydrozoan/anthozoan coelenterate hypothetical.

Gervillella, and high-level suspension-feeders (e.g. the pendent *Meleagrinella*). The numerous vagile ammonites (mainly *Amoeboceras*, less common perisphinctids) most likely formed a third trophic group, namely scavengers (Lehmann 1975) or predators.

G. *Chlamys*/*Nanogyra nana* association

Description. Eighteen collections with 2908 specimens have been grouped into this association. *N. nana* is with 52·1% the dominant species (text-fig. 14) followed by *C.* (*R.*) *fibrosa*, *C.* (*R.*) *superfibrosa*, and *C.* (*C.*) *qualicosta*. The burrowing echinoid *Nucleolites scutatus* and the shallow-burrowing bivalve *Sowerbya triangularis* complete the trophic nucleus. The association is characterized by the dominance of pectinids and of *Nanogyra*. Bivalves comprise 93·8% of the fauna, gastropods 3·2%, echinoderms 1·7%, brachiopods 0·3%, and free-living serpulids 0·2%. The epifauna (86·1%; text-fig. 11) consists mainly of cemented *Nanogyra* and byssally attached pectinids, the infauna (12·6%) predominantly of shallow burrowers like *Sowerbya*, *Trautscholdia*, and *Isocyprina*. Infaunal gastropods, *Nucleolites*, and deep-burrowing bivalves are of lesser significance as are semi-infaunal animals (*Gervillella*, *Pinna*). For the first time, deposit-feeding nuculids (1·1%) occur in an association more than just as scattered individuals. Trace fossils show a very high diversity (eight species) and medium abundance. The dominant ichnospecies are *Spongeliomorpha suevica* var. B, *Planolites* sp., and the burrow of a worm-shaped animal, *Cylindrichnus concentricus*. The over-all diversity is high (text-fig. 3). No species occur in life position except *Nanogyra* and other



TEXT-FIG. 14. Trophic nucleus and attempted reconstruction of the *Chlamys*/*Nanogyra nana* association (G). Length of bar, 4 cm. 1, *Nanogyra nana*; 2, *Chlamys fibrosa*; 3, *Chlamys superfibrosa*; 4, *Chlamys qualicosta*; 5, *Nucleolites scutatus*; 6, *Spongeliomorpha suevica*; 7, *Cylindrichnus concentricus*; 8, *Planolites* sp.; benthic algae hypothetical.

cemented forms and the percentage of specimens preserved with both valves is low (2·9%). 5% of the fauna are encrusted by various serpulids (*Cycloserpula*, *Dorsoserpula*, *Pentaserpula*), the bivalves *Nanogyra* and *Placunopsis*, bryozoans, and the foraminifera *Nubeculinella*. *Lithophaga inclusa* and cirripedes account for the few bored specimens (0·1%). Fragmentation varies between 30 and 98% and is usually around 90%. Orientation of shells could be measured in one collection; convex-up shells dominated (convex-up: convex-down = 100:65; oblique: 41). 5·3% of the fauna, predominantly burrowing forms (*Pleuromya*, *Palaeonucula*, *Protocardia*) more rarely epifaunal elements, are preserved as steinkerns. Only rarely do specimens exhibit signs of wear but commonly show algal envelopes when found in oolites or bioclastic limestones.

The *Chlamys*/*N. nana* association occurs in a wide range of substrates and facies types, in clays as well as in oolites whereby a certain preference for sandstones and impure limestones was noted. In several collections bored and encrusted pebbles are associated with the fauna.

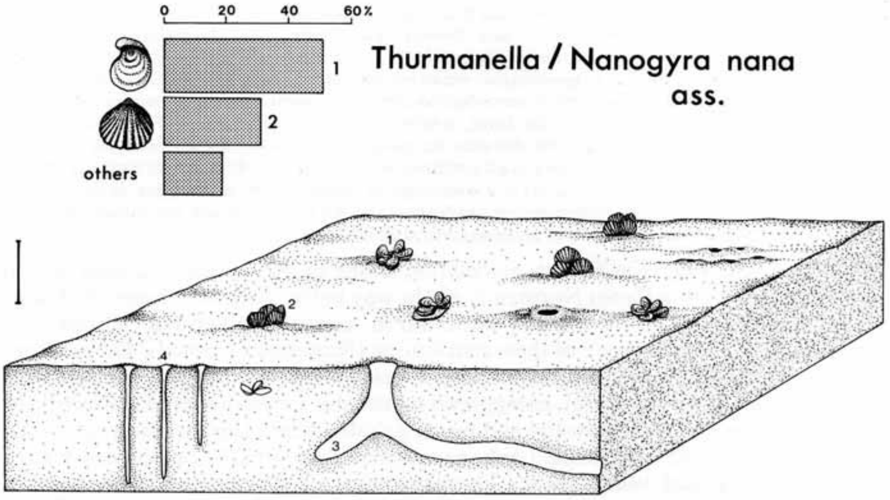
Discussion. The *Chlamys*/*N. nana* association is one of the commonest associations in the Corallian, found from Normandy all the way to the Yorkshire coast. Although its characteristic members can also be found in nearly all other associations, it is here that they reach the peak of their distribution (*Nanogyra* excepted). The environment in which this association accumulated was quite varied, judging from its wide range of facies, but a fairly high energy level is probable for most samples. Reworking was a common feature (encrusted and bored pebbles, high fragmentation rate, algal envelopes) and some species like *Lopha genuflecta* reacted in developing occasionally extremely thick and heavy shells. The percentage of still bivalved specimens is insignificant and no forms are preserved in life position. The substrate was of little attraction for the infauna as the cemented and byssally attached epifauna is the dominating faunal element. *Nanogyra* growing on dead shells formed little clusters on the sea floor and the pectinids similarly may have used shell material for fixation of their byssus.

Apart from this high-energy variety, a few collections seem to be derived from a low-energy environment represented by clays and silts. There, the fauna is better preserved and the infauna is of greater abundance and diversity with some deposit-feeding *Procerithium*, *Discomiltha*, and *Palaeonucula* occurring besides infaunal suspension-feeders (*Pseudomelania*).

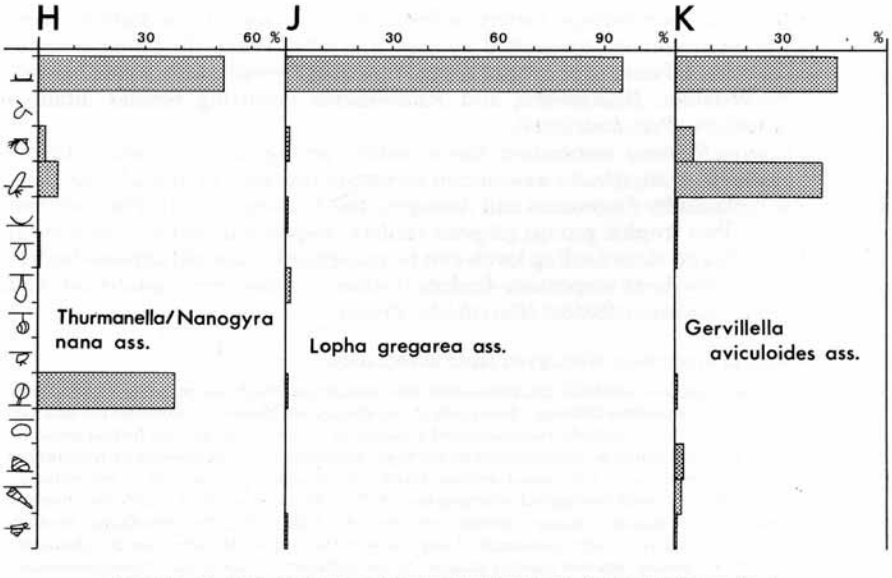
The *Chlamys*/*N. nana* association has a similar ecological composition to the oyster/*Isognomon promytiloides* association (compare text-figs. 11 and 21) but there *Chlamys* is replaced by *Isognomon* and *Nanogyra* has to compete with *Plicatula* and other oysters. Two trophic groups (deposit-feeders, suspension-feeders) are present in association G and three feeding levels can be recognized: infaunal deposit-feeders (*Palaeonucula*), low-level suspension-feeders (*Chlamys*, *Pleuromya*, *Sowerbya*), and medium-level suspension-feeders (*Gervillella*, *Pinna*).

H. *Thurmanella acuticosta*/*Nanogyra nana* association

Description. Three collections with 921 specimens form this association which has been encountered only in Yorkshire. The trophic nucleus (text-fig. 15) consists of two species, the bivalve *N. nana* and the brachiopod *Thurmanella acuticosta*. *Gervillella aviculoides* and a species of '*Terebratula*' are two further common faunal elements. The association is characterized by the high percentage of rhynchonellid or terebratulid brachiopods which otherwise are a rare faunal element. Hardly any infauna is present (0·9%), but epifaunal cemented bivalves (52·5%), pedicle-attached brachiopods (38·5%) and, to lesser extent, epifaunal byssally attached bivalves (2·0%; mainly *Chlamys*) prevail (text-fig. 16). With 5·8%, the semi-faunal bivalves (*Gervillella*, *Pinna*) are relatively well represented. Long stems of the crinoid *Millericrinus* are commonly found on the bedding planes; starfish ossicles abound in the sediment. Trace fossils (*Spongeliomorpha suevica* var. B and *Skolithos*) are of low diversity and medium abundance. The over-all diversity is similarly



TEXT-FIG. 15. Trophic nucleus and attempted reconstruction of the *Thurmanella acuticosta/Nanogyra nana* association (H). Length of bar, 2 cm. 1, *Nanogyra nana*; 2, *Thurmanella* sp.; 3, *Spongeliomorpha suevica*; 4, *Skolithos* sp.



TEXT-FIG. 16. Ecological composition of associations H–K. Legend in text-fig. 6.

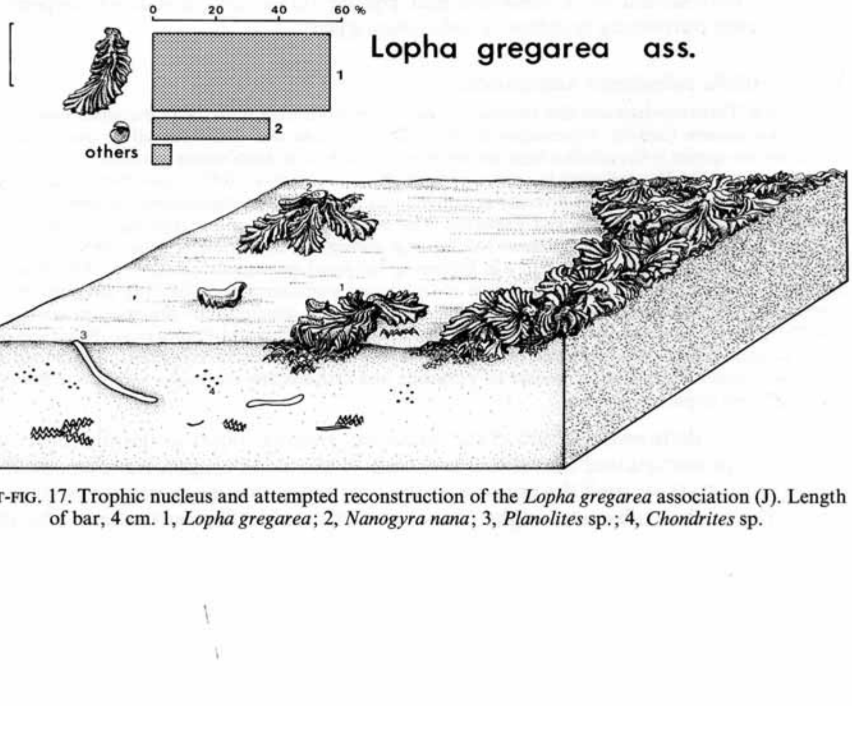
very low (text-fig. 3). Of the uncemented fauna 57·6%, mainly *Thurmanella* and '*Terebratula*', occur in life position as do most cemented *Nanogyra*, and 39% of the specimens are still bivalved. Only a few specimens are encrusted with the bryozoan *Berenicea* or with *Nanogyra*, even less are bored by polychaetes. Fragmentation ranges from 65 to 75%. All faunal elements are preserved with their shells.

The three collections show a distinct substrate preference occurring in oolitic/sandy limestones and oolitic calcareous sandstones.

Discussion. As only thick-shelled aragonitic burrowers are preserved (*Myophorella*), some preservational bias cannot be excluded, with the thin-shelled species dissolved during diagenesis. Apart from this, the *Thurmanella*/*Nanogyra* association is the remnant of an ancient community. This can be inferred from the high percentage of fossils still bivalved and in life position. Hardly any transport has been involved: *Nanogyra* and the brachiopods are found as small clusters with calcite or geopetal fills dispersed on the bedding plane as they were originally on the sea floor. Partly articulated *Millericrinus* also indicate that the fauna is autochthonous. The low percentage of bored and encrusted shells indicates continuous sedimentation; the substrate and faunal composition suggest moderate currents. Deposit-feeders are not represented, but the abundant starfish ossicles indicate that algal grazing, scavenging, or predatory starfish played an important role in the ecosystem. Three feeding levels can be distinguished: infaunal deposit-feeders (crustaceans) low-level suspension-feeders (e.g. the producer (worms, phoronids?) of *Skolithos*, *Myophorella*, *Nanogyra*, brachiopods), medium-level suspension-feeders (*Gervillella*, *Pinna*), and high-level suspension-feeders (*Millericrinus*).

J. *Lopha gregarea* association

Description. The *L. gregarea* association is represented by 616 specimens in six collections. The trophic nucleus (text-fig. 17) consists of two epifaunal cemented bivalves: *L. gregarea* and *N. nana*. The association



TEXT-FIG. 17. Trophic nucleus and attempted reconstruction of the *Lopha gregarea* association (J). Length of bar, 4 cm. 1, *Lopha gregarea*; 2, *Nanogyra nana*; 3, *Planolites* sp.; 4, *Chondrites* sp.

is characterized by *L. gregarea* which reaches here the peak of its distribution. Bivalves (98·5%) dominate the association with serpulids (0·8%) and brachiopods (0·6%) forming the rest, whilst gastropods are missing. Trace fossils are of low abundance and diversity; they are represented by *Chondrites* and pyritic tubes. The over-all diversity is very low (text-fig. 3). Except for a few epifaunal byssally attached bivalves (1·0%) and deep-burrowing bivalves (1·3%) the fauna is dominated by cemented bivalves (95·3%; see text-fig. 16). No uncemented forms are preserved in life position but the majority of *Lopha* and *Nanogyra* occur in life position forming low biostromes. 11·6% of the specimens are still bivalved. Due to the predominance of epifauna, 57·6% of the fauna are encrusted by *Nanogyra*, the foraminifera *Nubeculinella*, the bryozoans *Berenicea* and *Stomatopora*, and various serpulids (*Cycloserpula*, *Dorsoserpula*, and *Pentaserpula*). 4% of the fauna are bored; the animals responsible being the bivalve *Lithophaga inclusa* and a phoronid. Fragmentation varies between 75 and 90%. Most specimens are preserved with their shell intact except some deep-burrowing *Pholadomya* which occur in steinkern preservation.

Discussion. Only present in Normandy, the *Lopha gregarea* association exhibits a similar ecological composition as the *Nanogyra* association (R), but there *Lopha* is replaced by *Nanogyra* which is the only dominant faunal element. The environment is very similar to that of association A (see p. 347), i.e. relatively low rates of sedimentation and only interludes of high-energy conditions. This led to a stable substrate upon which extensive oyster beds grew up to 20 cm high. These beds could be followed laterally for several hundred metres. The dense mass of *L. gregarea* provided in turn an ecological niche for smaller encrusters like *Nanogyra* and the numerous serpulids. Whilst some collections represent the *in situ L. gregarea* community of Upper Jurassic times, in some others the shell beds have been broken up and clusters of individuals scattered on the sea floor, indicating the destruction of the community by strong currents. The fact that a large part of the sea floor was covered with these oyster beds is probably responsible for the extremely low percentage of burrowing fauna.

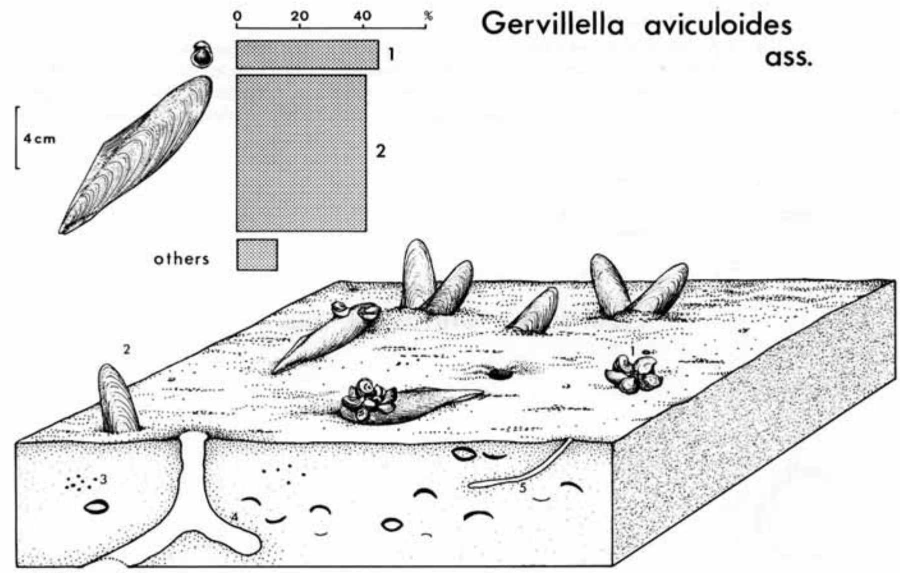
Only two feeding levels can be distinguished: infaunal deposit-feeders (sipunculoid worms?) represented by *Chondrites* and pyritic tubes, and low-level suspension-feeders (rare burrowing bivalves, *Lopha*, *Nanogyra*).

K. *Gervillella aviculoides* association

Description. Three hundred and fifty-two specimens in three collections form the *G. aviculoides* association. Its trophic nucleus (text-fig. 18) consists of the bivalves *N. nana* and semi-infaunal *G. aviculoides*. The characteristic species is *Gervillella* which reaches here the peak of its distribution. As usual, bivalves dominate the fauna (94·6%) followed by gastropods (4·3%), brachiopods (0·6%), and free-living serpulids (0·6%). The fossils are of medium diversity and abundance; the dominant ichnogenera comprise *Chondrites*, *Spongeliomorpha suevica* var. B, and *Planolites*. The over-all diversity is low (text-fig. 3). Semi-infaunal bivalves (41·8%) and cemented epifauna (46·3%; e.g. *Nanogyra*) are of nearly equal importance whilst the byssally attached epifauna (5·1%; e.g. *Chlamys*), epifaunal gastropods (2·3%; e.g. *Ampullina*), and infaunal gastropods (2·0%; *Pseudomelania*) are of lesser significance (text-fig. 16). Infaunal bivalves represented solely by *Isocyprina* and *Cucullaea* are very rare. No specimens are preserved in life position, but 27·1% are still bivalved. 7·4% of the fauna is encrusted by *Nanogyra* and *Pentaserpula*, bored specimens were not encountered. Fragmentation ranges from 50 to 75%. All specimens are preserved with their shell.

The *G. aviculoides* association occurs in Yorkshire and Oxfordshire and shows a substrate preference for oolites and impure limestones.

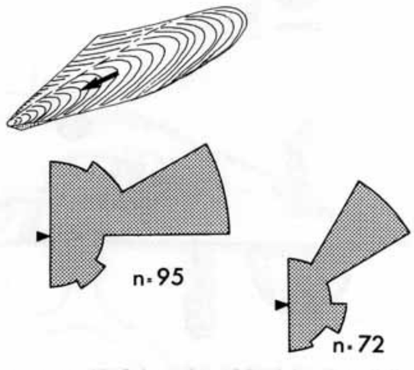
Discussion. Calcite preservation of the fauna and absence of any aragonitic burrowers point to a preservational bias of the association but as all aragonitic gastropods are preserved with their shell the absence of the burrowing bivalves seems to be genuine. Thus, the coarse substrate might have been unsuitable for burrowers. The three



TEXT-FIG. 18. Trophic nucleus and attempted reconstruction of the *Gervillella aviculoides* association (K). 1, *Nanogyra nana*; 2, *Gervillella aviculoides*; 3, *Chondrites* sp.; 4, *Spongeliomorpha suevica*; 5, *Planolites* sp.

collections represent different stages of reworking of an ancient *G. aviculoides* community, ranging from a sample from the Tabular Hills (Yorkshire) where nearly all *Gervillella* are preserved with both valves to a sample from Shellingford Cross Roads Quarry, Berkshire, where most specimens are one-valved and show current orientation (text-fig. 19). But even there, the transport involved must have been minimal as the Gervillella range from 3·5 to 15·0 cm in size and are well preserved. Thus, the *G. aviculoides* association can be regarded as the partially reworked authochthonous relic of an ancient community which seems to have thrived in a relatively high-energy environment.

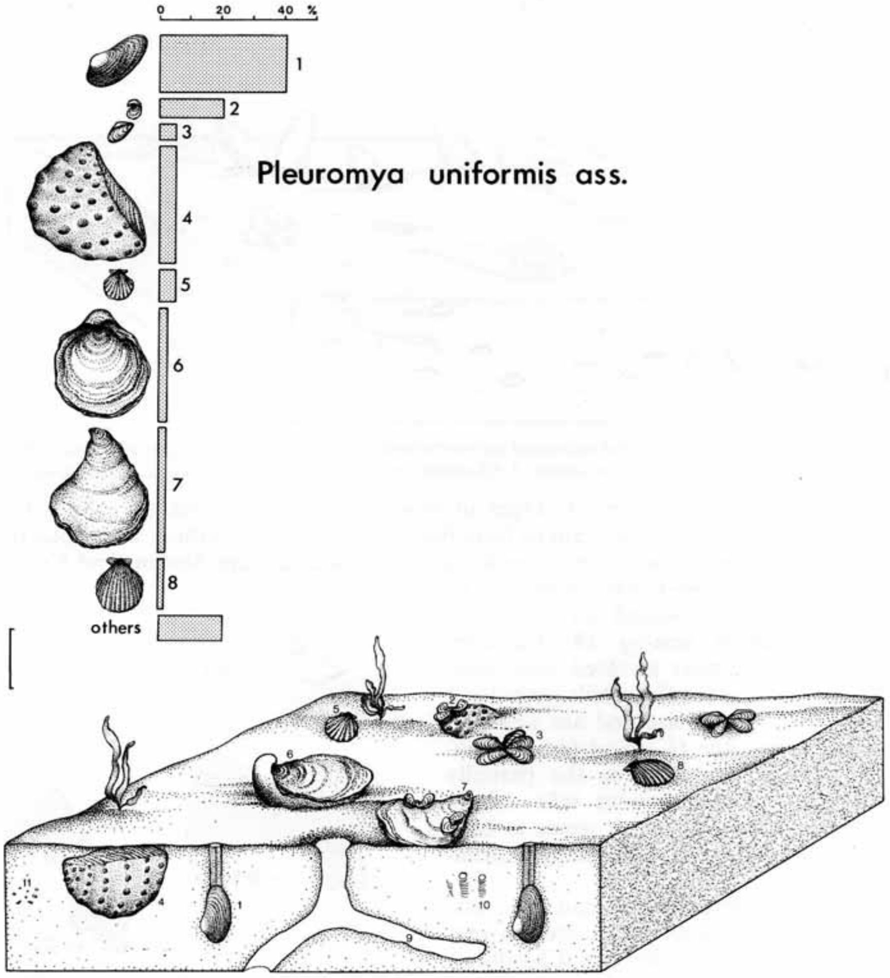
Three feeding levels can be distinguished: infaunal deposit-feeders represented by *Planolites* and *Chondrites*, low-level suspension-feeders (e.g. *Isocyprina*, *Nanogyra*), and medium-level suspension-feeders (*Gervillella*, large *Plagiostoma*).



TEXT-FIG. 19. Orientation of flat-lying *Gervillella aviculoides* in the *Gervillella aviculoides* association. Bedding planes of fallen blocks, Osmington Oolite Group, Shellingford Cross Roads Quarry, Berkshire.

L. *Pleuromya uniformis* association

Description. The *P. uniformis* association is with twenty-eight collections and 3272 specimens the commonest of the Corallian invertebrate associations, occurring predominantly in Dorset and, to a lesser extent, in Yorkshire. The trophic nucleus (text-fig. 20) consists of eight species of bivalves. *P. uniformis* occupies the first-rank position being followed by *N. nana*, *'Mytilus' varians*, *Myophorella clavellata*, *Chlamys*

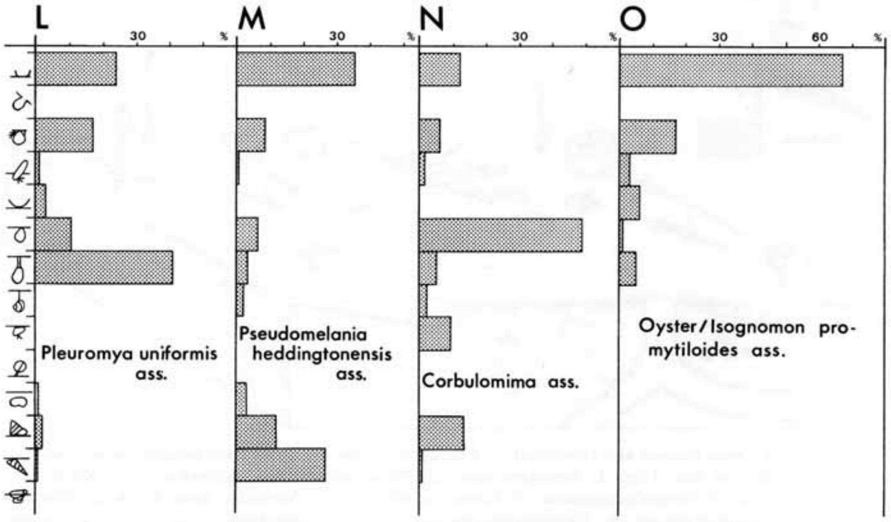


TEXT-FIG. 20. Trophic nucleus and attempted reconstruction of the *Pleuromya uniformis* association (L). Length of bar, 5 cm. 1, *Pleuromya uniformis*; 2, *Nanogyra nana*; 3, *'Mytilus' varians*; 4, *Myophorella clavellata*; 5, *Chlamys fibrosa*; 6, *Gryphaea dilatata*; 7, *Deltoideum delta*; 8, *Chlamys midas*; 9, *Spongeliomorpha suevica*; 10, *Teichichnus rectus*; 11, *Chondrites* sp.; benthic algae hypothetical.

fibrosa, *Gryphaea* (*B.*) *dilatata*, *Deltoideum delta* and *C.* (*R.*) *midas*. Two species, *P. uniformis* and '*M.*' *varians*, characterize the association reaching in it the peak of their distributions. As usual bivalves dominate the fauna with 96·1%; gastropods (2·6%), echinoderms (1·0%), brachiopods, serpulids, and sponges form the rest. The trace-fossil fauna is both very diverse and abundant; the more important members are *Spongeliomorpha suevica* var. B, *Chondrites*, *Teichichnus rectus*, and *Cylindrichnus concentricus*. The over-all diversity is very high (text-fig. 3). Epifauna and infauna are nearly equal in numbers (text-fig. 21), the semi-fauna represented by *Modiolus*, *Pinna*, and *Gervillella* being only of little importance (1·1%). Deep-burrowing bivalves like *Pleuromya* and *Pholadomya* (40·9%) dominate the infauna, shallow-burrowing bivalves like *Myophorella*, *Isocyprina*, and astartids account for 10·5% of the fauna; the rest is formed by the echinoid *Nucleolites*, the gastropod *Pseudomelania*, and some mucus-tube feeding bivalves (*Discomiltha*). In the epifauna, cemented bivalves (mainly *Nanogyra*) and byssally attached pectinids (*Chlamys*, *Camptonectes*) and *Isognomon* prevail. Less common are free-resting (*Gryphaea*) or swimming forms (*Entolium*) and some herbivorous or scavenging gastropods. Only 2·8% of the fauna occur in life position but 48·7% of the specimens are still preserved with both valves. The number of encrusted and bored specimens is fairly low. Epizoans are the foraminifera *Nubeculinella* and the bivalves *Nanogyra*, *Lopha*, '*Ostrea*', and *Placunopsis*. *Lithophaga inclusa* and phoronids account for the borings. Fragmentation ranges from 5% to more than 95% and is usually at one end of the scale. In two collections a preferred convex-up orientation of shells larger than 2 cm has been noted, the percentage of shells in an oblique position being relatively high. A large part (39·6%) of the fauna is preserved as steinkerns, mainly the burrowing bivalves *Pleuromya*, *Pholadomya*, and *Myophorella* as well as many gastropods (especially *Ampullina* and pleurotomariids). Only rarely do specimens show signs of wear or exhibit algal envelopes.

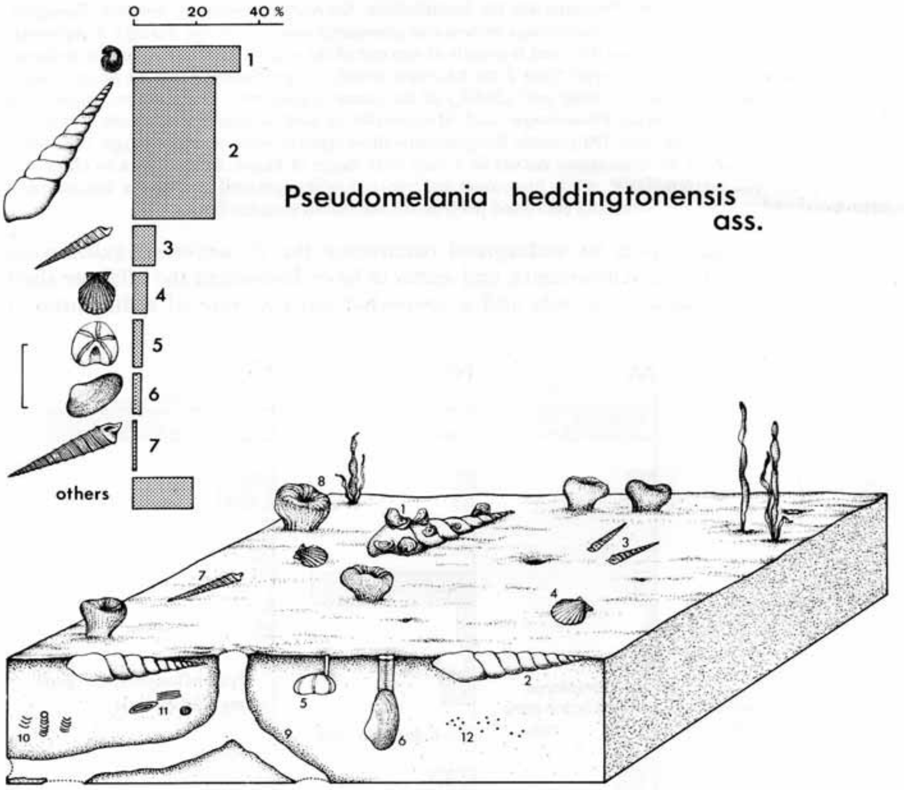
The *Pleuromya uniformis* association occurs in a very wide range of facies, from oolites to clays, but shows a preference for intraclastic, sandy limestones and fine- to medium-grained sandstones. Occasionally drift-wood and in one case bored and encrusted pebbles are associated with the fauna.

Discussion. Judging from its widespread occurrence the *P. uniformis* association thrived in a variety of environments, and seems to have dominated the offshore shelf regions where moderate currents and a somewhat reduced rate of sedimentation



TEXT-FIG. 21. Ecological composition of associations L–O. Legend in text-fig. 6.

favoured deep burrowing, as well as the even more rigorous shallow subtidal bar and nearshore environments. In some collections the composition of the fauna indicates a gradation into the condensed version of the *Myophorella* association, and the high density of the fauna, and shell beds which accumulated rather by non-deposition and only rarely by current action confirm this observation. Other collections represent a fairly true picture of the ancient *Pleuromya* community: *Pleuromya* and clusters of '*Mytilus*' *varians* (which most likely lived like the present-day *M. edulis*) in life position indicate that hardly any disturbance has taken place. In general the high percentage of bivalved specimens, the concentration of the fauna in small pockets, and the good preservation of most specimens demonstrate that transport played only a very subordinate role in the formation of the association. The low



TEXT-FIG. 22. Trophic nucleus and attempted reconstruction of the *Pseudomelania heddingtonensis* association (M). Length of bar, 4 cm. 1, *Nanogyra nana*; 2, *Pseudomelania heddingtonensis*; 3, *Nerinella* sp.; 4, *Chlamys fibrosa*; 5, *Nucleolites scutatus*; 6, *Pleuromya uniformis*; 7, *Nerinella cyane*; 8, sponge *Rhaxella* (hypothetical reconstruction); 9, *Spongeliomorpha suevica*; 10, *Teichichnus rectus*; 11, *Cylindrichnus concentricus*; 12, *Chondrites* sp.; benthic algae hypothetical.

percentage of specimens in life position and, at the same time, the high percentage of bivalved fauna is in many collections probably due to the very intensive bioturbation, especially of burrowing decapods.

Three or four trophic groups are represented in the association: deposit-feeders, suspension-feeders, herbivores (e.g. *Bathrotomaria*), and possibly, scavengers (*Ampullina*?). Two feeding levels can be recognized: infaunal deposit-feeders indicated by *Planolites*, *Cylindrichnus*, *Chondrites*, and *Teichichnus*, deposit-feeders at the depositional interface (the rare *Discomiltha*) and low-level suspension-feeders (e.g. *Pleuromya*, *Myophorella*, pectinids).

M. *Pseudomelania heddingtonensis* association

Description. The *P. heddingtonensis* association is, with sixteen collections and 2194 specimens, fairly common in the Corallian. The trophic nucleus consists of seven species (text-fig. 22). *N. nana* occupies the first rank position followed by two gastropod species, *P. heddingtonensis* and *Nerinella* sp. The pectinid *Chlamys* (*R.*) *fibrosa*, the echinoid *Nucleolites scutatus*, the bivalve *Pleuromya uniformis* and the gastropod *Nerinella cyane* form the rest. *Pseudomelania heddingtonensis* reaches in this association the peak of its distribution and thus forms its characteristic species. Bivalves account for only 56·6% of the fauna and gastropods (39·7%) are a very important faunal element. Echinoderms (3·5%), brachiopods (0·1%), and sponges (0·04%) are of lesser significance. Trace fossils are of a high diversity and only medium abundance. The dominant forms are *Spongeliomorpha suevica* var. B, *Chondrites* sp., *Teichichnus rectus*, and *Cylindrichnus concentricus*. The over-all diversity is high (text-fig. 3). Infauna and epifauna are of nearly equal importance, the semi-fauna being hardly represented (0·6%). Amongst the epifauna (text-fig. 21), cemented bivalves form the largest group (35·5%; mainly *Nanogyra*), followed by gastropods like *Nerinella*, *Bathrotomaria*, *Coelostylina*, *Procerithium*, and *Ampullina* (13·1%), and by byssally attached bivalves (8·4%; mainly pectinids and limids). The infauna is dominated by the gastropod *Pseudomelania*. The rest consists of deep-burrowing (e.g. *Anisocardia*, *Isocyprina*) bivalves as well as echinoids (*Nucleolites*, *Pygaster*). No elements of the fauna have been found in life position except cemented bivalves; 9% of the specimens are still preserved with both valves. *Nanogyra*, *Dorsoserpula*, and the foraminifera *Nubeculinella* encrust 6% of the fauna; 0·2% are bored by the bivalve *Lithophaga inclusa* and by polychaetes. Fragmentation ranges from 20 to 98% and is usually around 90%. The thin-shelled organisms are preferredly fragmented whilst the thick shells of, for instance, *Gervillella* and *Pseudomelania* have been less affected. In seven collections orientation of shells larger than 2 cm has been measured (Table 3). The overwhelming majority of the shells occurs convex-up and in four collections imbrication has been observed. 7·2% of the fauna occurs in steinkern preservation. Amongst them are many deep-burrowing bivalves, some shallow burrowers, and most gastropods except *Pseudomelania*. Occasionally shells exhibit algal envelopes, more rarely are they worn.

TABLE 3. Shell orientation in the *Pseudomelania heddingtonensis* association. Only shells with a diameter larger than 2 cm have been counted. The asterisk marks collections in which imbrication has been encountered.

Collection	Convex-up	Convex-down	Oblique
P II 1b	100	12	9
*TB II 10 top	100	20	23
TB II 10 base	100	29	19
*TB II 14	100	19	28
*TB II 17	100	40	30
*TB II 18	50	13	33

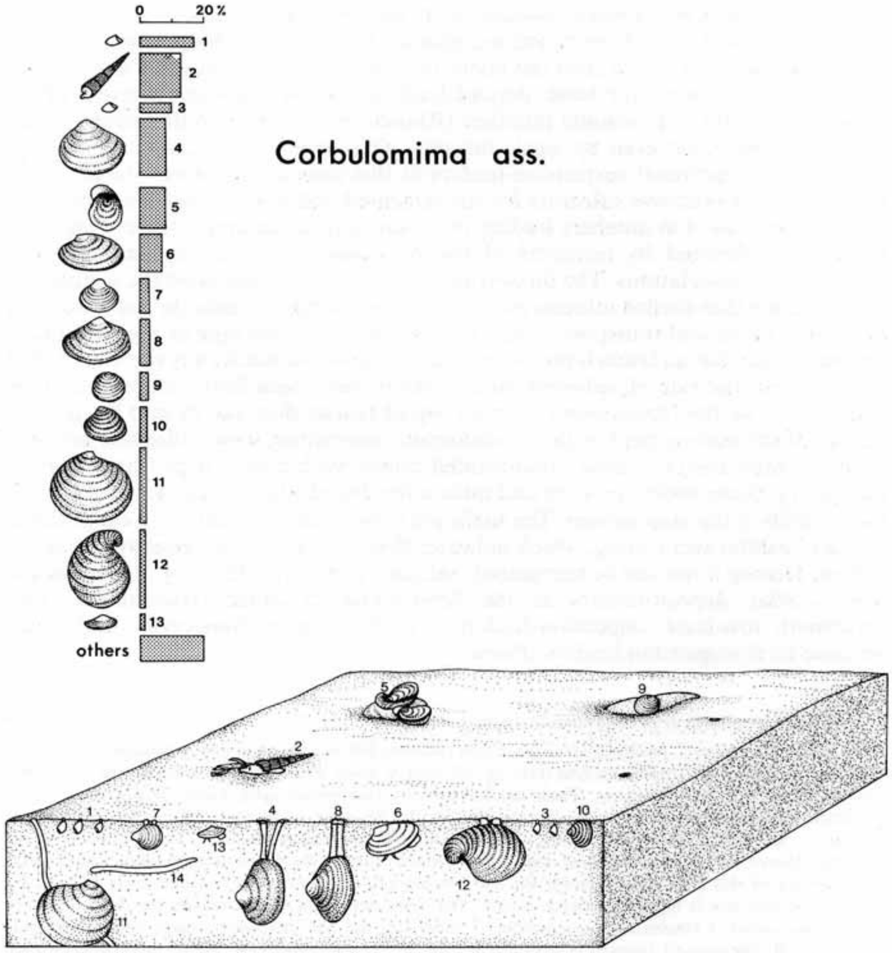
Discussion. The *P. heddingtonensis* association is widespread in the Malton Oolite of the Vale of Pickering, Yorkshire, but is also found in Normandy and Dorset.

Substrate, algal envelopes, low percentage of bivalved specimens, high fragmentation rate, convex-up orientation, and imbrication of shells testify a high-energy environment for most samples. Lateral transport must have played a role, so that sorting of the fauna certainly took place. Nevertheless a large-scale lateral transport can be excluded, as in some samples *Pseudomelania* are preserved with their calcareous operculum still in place. As many of the oolites are micritic and alternate with thin bands of marly oolite, stable, less rigorous conditions must have prevailed at times which enabled the colonization of the substrate. With return of the high-energy regime, the fauna was then frequently washed out and redeposited under current action. The existence of an ancient *Pseudomelania* community is further supported by a few samples from Dorset where a finer-grained sediment (probably stabilized by the sponge *Rhaxella* whose spicules occur abundantly in the substrate) and a higher percentage of bivalved specimens, together with a low fragmentation rate (20%), indicate a low-energy environment with only little disturbance of the fauna. Thin-shelled burrowing bivalves (*Pholadomya*, *Pleuromya*) are quite common in these samples and indicate that in the collections from the oolites these shells were eliminated during reworking. The reconstruction of the life habits of fossil gastropods is conjectural. The pleurotomariids *Bathrotomaria*, *Obornella*, and *Pleurotomaria* might have been herbivores. Vogel (1968) argued that nerineids belonged to the liberosessile epifauna due to their heavy shell and the manner in which a rudist encrusted the shell of one species. *Nerinella* and other nerineids are usually found in high-energy environments often in association with reefs (e.g. Janicke 1970; see also association Q) which strengthens Vogel's argument. *Ampullina* probably belonged to the epifauna as well feeding on algae or plant detritus, scavenging or even predating. The high-spired, thick-shelled *Pseudomelania* in turn could well have lived as a very shallow burrower feeding by ciliary activity, whilst the species of *Procerithium* present was probably a deposit-feeder. The large number and diversity of gastropods in the *Pseudomelania* association accounts for the large number of trophic groups present: deposit-feeders, suspension-feeders, herbivores (*Bathrotomaria*), and possibly scavengers (*Ampullina*?). Two feeding levels can be distinguished: infaunal deposit-feeders represented by *Nucleolites*, *Teichichnus*, *Cylindrichnus*, *Planolites*, and *Chondrites*, and low-level suspension-feeders (e.g. *Pseudomelania*, *Pleuromya*).

N. *Corbulomima* association

Description. Five collections with 836 specimens constitute the *Corbulomima* association. The very diverse trophic nucleus (text-fig. 23) contains thirteen species starting with *Corbulomima* sp. A, *Procerithium* (*R.*) *struckmanni*, *C. suprajurensis*, *Tancredia subplanata*, *Nanogyra nana*, and *Palaeonucula menkii*. The remaining seven species (*Protocardia dyonisea*, *Thracia depressa*, *Placunopsis duriuscula*, *Trautscholdia extensa*, *Discomiltha rotundata*, *Cercomyopsis striata*, and *Mesosacella* sp.) are of lesser significance (altogether 15·2% of the fauna). Four bivalve species are characteristic of this association, namely *Corbulomima* sp. A, *C. suprajurensis*, *Tancredia subplanata*, and *Palaeonucula menkii*, and one gastropod, *Procerithium struckmanni*. Bivalves (84·7%) and gastropods (14·1%) dominate the association; brachiopods (0·6%), echinoderms (0·4%), and decapods (0·2%) making up the remainder. Trace fossils are present in two of the five collections and consist of *Chondrites* sp., *Planolites* sp., *Teichichnus rectus*, and *Spongeliomorpha suevica* var. B. Abundance and diversity of the traces are both medium. The over-all diversity of the benthos is medium (text-fig. 3).

Some pectinids, arcids, free-swinging *Pteroperna*, and *Procerithium* compose the epifauna (31·9%, text-fig. 21); the association is dominated by the infauna (66·5%), semi-infaunal bivalves (*Pinna*) being fairly insignificant (1·6%). The diverse infauna is represented by shallow-burrowing suspension-feeders (48·8%) like *Corbulomima*, *Tancredia*, and astartids, deposit-feeding bivalves (9·6%; *Mecosacella*, *Palaeonucula*), and less commonly by deep-burrowing suspension-feeders (e.g. *Pleuromya*, *Cercomya*), deposit-feeding gastropods (*Dicroloma*), mucus-tube feeders (*Discomiltha*), echinoids (*Nucleolites*), or brachiopods (e.g. *Lingula*). No specimens occur in life position and only 6·3% are still bivalved. Encrusted and bored



TEXT-FIG. 23. Trophic nucleus and attempted reconstruction of the *Corbulomima* association (N). 1, *Corbulomima* sp. A; 2, *Procerithium struckmanni*; 3, *Corbulomima suprajurensis*; 4, *Tancredia subplanata*; 5, *Nanogyra nana*; 6, *Palaeonucula menkii*; 7, *Protocardia dyonisea*; 8, *Thracia depressa*; 9, *Placunopsis duriuscula*; 10, *Trautscholdia extensa*; 11, *Discomiltha rotundata*; 12, *Ceratomyopsis striata*; 13, *Mesosacella* sp.; 14, *Planolites* sp.

specimens are rare (0·6% and 1·1% respectively); the borers are represented by phoronids and another, unknown organism; the epizoans by *Placunopsis*, *Nanogyra*, and *Serpula*. Fragmentation varies between 50 and 95% and is usually around 80%. Part of the infauna, especially *Corbulomima*, *Pleuromya*, and *Discomiltha*, as well as some gastropods (*Procerithium*) are preserved as steinkerns.

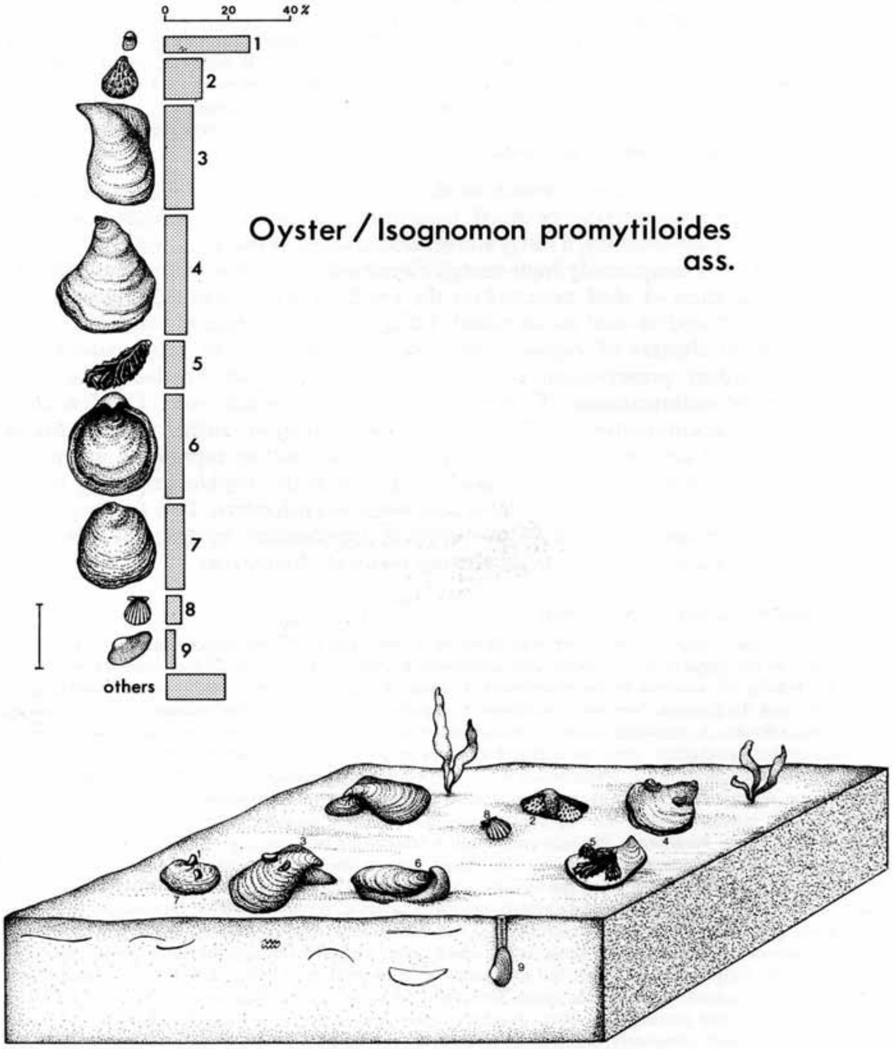
The *Corbulomima* association occurs in a narrow facies range, i.e. in clays, silts, and fine-grained sandstones. One collection, however, was recovered from oolites.

Discussion. The *Corbulomima* association is the only association in the Corallian where infaunal deposit-feeders are significant. This trophic group favours a fine-grained substrate which is also the facies in which they occur in the Corallian. By churning the sediment for food, deposit-feeders increase the water content of the sediment near the depositional interface (Rhoads 1970) and such thixotropic muds are easily suspended even by weak currents. This may be the reason for the low percentage of epifaunal suspension-feeders in this association. Where larger shells provided more extensive substrate for the cemented and byssally attached epifauna, the latter increased in numbers leading to a change in community: these shell pavements are colonized by members of the *N. nana*/*Chlamys* or oyster/*Isognomon promytiloides* associations. The thixotropic muds probably facilitated the winnowing of the mainly thin-shelled infauna even by relatively weak currents. *In situ* reworking or small-scale lateral transport is indicated by the low percentage of bivalved fauna and by the fact that no fauna is preserved in life position. As hardly any shells are bored or encrusted, the rate of sedimentation seems to have been fairly continuous. One collection from the Osmington Oolite Group of Dorset does not fit into the general picture of the environment of the *Corbulomima* association. This collection has been found in high-energy, planar cross-bedded oolites with a very high fragmentation rate (95%). Some shells are worn and quite a few bored (this sample accounts for all bored shells of the association). The shells are found in a lumachelle 2–3 cm in thickness and exhibit size sorting, which indicates that they have undergone transport.

Four feeding levels can be recognized: infaunal deposit-feeders (e.g. *Palaeonucula*, *Mesosacella*), deposit-feeders at the depositional interface (*Discomiltha*, *Procerithium*), low-level suspension-feeders (e.g. *Pleuromya*, *Nanogyra*), and intermediate-level suspension-feeders (*Pinna*).

O. Oyster/*Isognomon promytiloides* association

Description. The oyster/*I. promytiloides* association contains 459 specimens in nine collections. Cemented epifauna dominates the trophic nucleus (text-fig. 24) with *N. nana*, *Plicatula weymouthiana*, and *I. promytiloides* on the first-rank positions. These are followed by *Deltoideum delta*, *Lopha gregarea*, *Gryphaea* (*B.*) *dilatata*, '*Ostrea*' sp., *Chlamys* (*R.*) *fibrosa*, and, finally, *Pleuromya uniformis*. Other cemented bivalves include *L. solitaria*, *Placunopsis radiata*, *P. duriuscula*, '*Ostrea*' *quadrangularis*, and *Praeexogyra* sp. *D. delta*, '*Ostrea*' sp., *P. weymouthiana*, and *I. promytiloides* reach their distribution maxima and are thus characteristic of this association. Except for one brachiopod, the association consists solely of bivalves. Trace-fossil diversity is high, abundance is low. The more important forms include the deposit-feeders *Teichichnus rectus*, *Cylindrichnus concentricus*, *Chondrites*, and the crustacean-made *Spongeliomorpha suevica* var. B. The over-all diversity is medium (text-fig. 3). The epifauna (90·4%) dominates the ecological spectrum and is represented by cemented forms (67·1%; see trophic nucleus), byssally attached bivalves (17·0%), and free-living species (e.g. *Gryphaea*; 6·1%). Semi-infaunal bivalves (*Modiolus*, *Gervillella*) are of lesser significance (3·0%) as are deep burrowers (5·0%; e.g. *Pleuromya*, *Pholadomya*). The remaining ecological groups are rare or missing (text-fig. 21). Only 1·3% of the fauna is in life position but 15·03% of the bivalves are preserved with both valves (mainly *Pleuromya*, *Isognomon*, and *Plicatula*). 26·8% of



TEXT-FIG. 24. Trophic nucleus and attempted reconstruction of the Oyster/*Isognomon promytiloides* association (O). Length of bar, 6 cm. 1, *Nanogyra nana*; 2, *Plicatula weymouthiana*; 3, *Isognomon promytiloides*; 4, *Deltoideum delta*; 5, *Lopha gregarea*; 6, *Gryphaea dilatata*; 7, '*Ostrea*' sp.; 8, *Chlamys fibrosa*; 9, *Pleuromya uniformis*; benthic algae hypothetical.

the fauna are encrusted by a diverse fauna of epizoans such as *L. gregarea*, *L. solitaria*, *Nanogyra*, *Plicatula*, *Placunopsis*, the foraminifera *Nubeculinella*, various serpulids (*Dorso-*, *Cyclo-*, and *Pentaserpula*) as well as the bryozoans *Berenicea* and *Stomatopora*. Phoronids, *Lithophaga inclusa*, and cirripedes bored 9·8% of the fauna. The percentage of fragmentation is high, i.e. between 80 and 98%. Most burrowing species are preserved as steinkerns, the rest with their shell. In some collections part of the epifauna, especially oysters and *Isognomon*, is very worn and intensively bored and encrusted.

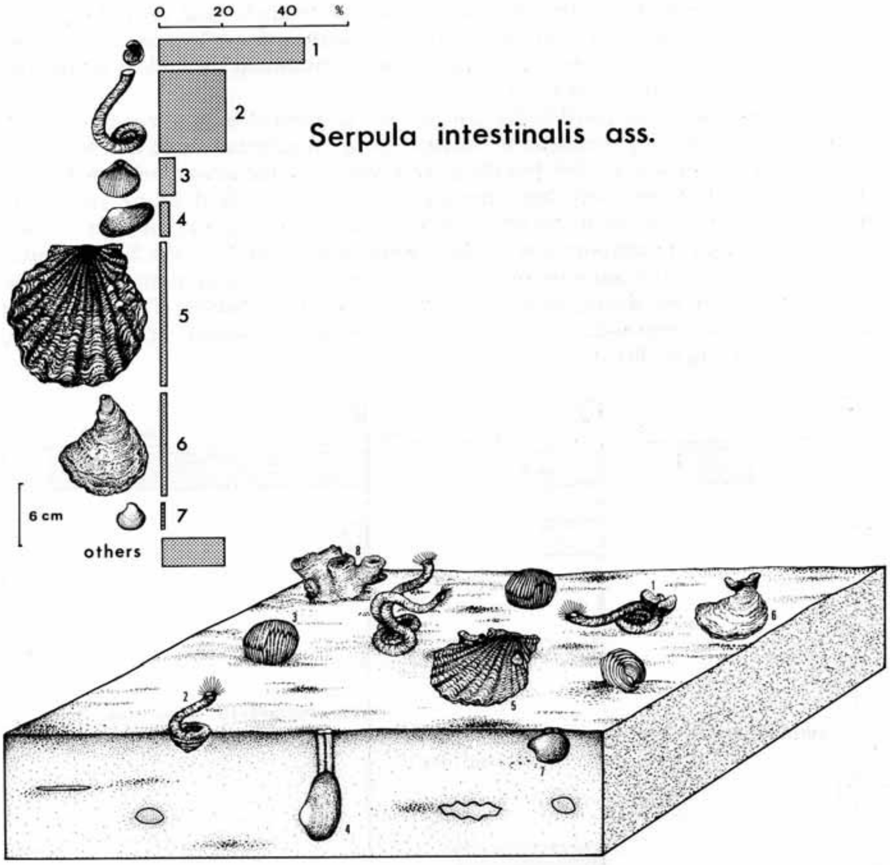
The oyster/*I. promytiloides* association exhibits a clear substrate and facies preference occurring mainly in Fe-oolitic argillaceous limestones and marls.

Discussion. The environment in which most of the oyster/*I. promytiloides* association accumulated was similar to that of the *M. bipartitus*/*P. alduini* and *L. gregarea* associations, i.e. slow sedimentation, a fairly stable, fine-grained substrate, occasional influx of Fe-ooliths, and temporarily high-energy conditions. The slow sedimentation rate led to accumulation of shell material on the sea floor which was often intensively encrusted and bored as well as corroded. Large '*Ostrea*' commonly served as substrate for small clusters of *Lopha*, *Nanogyra*, and *Plicatula*. In some collections, however, excellent preservation of the epifauna, often still bivalved, indicates relatively rapid sedimentation. Transport played only a minor role. The few shell layers present accumulated *in situ* due to non-deposition, rather than through current action. Thus the oyster/*I. promytiloides* association represents again the remnant of an ancient community. An inhomogeneous trophic grouping is the result of the presence of deposit-feeders and suspension-feeders. Two feeding levels could be recognized: infaunal deposit-feeders represented by trace fossils, and low-level suspension-feeders (e.g. burrowing bivalves, *Nanogyra*).

P. *Serpula intestinalis* association

Description. Four collections with 638 specimens have been grouped into this association which was found only in the uppermost Corallian and lowermost Kimmeridgian of the Dorset coast. The trophic nucleus (text-fig. 25) consists of the ubiquitous *N. nana*, *S. intestinalis*, the brachiopod *Torquirhynchia inconstans*, and the bivalves *Pleuromya uniformis*, *Ctenostreon proboscideum*, *Deltoideum delta*, and *Anisocardia isocardioides*. *S. intestinalis* and *C. proboscideum* only rarely occur elsewhere and *T. inconstans* is confined to this association; these three therefore serve as its characteristic species. Bivalves form 69·6% of the fauna, gastropods 4·5%, brachiopods 4·7%, and free-living serpulids 21·2%. No trace fossils occur except some indistinct tubes most likely left by deposit-feeders. The over-all diversity is medium (text-fig. 3). Semi-infaunal bivalves (1·6%) are represented by *Modiolus*, the infauna (12·4%) by deep-burrowing bivalves (*Goniomya*, *Pleuromya*, *Pholadomya*), shallow-burrowing bivalves (e.g. *Anisocardia*, *Protocardia*, *Isocyprina*), and some gastropods (text-fig. 26). Most species (86·0%) belong to the epifauna. They are either cemented bivalves (48·4%; e.g. the oysters *Nanogyra*, *Deltoideum*), byssally attached bivalves (6·7%; e.g. *Isognomon*, *Chlamys*), free-resting animals like the bivalves *C. proboscideum*, *S. intestinalis*, and some gastropods (e.g. *Bathrotomaria*, *Pleurotomaria*). Another faunal element are small colonies of corals, mainly *Thecosmilia annularis* and *Thamnasteria* which occur scattered throughout the samples, especially those from the Ringstead Coral Bed. No specimens of the uncemented fauna occur in life position, but 23·6% are still bivalved. 13·5% of the fauna have been encrusted by the foraminifera *Nubeculinella*, the bivalve *Nanogyra*, and the serpulids *Dorsoserpula*, *Cycloserpula*, and *Pentaserpula*. In addition, specimens of *S. intestinalis* were commonly found to be infested by the hydroid *Protulophila gestroi*. (For detailed discussion of this commensalism see Scrutton 1975). 10·5% of the shells are bored by the bivalve *Lithophaga inclusa*, cirripedes, polychaetes, phoronids, and some unknown organisms. The degree of fragmentation is fairly low and varies between 10 and 50%. Altogether, 15·7% of the fauna are preserved as steinkerns, mainly the infaunal bivalves as well as gastropods and the rare ammonites.

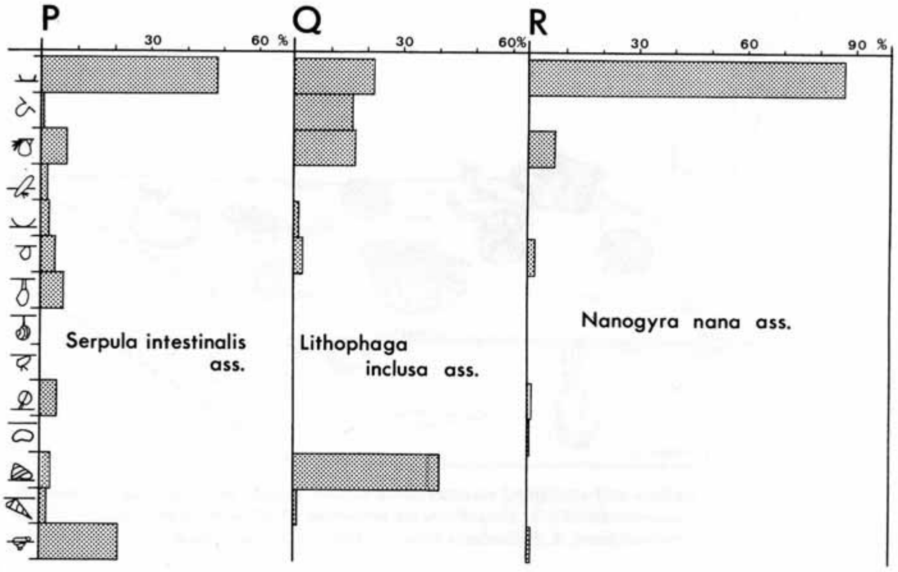
The *S. intestinalis* association exhibits a clear preference for clay with a varying amount of Fe-hydroxide ooliths. In two samples from the basal Kimmeridgian, reworked phosphate pebbles and phosphate steinkerns, partly encrusted with *Nanogyra*, are common.



TEXT-FIG. 25. Trophic nucleus and attempted reconstruction of the *Serpula intestinalis* association (P). 1, *Nanogyra nana*; 2, *Serpula intestinalis*; 3, *Torquirhynchia inconstans*; 4, *Pleuromya uniformis*; 5, *Ctenostreon proboscideum*; 6, *Deltoideum delta*; 7, *Anisocardia isocardioides*.

Discussion. The *S. intestinalis* association is tied to a specific environment in which non-deposition and reworking played a certain role. Two collections come from the uppermost Corallian, the Ringstead Coral Bed, the other two from the basal Kimmeridgian, the *Torquirhynchia* Bed. Although Brookfield (1973*b*) maintains that *Torquirhynchia* occurs only in the basal Kimmeridgian, it has also been found occasionally in the Ringstead Coral Bed. Corals are only found in the latter. They never formed reef-like structures but small isolated colonies growing on a consolidated substrate. In the lower Kimmeridgian, clay was deposited at a very slow rate with occasional influx of Fe-ooliths which are distributed in the form of small seams in the sediment. Encrusted pebbles and steinkerns indicate that reworking took place. The same association is present in both uppermost Corallian and lowermost Kimmeridgian which indicates that no change in environment took place across the stage boundary (see also Talbot 1973).

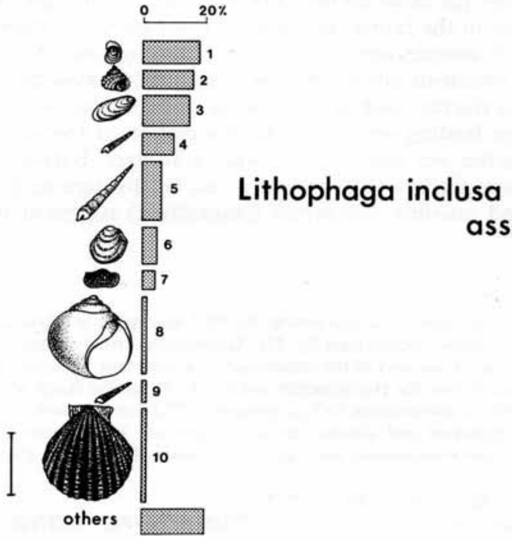
S. intestinalis seems adapted to have lived on fine-grained substrate (text-fig. 25). The asymmetry of *Torquirhynchia* is thought to be an adaptation to life in a tidal environment (Brookfield 1973*b*), but there are doubts as to the validity of Brookfield's interpretation. The relatively high percentage of still bivalved fauna (not only burrowers but also epifaunal species!) suggests that reworking was only on a small scale and that lateral transport was of little significance. Therefore, the *S. intestinalis* association, too, is the autochthonous relic of an ancient community. Only one feeding level can be distinguished: low-level suspension-feeders (*S. intestinalis* burrowing fauna, pectinids). *Bathrotomaria* represent a second trophic group, probably browsing herbivores.



TEXT-FIG. 26. Ecological composition of associations P–R. Legend in text-fig. 6.

Q. *Lithophaga inclusa* association

Description. Represented by 1421 specimens in fifteen collections the *L. inclusa* association has been found in Yorkshire, Oxfordshire, and Normandy. Ten species form the trophic nucleus (text-fig. 27) in which *N. nana* takes the first place followed by *Metriomphalus muricatulus, L. inclusa, Procerithium* sp. 1, *Nerinella* sp., *Plagiostoma zonatum*, and *Barbatia* (*Acar*) sp. The remaining three species are *Procerithium* sp. 2, *Ampullina* sp., and *Chlamys* (*Chl.*) *nattheimensis*. *L. inclusa, M. muricatulus*, and *Procerithium* sp. 1 reach in this association the peak of their distribution and are thus characteristic of it. Bivalves (57·8%) and gastropods (14·9%) dominate the fauna; brachiopods and echinoids are very rare except for abundant spines of *Plegiocidaris florigemma*. The only trace fossil found, and that only in one collection, is *Chondrites*. The over-all diversity is high (text-fig. 3). The majority (79·4%) of the specimens belong to the epifauna, the rest is infauna as semi-infaunal organisms are very rare (text-fig. 26). The epifauna is shared by cemented bivalves (21·8%; mainly *Nanogyra*), byssally attached bivalves (16·5%; e.g. *Plagiostoma, Barbatia, Chlamys*), and free-living gastropods (38·5%; e.g. *Metriomphalus, Procerithium*). Corals, also members of the epifauna, are very common but have not been included in the statistics. The commonest forms include *Montlivaltia* sp., *Thamnasteria concinna*, *Thecosmilia annularis*, *Isastrea explanata*, and *Rhabdophyllia phillipsi*. The infauna (20·4%) is dominated by the rock-boring bivalve *Lithophaga*. Deep- and shallow-burrowing bivalves are of only little significance. 19·8% of the uncemented fauna is in life position, mainly *Lithophaga*, and 29·9% of the organisms are still bivalved (again mainly *Lithophaga*). Only 1% of the fauna excluding corals are encrusted by the foraminifera *Nubeculinella*, the bivalves *Nanogyra* and *Plicatula*, two species of *Serpula* (*Dorsoserpula, Cycloserpula*), and the bryzoans *Berenicea* and *Stomatopora*. 0·9% are bored by polychaetes, phoronids, and *Lithophaga*. Fragmentation is usually fairly high, between 75 and 98%. Nearly half the fauna (47·2%) is preserved as steinkerns or moulds, mainly gastropods, arcids, and some burrowing bivalves.



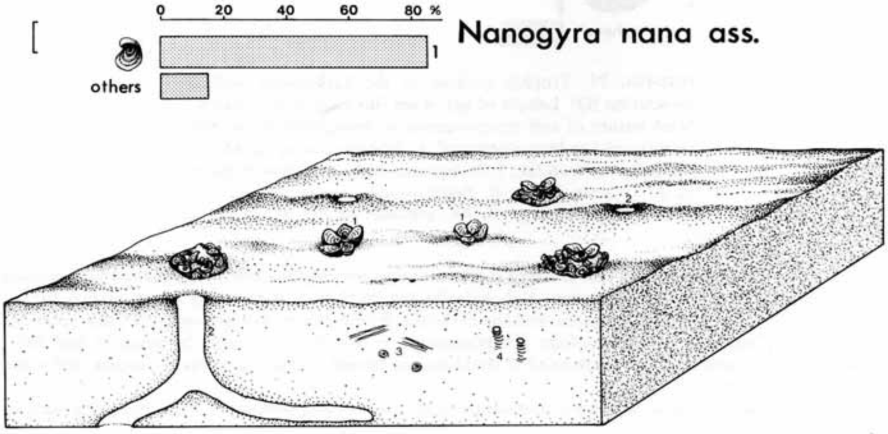
TEXT-FIG. 27. Trophic nucleus of the *Lithophaga inclusa* association (Q). Length of bar, 4 cm. Because of the complicated nature of reef environments no reconstruction of the association has been attempted. 1, *Nanogyra nana*; 2, *Metriomphalus muricatulus*; 3, *Lithophaga inclusa*; 4, *Procerithium* sp. 1; 5, *Nerinella* sp.; 6, *Plagiostoma zonatum*; 7, *Barbatia* sp.; 8, *Ampullina* sp.; 9, *Procerithium* sp. 2; 10, *Chlamys nattheimensis*.

The *L. inclusa* association occurs predominantly in biomicrites and biosparites thus showing a marked substrate preference.

Discussion. As the reef environment in the Corallian will be the subject of a more detailed later study, the discussion here is fairly short. The *L. inclusa* association has been found in three reefal environments: (*a*) in the reef itself, (*b*) in small pockets of lime mud within the reef, and (*c*) in the reef talus. Autochthonous in the first two environments, it also occurs in form of parautochthonous faunal elements in (*c*), there usually partly fragmented and worn (e.g. Wheatley Limestone of Oxfordshire and Berkshire). The Corallian reefs, only small structures at the most 6 m thick but usually far less, have been described in detail already by Arkell (1928, 1935) who compared them with Recent reefs in the Red Sea. Arkell also recognized a typical reef fauna which is more or less equivalent to the reef association described here. A reef provides far more niches than the usually fairly uniform sea floor and this is also reflected in the fauna. Herewith a few examples: *Barbatia* (*Acar*) dwelt as a byssate nestler in crevices amongst corals; *Lithophaga* and the numerous epizoans found extensive substrate on corals, burrowers like *Protocardia* lived in small pockets of lime mud within the reef and *Metriomphalus muricatulus* as well as *Procerithium* sp. 1 were browsers feeding on algae. The description of feeding levels in a reef is a very complex matter but low-level suspension-feeders (burrowing bivalves), and high-level suspension-feeders (e.g. corals) could be distinguished. Herbivores (e.g. *Metriomphalus*) and possibly scavengers (*Ampullina*?) represent two more trophic groups.

R. *Nanogyra nana* association

Description. The *N. nana* association is represented by 3037 specimens in fifteen collections. *N. nana* is the only member of the trophic nucleus (text-fig. 28). Although occurring in nearly all other associations as well, often even as a significant part of the community, it is here that *Nanogyra* reaches the peak of its distribution (85·3%) and is thus the characteristic species. 97·0% of the fauna are bivalves; gastropods (0·5%), brachiopods (0·8%), echinoderms (0·7%), sponges (0·2%), and serpulids (0·7%) forming the rest. Trace fossils are very abundant and diverse, the most important ichnospecies being *Spongeliomorpha suevica* var. B, *Cylindrichnus concentricus*, and *Teichichnus rectus*. The over-all diversity is medium (text-



TEXT-FIG. 28. Trophic nucleus and attempted reconstruction of the *Nanogyra nana* association (R). Length of bar, 1 cm. 1, *Nanogyra nana*; 2, *Spongeliomorpha suevica*; 3, *Cylindrichnus concentricus*; 4, *Teichichnus rectus*.

fig. 3). Epifaunal cemented bivalves (*Nanogyra* and some other oysters) account for most of the fauna (86·8%) and the only other important group are epifaunal byssally attached bivalves (7·2%; e.g. various species of *Chlamys*). The remaining ecological groups are fairly insignificant, e.g. the infauna totals 3·4% (text-fig. 26). Only 2·9% of the fauna are preserved with both valves, and of the uncemented fauna, only 0·2% are in life position (some deep-burrowing *Pleuromya*). Encrusted are 4·7% of the fauna by one or more of the following epizoans: the oysters *Nanogyra*, *Lopha gregarea*, the serpulids *Cycloserpula*, *Pentaserpula*, *Tetraserpula*, and *Dorsoserpula*, the foraminifera *Nubeculinella*, and thecideacean brachiopods. Only two specimens are bored by the bivalve *Lithophaga inclusa* and cirripedes. Nearly all faunal elements are preserved with their shell except some aragonitic forms (some gastropods and thin-shelled burrowing bivalves). In bioclastic limestones specimens are not infrequently coated with algal envelopes; more rarely specimens are worn.

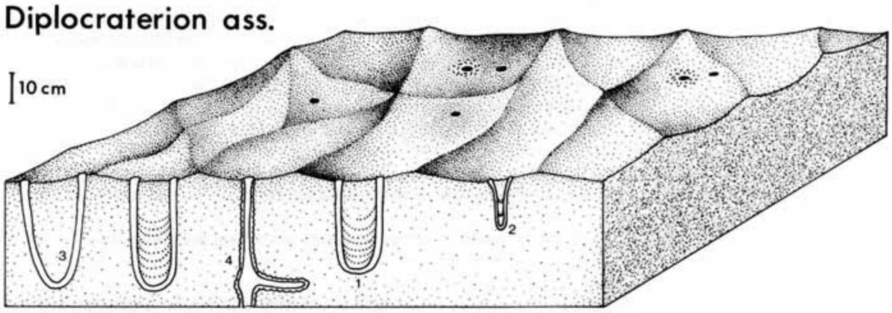
The *Nanogyra nana* association exhibits a medium substrate range occurring predominantly in sandstones and impure limestones occasionally with shell beds.

Discussion. The *Lopha gregarea* association (J) has a similar ecological composition to the *N. nana* association (text-figs. 16, 26), but there *L. gregarea* replaces *Nanogyra* as the dominant species. *Nanogyra* must have been adapted to live in a wide range of environments provided that suitable substrate (e.g. shell material) was present. It was probably an opportunistic species, which took over when other species of the same ecological niche (e.g. *Lopha*) could no longer compete, due to unfavourable conditions. An unstable environment is indicated by the low diversity. Which factor was responsible for the eurytopic behaviour is not clear. Settling behaviour of the larvae most likely played an important role. The *N. nana* association probably thrived in a fairly high-energy environment, indicated by the shell beds, specimens with algal envelopes, and coarse sediment. Small-scale transport was probably a frequent event and most collections are the parautochthonous relic of the ancient community. In some cases, however, *Nanogyra* seems to have been embedded more or less in life position, i.e. forming small clusters on an otherwise fairly barren sea floor.

More than 99% of the fauna are suspension-feeders, solely a few *Discomiltha*, *Procerithium*, and trace fossils represent deposit-feeders. Two feeding levels can be recognized: infaunal deposit-feeders (trace fossils) and low-level suspension-feeders (e.g. *Pleuromya*, *Anisocardia*). Some (?)herbivorous gastropods (*Bathrotomaria*) account for a third trophic group.

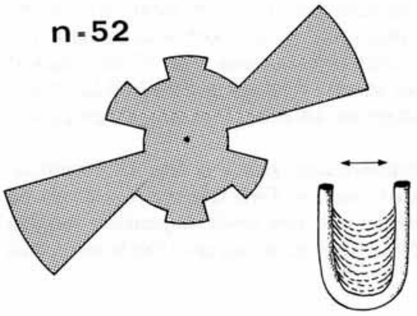
S. *Diplocraterion* association

Discussion. Fürsich (1975) recognized three trace-fossil associations in the Corallian. Two of them, the *Teichichnus* and the *Rhizocorallium* associations, occur together with associations of the body fauna, the third, however, the *Diplocraterion* association, is not found with any of the associations described under A to R. The *Diplocraterion* association (text-fig. 29) has been found in eleven samples from Oxfordshire, Dorset, and Normandy. It is characterized by burrows of suspension-feeding crustaceans and 'worms', i.e. *D. parallelum*, *D. habichi*, *Spongeliomorpha nodosa*, *S. saxonica*, and *Arenicolites variabilis*. Associated with them are *Planolites* sp., and less commonly *S. suevica* var. A and var. B, *Chondrites* sp., and *Cylindrichnus concentricus*. Most of the burrows are deep, and in the case of *D. parallelum* frequently show adjustment to either erosion or sedimentation by vertical shifting of the burrow. Orientation of burrows is encountered occasionally (text-fig. 30). The sediments



TEXT-FIG. 29. Attempted reconstruction of the *Diplocraterion* association (S). 1, *Diplocraterion parallelum*; 2, *Diplocraterion habichi*; 3, *Arenicolites variabilis*; 4, *Spongeliomorpha nodosa/ saxonica.*

in which the burrows occur are predominantly fine- to medium-grained well-sorted sands and oolites. Sedimentary features are commonly associated with the trace fossils, notably oscillation ripples, large-scale planar or trough cross-bedding as well as herringbone cross-bedding and flaser bedding. The *Diplocraterion* association occupied a high-energy environment such as very shallow subtidal or intertidal areas (Fürsich 1975). This environment must have been too rigorous for most of the bivalves and gastropods which dominate the remaining Corallian associations. In addition, removal of the body fauna by transport or breakage by frequent reworking could account for the non-preservation of any shells. The harsh environment allowed only animals to flourish which could adjust well to the unstable substrate, i.e. deep and rapid burrowers. Many niches occupied in the other associations are therefore here vacant due to the environmental stress.



TEXT-FIG. 30. Orientation of *Diplocraterion parallelum*. Fallen block from the Bencliff Grit, Berkshire Oolite Group, Bowleaze Cove, Dorset.

Disturbed assemblages

Only four of the 170 samples collected in the Corallian could not be grouped with any of the above associations. Their usually fairly large trophic nucleus either contains important faunal elements of *several* associations or else indicates selective removal or accumulation of certain elements from *one* association. In both cases, the structure and composition of the original community are distorted. There are two agents which cause disturbed assemblages: (*a*) currents which cause mixing and/or impoverishment of communities by transportation; (*b*) reduced sedimentation which causes mixing by superimposition of several communities, that is condensation. Both cases are represented, although one or the other assemblage might have been created by a combination of the two agents.

In Table 4 some characteristic features of the four collections are given. When comparing them, sample BH4 from the Osmington Oolite Group at Black Head, Dorset Coast, differs in having the highest fragmentation rate, no bivalved specimens and a different trace fossil suit (suspension-feeders); sedimentary structures are preserved and indicate a high-energy environment. Clearly, this sample is the result of transport especially as the shells form a thin lumachelle in the otherwise unfossiliferous oolite. Sample SPB from the Shell cum Pebble Bed of Beckley, Oxfordshire, in turn, is a typical example of mixing caused mainly by condensation as the low fragmentation rate and the high percentage of still bivalved and encrusted specimens indicate. The remaining two samples occupy an intermediate position and probably both, reduced sedimentation and transport by currents, played a role in their formation. Recognition of disturbed assemblages is of prime importance for environmental interpretation as well as to avoid making mistakes in reconstructing ancient communities and their structure.

TABLE 4. Some characteristics of mixed assemblages.

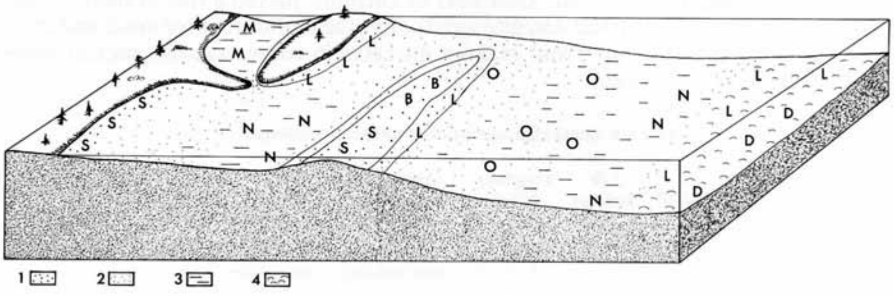
Collection	n_s	Bi-valved %	Life position %	Fragmentation %	Associated sedimentary structures	Trace fossils	Encrusted %	Origin by
BH 4	9	0	0	95	Large-scale planar cross-bedding	*Skolithos*, *Arenicolites*	9·90	Transport
BH 31	6	7·47	0	70	None	*Chondrites* *Planolites*	9·04	Transport and condensation
BH 25	13	11·64	0	90	None	*Chondrites*, *Planolites*	9·84	
SPB	10	20·20	0	50	None	*Planolites*	27·77	Condensation

n_s = number of species in the trophic nucleus.

ENVIRONMENTAL DISTRIBUTION OF CORALLIAN BENTHIC ASSOCIATIONS

The value of the associations as environmental indicators and their relationship to various facies types has been discussed elsewhere (Fürsich 1976*b*) so that only a summary is presented here. When the distribution of the associations was plotted against the sections of the Normandy and Dorset Corallian no cyclic sequence (representing transgressive and regressive phases) could be observed, in contrast to the sedimentary and trace-fossil evidence (Talbot 1973; Fürsich 1976*b*). Thus it seems that within shallow-water deposits of only moderate variations in depth the benthic fauna is not a useful tool for interpreting bathymetry. This is partly due to the fact that some abundant epifaunal species (e.g. *Chlamys*, *Nanogyra*) occur in a wide variety of substrates and that the others, though substrate-related, are not necessarily depth-related.

Despite this, several associations proved to be characteristic of certain environments, especially when certain types of substrates were commonly found in a characteristic bathymetric position. The distribution of these associations in the Corallian is shown in text-fig. 31. For instance, the *Pseudomelania heddingtonensis* association (M) is characteristic of lagoons with lime mud or of sheltered lagoon-like environments. The oyster/*Isognomon promytiloides* association (O) in turn preferred offshore muds and sands. Offshore condensed calcareous sandstones and sandy limestones were populated by members of the *Myophorella clavellata* (D) and *Pleuromya uniformis* (L) associations. The latter is also typical of subtidal sands, whilst the *Corbulomima* association (N) preferred silty muds of low-energy bays or the offshore shelf. High-energy environments such as near intertidal bars or intertidal sands and silts were usually devoid of body fauna but exhibit a distinct trace-fossil suite, the *Diplocraterion* association (S). The *Pinna* association (B) is typical of a similar environment, i.e. current-swept near intertidal bars. Finally, the *Lithophaga inclusa* association (Q) is restricted to the patch reef environment and to coral thickets or low coral biostromes. In contrast, several associations were found to be fairly independent of the environment. They consist mainly of epibenthic bivalves (e.g. in the *Chlamys*/*Nanogyra nana* (G) and *N. nana* (R) associations) and occur over most of the Corallian. Thus several Corallian benthic associations, although not useful as bathymetric indicators, are indicative of particular facies and thus aid the reconstruction of the palaeogeographic and environmental set-up of the Middle and Upper Oxfordian of north-west Europe.



TEXT-FIG. 31. Facies distribution of some Corallian associations. B = *Pinna* ass.; D = *Myophorella clavellata* ass.; L = *Pleuromya uniformis* ass.; M = *Pseudomelania heddingtonensis* ass.; N = *Corbulomima* ass.; O = Oyster/*Isognomon promytiloides* ass.; S = *Diplocraterion* ass.; 1, sand; 2, silt; 3, clay, argillaceous/micritic limestones; 4, condensed sandstones and limestones.

COMPARISONS WITH OTHER MESOZOIC BENTHIC ASSOCIATIONS

Benthic community studies have been carried out especially in the Silurian, Cretaceous, and the Recent. Different approaches and presentation of data make a straightforward comparison very difficult as does the degree of splitting or lumping of data into 'communities'. Furthermore, often only part of the fauna, for instance, brachiopods (e.g. Calef and Hancock 1974; Boucot 1975), has been taken into consideration, and other elements like the infauna have been neglected. Some standardization is needed in the approach to associations, as well as an agreement on the definition of benthic associations or 'communities'. Only then can direct comparison between benthic associations become meaningful and allow sound inferences about community evolution. Thus the following comparisons are of a tentative nature only.

The Lower Oxford Clay associations (*Callovian*) *of central England*. As no other Middle and Upper Oxfordian data are available yet, the nearest comparison is with the Lower Oxford Clay associations of central England (Duff 1975). Duff divided the fauna into ten biofacies associations, some of them showing only slight variations in faunal composition. For instance, the difference between the blocky claystone, *Meleagrinella* shell bed, and the deposit-feeder bituminous shale biofacies consists in the different order in which faunal elements are arranged in the trophic nucleus. As we know from present-day communities, the faunal composition of samples from the same community can vary to a large extent; thus the three biofacies types might represent only variations of one association. None of Duff's associations are found in the Corallian but his *Grammatodon*-rich bituminous shale biofacies resembles to some extent the *Corbulomima* association (N). Both have, in prominent position, an epifaunal (?)deposit-feeding gastropod (*Procerithium*), the small infaunal suspension-feeding bivalve *Corbulomima*, and the infaunal deposit-feeder *Palaeonucula*. Other genera of the trophic nucleus common to both associations are *Mesosacella* and *Thracia*. Pendent bivalves like *Meleagrinella* and *Bositra* in the Callovian are represented by *Pteroperna pygmaea* in the Corallian but are there of lesser significance. The *Corbulomima* association also resembles, to some extent, the Callovian Nuculacean shell bed and *Grammatodon* shell-bed biofacies which also consist of similar faunal elements. The substrate is identical in the Corallian and Callovian (i.e. mud), and so is the bathymetric position, i.e. low energy but well-aerated offshore subtidal.

Middle and Upper Jurassic bivalve associations of Wyoming and South Dakota. Wright (1973, 1974) distinguished six bivalve assemblages, mainly from the Middle Jurassic of Wyoming and South Dakota which inhabited open shelf, littoral, and lagoon areas. The Bajocian *Pleuromya subcompressa* assemblage is similar to the Corallian *P. uniformis* association, both being relatively diverse and having roughly equal numbers of epifauna and infauna. Genera common to both trophic nuclei are *Pleuromya* and *Gryphaea*. *Camptonectes* in the Bajocian is replaced by *Chlamys* in the Corallian, *Ostrea* by *Deltoideum*. The *P. subdepressa* assemblage inhabited the open-shelf living on firm lime mud, which is also the environment in which part of the *P. uniformis* association in the Corallian is found.

Coloradoan (*Cretaceous*) *macroinvertebrate assemblages from the Central Western Interior*. Kauffman (1967) described twenty-six macroinvertebrate assemblages from the Cretaceous of the Central Western Interior of U.S.A. of which at least two have counterparts in the Corallian. His *Pinna* assemblage (K) is dominated by *Pinna* and occurs in shallow-water massive sandstones which is exactly the environment of the Corallian *Pinna* association (B). His plicate oyster assemblage (M) consisting mainly of *Lopha* which formed local clusters and restricted biostromes on many shallow-water nearshore calcarenites may be compared to the Corallian *Lopha gregarea* association (J) which similarly formed small biostromes but obviously inhabited a somewhat quieter and deeper offshore environment with a mud substrate (Fürsich 1976*b*).

Lower Cretaceous benthic communities from the Southern Western Interior Basin. Scott (1974) recognized an *Arenicolites* association indicative of the upper shoreface when studying the benthic faunas in the Lower Cretaceous of the Southern Western Interior of the U.S.A. This association can be compared with the Corallian *Diplocraterion* association which is also devoid of body fauna and indicative of a high-energy environment. The Corallian *Corbulomima* association combines most elements of Scott's (1970, 1974) *Corbula–Breviarca* and *Nucula–Nuculana* associations, consisting mainly of shallow infaunal suspension-feeders and infaunal deposit-feeders. Both of Scott's associations and the *Corbulomima* association occur in the same substrate (mud, clayey silty sandstones) and roughly similar environments (lower shoreface to open sea).

CHARACTERISTIC FEATURES OF THE CORALLIAN ASSOCIATIONS

1. *Nanogyra nana.* In most associations, the oyster *N. nana* occupies one of the first ranks of the trophic nucleus, except for the *Pinna*, *Discomiltha*, and *Corbulomima* associations. Usually, *Nanogyra* forms clusters either on the sediment or on other shells; shells covered with spat are quite frequent. The widespread occurrence and mode of distribution indicate that *Nanogyra* most likely acted as an opportunistic species (Levinton 1970) being extremely eurytopic and having few requirements besides hard substrate and more or less fully marine conditions. A similar distribution pattern and mode of life is recorded of small *Exogyra* (e.g. *E. columbella*) from the Cretaceous of the Central Western Interior (Kauffman 1967). These species might have filled the niche in the Coloradoan, which was occupied by *Nanogyra* in the Corallian.

2. *Chlamys.* Another conspicuous element of the Corallian fauna are several species of *Chlamys*, being the dominant group amongst the byssally attached epifauna. Not only characteristic of the *Chlamys*/*N. nana* association (G), they also occur in most trophic nuclei of the other associations. Although *Chlamys* ranges from the Triassic to the Recent, it does not play a role in the Cretaceous macroinvertebrate associations so far studied (Kauffman 1967; Scott 1970, 1974) nor in the other Jurassic benthic associations (Wright 1973, 1974; Duff 1975). The absence of *Chlamys* from the Lower Oxford Clay is most likely the result of a lack of suitable substrate (they are also rare in the Corallian *Corbulomima* association which occurs in a similar facies). In the Middle and Upper Jurassic of Wyoming and South Dakota the niche seems to have been filled by *Camptonectes* which are very widespread, and form the dominant element of the *C. bellistriatus* assemblage (Wright 1974).

3. *Scarcity of brachiopods and crinoids.* Brachiopods and crinoids are virtually absent from the Corallian of England and Normandy except for two horizons:

Torquirhynchia inconstans is a common faunal element in the top Corallian and basal Kimmeridgian, and clusters of the rhynchonellid *Thurmanella* dominate, together with *Nanogyra*, part of the Hambleton Oolite of Yorkshire. In the latter horizon the crinoid *Millericrinus* is also a conspicuous faunal element. The appearance of *Torquirhynchia* at the Oxfordian/Kimmeridgian boundary in England and Normandy most likely is connected to the transgression which took place at the base of the Ringstead Coral Bed (Talbot 1973) and which enabled the asymmetric and therefore specialized *Torquirhynchia* to spread over a large area. Species of *Torquirhynchia* have been found, in similar stratigraphical positions, over much of Central and Western Europe, and possibly on the Russian platform (Childs 1969). The abundance of *Thurmanella* in certain beds of the Hambleton Oolite forming small clusters suggests that it, too, can be regarded as an opportunistic species especially as the other main faunal component is *N. nana*. This assumption is also supported by the low diversity of the fauna (see also Fürsich 1976*a*).

The scarcity of brachiopods and crinoids, both stenohaline groups, seems to point to lowered salinity as the reason for their restricted distribution. However, other stenohaline groups like ammonites, starfish, and especially echinoids, are not uncommon and in the latter case even form distinct associations, so that changes in salinity do not seem to be responsible. Unsuitable (shifting) substrates can also be discounted, as byssally attached bivalves are very widespread. Brachiopods constitute an important part of the fauna of the sponge reefs on the Swabian Alb and also on the high-energy carbonate platform of the Swiss Jura Mountains (author's field observation), both in age comparable to the Corallian. The deeper bathymetric position of the sponge reefs, where brachiopods dominate the epifauna, suggests that there brachiopods still held the niches which were occupied by bivalves in the shallower parts of the epicontinental sea. However, this niche replacement cannot explain the abundance of brachiopods in the very shallow carbonate platform sediments of the Swiss Jura Mountains during parts of the Middle and Upper Oxfordian. In equivalent environments in Dorset and Normandy (e.g. Osmington Oolite Group, Oolithe de Trouville) brachiopods do not occur. Differences in food supply combined with competition with the more efficiently feeding bivalves cannot explain this distribution pattern either, as near landmasses (in the case of England and Normandy) food supply was surely at least equivalent to that on the Swiss carbonate platform which bordered the Tethys. The least unsatisfactory explanation which can be offered is that the articulate brachiopods with their very short free-swimming larval period (probably a few hours or at the most a few days according to Rudwick 1970) were at a great disadvantage when colonizing large areas. When dispersal took place from a source area near the border Tethys/epicontinental sea—and the continual decrease of the abundance of brachiopods from Switzerland through France into England seems to support this—the short free-swimming larval stage, combined with competition from bivalves and unstable environments (due to several transgressions and regressions) might account for the scarcity of brachiopods over most of the Corallian of England and Normandy.

Articulate brachiopods are also rare in the Lower Oxford Clay of Central England (Duff 1975), probably due to the unsuitable substrate which presented difficulties in anchorage for most species and could easily clog their filter-feeding system.

Except for *Kallirhynchia myrina* in the late Callovian and early Oxfordian, brachiopods form no part of the benthic assemblages of the Middle and Upper Jurassic of Wyoming and South Dakota (Wright 1973), perhaps also for similar reasons as in the Corallian. Brachiopods are of no importance in any of the Cretaceous benthic assemblages. Perhaps their role in the Jurassic and Cretaceous epicontinental sea was chiefly confined to their appearance as opportunistic species, or specialists not being able to compete with bivalves under other ('normal') circumstances.

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APPENDIX

Localities of collections

Yorkshire:

FB	Cliffs at Filey Brigg, North of Filey (TA 131 815)
TB I	Betton Farm Quarries, Ayton (TA 002 856 and 001 855)
TB II	Crossgates Quarry, Seamers (TA 028 843)
P I	Disused quarries on Stonygate Moor (SE 868 849)
P II	Newbridge Quarry, Pickering (SE 800 860)
NG	North Grimston Hill Quarry (SE 84 67)
SQ	Spaunton Quarry (SE 722 868)
WQ	Whitewall Quarry (SE 791 697)
NRC	Nunnington Railway Cutting (SE 649 787)

Oxfordshire/Berkshire:

SH	Shellingford Cross Roads Quarry (SU 326 940)
CH	Cothill Quarry (SU 467 997)
B	Beckley Quarry (SP 570 108)
CR	Cross Roads Quarry, Oxford (SP 550 064)

Dorset:

BC	Cliffs east of Bowleaze Cove (SY 708 818)
HC	Redcliff Point (SY 711 816)
RB	Ringstead Bay (SY 755 813)
OS	Cliff east of Osmington Mills (SY 737 816)
OSM	Cliff at Osmington Mills (SY 735 816)
BR	Cliff at Bran Point (SY 742 813)
SC	Cliff below Sandsfoot Castle, and cliffs towards Weymouth (SY 675 774)
EF	Low cliffs at East Fleet, Weymouth (SY 652 772)
BH	Cliffs between Black Head (SY 729 819) and Shortlake (SY 722 819)

Normandy:

HLF	Cliffs (Falaises des Vaches Noires) between Houlgate and Villers-sur-Mer, 90 m west of the steps leading down to the beach from the camping 'Les Falaises'.
HLC	Cliffs (Falaises des Vaches Noires) between Houlgate and Villers-sur-Mer, 500 m west of the steps leading down to the beach from the camping 'Les Falaises'.
V	Cliffs (Falaises des Vaches Noires) south-west of Villers-sur-Mer.
BV	Low cliffs between Blonville-sur-Mer and Bénerville-sur-Mer.
MC	Small quarries on the slopes of Mount Canisy
HV	Cliffs between Trouville-sur-Mer and Hennequeville