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ADAPTATIONS OF BRITISH CHALK BIVALVIA

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ABSTRACT—Available museum collections have been utilised for a functional analysis of common members of the bivalve fauna of the Cretaceous Chalk Formation of England. It is concluded that many members of the fauna were able to inhabit their unusual environment by virtue of specialised adaptations. There is an apparent paucity of infaunal bivalves in true Chalk lithology, and the fauna is dominated by epifaunal animals. Adaptations found in members of the epifauna fitting them for life on a soft fine-grained substrate include the probable life habits of swimming, byssal attachment, cementation, and secretion of a gryphaeate lower valve. A remarkable case of parallel adaptation in *Spondylus spinosus* (J. Sowerby) and *Arctostrea colubrina ricordeana* (d'Orbigny) is related to their inferred adult life habit of lying free on the soft substrate. Specialised 'snowshoe' spines were secreted by these animals to help prevent their sinking into the Chalk ooze. An appendix contains a detailed functional analysis of *Spondylus spinosus* and *Plicatula inflata* (Sowerby), and it is demonstrated for the first time that *Spondylus spinosus* possessed an early ontogenetic stage of direct cementation.

INTRODUCTION

THE Cretaceous chalk rocks of Western Europe contain a fauna of somewhat unusual facies, and whilst the generic suite of bivalves present shows similarities to the faunas of earlier soft-bottom deposits (e.g. the Gault), there are important differences, particularly in the restricted number of supra-familial taxa found in the Chalk.

The study of museum material that forms the major part of this paper suggests that epifaunal Bivalvia that were able to live successfully under the sedimentological conditions of a chalk substrate all possessed some type of specialised adaptation. In the paper attention will be drawn to these varied adaptations, and an attempt made to interpret the whole bivalve fauna from an adaptive point of view.

Specific names throughout are based on the monograph of Woods (1899–1913); there has

been no attempt at their critical re-appraisal, though generic placement has been modernised in some cases. Generalisations that are made with respect to the Chalk bivalve fauna are based on qualitative examination of the collections in the Sedgwick Museum, Cambridge, the British Museum of Natural History, London, and the Institute for Geological Sciences, London. Though a quantitative field-oriented approach might have been preferable, such an approach is hampered by the overall paucity of fossils in individual chalk outcrops. As Rayner (1967, p. 377) notes: "Chalk is not normally rich in fossils and the very large numbers in museum collections, often beautifully preserved, are rather misleading and are due rather to long collecting from quarries and cliffs than to an original abundance". However, the larger collections have now been accumulating through so many years, and been

contributed to by so many different individuals, that they are surely broadly representative of the whole Chalk fauna—even if biased in detail. As such, these collections represent a valuable, generally untapped, source of data on Chalk fauna and ecology, and this paper attempts to portray major adaptive patterns in Chalk Bivalvia by functional study of museum material.

NATURE OF THE CHALK

Sedimentary and lithological characteristics.

—The Chalk Formation, of Upper Cretaceous Age, is over 1600' thick (Rayner, 1967, p. 317); its current subdivision and terminology in the U.K. are summarised in Text-figure 1. Obviously such a thickness of strata contains considerable lithologic variety, but the essential characters of the chalk have recently been well summarised by Smart *et al.* (1966, p. 114): "Chalk is, for the most part, a soft, remarkably pure limestone. M. Black (1953) found that ordinary white chalk was composed of two powders: the finer consisted of coccoliths and their disintegration products, that formed a matrix in which were embedded molluscan debris, foraminifera and 'spheres' or *Oligostegina*, comprising the coarser fraction. In soft chalk the coarser powder had particles between 100 microns and 10 microns in diameter, the finer between 4 microns and one-half micron. Colloidal clay mineral finer than one-half micron was present in appreciable quantities in chalk/marl and grey chalk, but in only very small amounts in white chalk. Coccoliths, the minute calcareous bodies produced by planktonic algae, were present in all stages of disintegration down to the individual component crystals. Of the larger particles, predominance of molluscan debris gave a gritty but friable rock; chalk with abundant foraminifera or spheres was apt to be rather hard or nodular, while preponderance of coccolith material gave common soft chalk. In contrast, modern precipitated oozes contained relatively little shell material and hardly a trace of coccoliths, but an abundance of minute aragonite crystals."

Though a first inspection suggests "the persistence of unusually stable conditions for the whole of the Chalk" (Nichols, 1959, p. 404), the Chalk is far from being one uniform lithology throughout. The Lower Chalk, in particular, has somewhat more terrigenous material, and nodular beds (whose origin and significance are discussed by Wood, *in* Worsam and Taylor, 1969, p. 43–45) are common at various horizons in the Middle and Upper

Chalk. The nodules are primarily due to diagenesis (calcite-cementation, see Lombard (1956), Hancock (1963)), and all gradations can be found between lumpy lithologies—where only some patches of chalk are hard relative to the remainder—and completely indurated beds of limestone. These latter lithologies are frequently referred to as "hardgrounds", and several hardground horizons are sufficiently thick and widespread to have received formal lithostratigraphic names (Text-fig. 1). Wood (*loc. cit.*, p. 43–44) is of the opinion that many of the hardgrounds may have been formed by pre-burial diagenesis, and therefore provided 'islands' or extensive platforms of hard-bottom conditions on an otherwise soft sea-floor. Such penecontemporaneous submarine cementation of soft sediment—giving rise locally to hard-bottom conditions—is being increasingly reported on modern sea-floors (e.g. Shinn, 1969).

Gross bedding in the Chalk generally consists of alternating bands of different hardness, occasional concentrations of fossils, or lines of flints (see, e.g., Smart *et al.*, 1966, pl. 5a). Fine sedimentary structures are very rarely preserved (Kennedy, 1969, p. 460), and it is tempting to relate their absence to intensive bioturbation of the sediment by the contemporary infauna (C. V. Jeans, *pers. comm.*).

Faunal characteristics, (a) Preservation.—Hard parts of many invertebrate phyla are composed of either aragonite or calcite. A comprehensive summary of the distribution of these polymorphs in bivalve molluscs is provided by Taylor, Kennedy and Hall, 1969 (see also Majewske, 1969, table 5). The shells of nearly all infaunal bivalves are composed entirely of aragonite, and—in view of the metastability of aragonite with respect to calcite at normal PT conditions—the question of differential preservation of these two minerals must be carefully considered before drawing ecological conclusions from the present distribution of bivalves in the Chalk. This problem was first recognized by Jukes-Browne (1904, p. 369), and an excellent brief summary may be found in Kennedy (1969, p. 462–465).

Aragonite is not generally preserved in the Chalk. For instance, *Spondylus* and *Inoceramus* both have calcitic external shell layers and aragonitic internal layers: all Chalk specimens of both genera are preserved without internal shell layers (and hence without dentition). Some recent writers (Jeffries, 1962; Hudson, 1967) have argued that the absence of aragonite may be at least partially due to its preferential dissolution on the bottom of the Chalk sea. Others (e.g., Kennedy and Hall, 1967)

FORMATION	ZONE	AGE	TIME-RANGE
UPPER CHALK (Chalk Rock)	<i>Liostrea lunata</i>	MAASTRICHTIAN	<i>Spondylus spinosus</i> <i>Arctostrea colubrina</i> <i>Plicatula inflata</i> <i>Entolium orbiculare</i> <i>Neithea quinquecostata</i> <i>Atræta nilssonii</i> <i>Pycnodonte vesicularis</i> <i>Arctostrea pusilla</i>
	<i>Belemnitella mucronata</i>	SENONIAN	
	<i>Goniotentis quadrata</i>		
	<i>Offaster pillula</i>		
	<i>Marsupites testudinarius</i>		
	<i>Vintacrinus socialis</i>		
	<i>Micraster coranginium</i>		
	<i>M. cortestudinarius</i>		
	<i>Holaster planus</i>	TURONIAN	
<i>Terebratulina lata</i>			
<i>Inoceramus labiatus</i>			
(Totternhoe Stone) LOWER CHALK	<i>Holaster subglobosus</i>	CENOMANIAN	
	<i>Schloenbachia varians</i>		

TEXT-FIG. 1.—Stratigraphy and terminology of the Chalk in the United Kingdom, together with approximate time ranges of selected bivalve species.

lay stress on the mechanism of post-depositional solution. Either way, however, the remains of animals presumed to have had aragonitic shells are not uncommonly preserved, generally in one of three ways (Jefferies, 1962; Kennedy, 1969) :

- (1) Replacement (or "normal") preservation: the shell is replaced by chalky calcite or by marcasite/pyrite; in the former case preservation is essentially as a (generally internal) mould (e.g., the Underwood Hall fauna listed in Worssam and Taylor, 1969, p. 52). This mode of preservation provides the most diverse aragonitic faunas in the Chalk, and is nearly always associated with hardground horizons (the *reussianum* fauna, see below).
- (2) Pebble preservation; the fossils occur as phosphatised or glauconitised internal moulds with patches of adherent sediment.
- (3) Oyster-cast preservation; moulds of (especially) ammonites and small gastropods occur on the attachment areas of oysters (commonly *Pycnodonte*).

Faunal characteristics, (b) General aspects.—Generalisations regarding faunal distributions are not rewarding, for the fauna varies

from one locality and bed to another in sympathy with local environmental conditions. The commonest fossils include echinoids, brachiopods and bivalves. Within the main body of the Chalk fossils are not rare, but their occurrence varies. Sometimes they are sparsely and evenly scattered through a thickness of rock (e.g., Band 3 of the Eastbourne succession; Kennedy, 1969, p. 507) and at other times they occur concentrated along a particular horizon (e.g., Band 9 of the Kent coastal section; Kennedy, 1969, p. 476-477).

The hardground horizons are faunally most important, for they often contain a fauna of aragonite-shelled bivalves, ammonites and gastropods, together with rich hexactinellid sponge assemblages, that is rarely found in other chalk lithologies. Voigt (1959) and Hofker (1959) have discussed the ecology and sedimentology of the hardgrounds in Europe, and have concluded that they almost invariably mark a disconformity, whose magnitude may in part be inferred from the extent to which an individual hardground is perforated by borings, and includes reworked pebbles.

A characteristic ammonite of hardgrounds is *Hyphantoceras reussianum* (d'Orbigny), and the hardground faunal assemblage is therefore informally termed the *reussianum* fauna in most British descriptions.

Inferred physical conditions.—Early estimates regarding deposition of the Chalk suggested a depth of between 100 and 500 fathoms (e.g., Woods, 1897). More modern work makes it clear that different horizons were probably deposited at markedly different depths, and anyway at depths generally less than about 150 fathoms. For instance, Burnaby (1962, based on foraminifera) postulated a depth of about 5 fathoms for the beginning and end of deposition of part of the Lower Chalk, with a maximum depth in between of some 50–100 fathoms, and suggested that the overlying Burwell rock may even have been deposited in water less than 2 fathoms in depth. Reid (1962, p. 277) suggests that the hexactinellid sponge fauna from the Chalk Rock indicates a depth “probably not less than ca. 50 fathoms, but not necessarily more than ca. 110 fathoms”.

In a detailed treatment of a limited thickness of Lower Chalk (the *plenius* Marls), Jefferies (1962) has estimated varying temperatures of deposition of between about 5° and 17°C. These temperatures are low by comparison with isotopic palaeotemperature estimates of 15–17°C (based on nektonic belemnites), 25–27° (based on benthic oysters), and even as high as 30° (many specimens of Chalk matrix) (Lowenstam and Epstein, 1954). Burnaby (1962, p. 607) has pointed out that this latter figure may be due to the very high proportion of coccolith material that is present in many Chalk matrices, and also records rhabdoliths (exclusively tropical at the present day) in the Lower Chalk of Cambridgeshire. The consensus of opinion seems to indicate shallow, warm to tropical conditions for bands rich in aragonitic fossils, and cooler (?deeper) conditions for bands in which aragonitic fossils are rare or absent (Kennedy, 1969, p. 465).

In spite of their being composed of markedly different materials, there is probably a close physical analogy to be drawn between the Chalk bottom and Recent foraminiferal oozes (cf. Pl. 2, figs. 5–6). Thus, though the Chalk bottom was certainly soft, it must also have been firm enough to have supported the substantial epifauna that is known to have existed. Though it might be suggested that the bottom surface was virtually a sediment suspension, general faunal evidence indicates that the sediment/water interface was probably very sharp.

The analysis of the bivalve fauna which follows also suggests that large areas of the Chalk bottom were very soft, but that there were local exposures and scattered boulders of penecontemporaneously cemented chalk forming sites where a hard-bottom community could

establish itself. Dead tests and shells also formed small “islands” populated by rich epifaunal communities. However, most of the sea floor, being soft, possessed an abundant though restricted infauna of echinoids, and a specialised and characteristic benthonic epifauna. Conditions of sedimentation were probably quiet, but locally highly turbid conditions could be generated by biotic or physical disturbance of the upper sediment layers.

INFAUNA

One of the most striking aspects of the preserved Chalk fauna is the rarity of infaunal bivalves. The problem is to decide whether the general absence of infauna is of primary biological nature, or whether it is a secondary character due to preferential dissolution of aragonitic shells (see Faunal characteristics above).

There can be little doubt that the *reussianum* fauna includes both elements indicative of a special hard-bottom facies (conveniently termed the *reussianum* fauna *sensu stricto*), and also elements (which may have been originally widespread) that have been preserved only by virtue of a particular combination of sedimentary and diagenetic conditions (though Wood, *in* Worssam and Taylor, 1969, p. 50, seems to imply one of these explanations must be true to the exclusion of the other). As most hardgrounds show some degree of disconformity at their top, they imply a temporary still-stand on the sea-floor and probably an exposed submarine rocky bottom, resulting from early diagenetic cementation. However, here and there, pockets of soft chalk would have provided a substrate for an aragonitic infauna, whose preservation was assured by the rapidly proceeding diagenetic cementation (see also the evidence for similar penecontemporaneous cementation of horizons rich in crustacean burrows, in Bromley, 1967). Infaunal bivalves preserved in such a way are commonest in hardgrounds, and include *Pinna*, *Pholadomya*, *Corbis*, *Cuspidaria*, *Freiastarte*, *Goniomya*, *Mesosacella*, *Nucula*, *Nuculana*, *Nicaniella*, *Cardita*, *Cardium*, *Trapezium*. (pers. obs.; Worssam and Taylor, 1969, p. 51–53). Many of these forms have also been reported from the main body of the Chalk (Wright, 1935, in association with ammonite shells; Davis, 1926, inside irregular echinoid tests), suggesting that this infaunal element of the *reussianum* assemblage was also the typical infauna of the majority of the Chalk soft-bottom.

Amongst the Chalk infauna, the high per-

centage of inferred deposit feeders (mainly protobranchs), and the small size of most of the other species is consistent with communities known to be living today on areas of very soft, fine-grained sediment (Craig and Jones, 1966; Purdy, 1964). It contrasts markedly with the large, robust infaunal bivalves that are typical of shallower coarsely clastic substrates. In typical Cenomanian faunas of Devon (contemporaneous with the Lower Chalk and generally interpreted as indicating shallow water, and perhaps a shoreline, in that region—see, e.g., Smith, 1957), the infaunal suspension feeding element is dominant, and includes large *Pholadomya*, *Thracia*, *Myophorella*, *Cardita*, “*Cyprina*”, *Crassatella* and “*Lacvivitrigonia*”. Such a rich association serves to highlight the fact that—with virtually no significant exceptions, and notwithstanding the problems of diagenesis and preservation—this Cenomanian generic suite is completely absent from the typical facies of the Middle and Upper Chalk. The relative paucity of infauna also invites the speculation that the absence of competing bivalve infauna might help to explain the enormous success of infaunal echinoids in the Chalk sea (cf. Nichols, 1959, p. 404–6).

HARD-BOTTOM EPIFAUNA

The *reussianum* fauna *sensu stricto* may be viewed as an assemblage of species typical of hard-bottom conditions, and supports the opinions of earlier writers (e.g., Voigt, 1959; Lombard, 1956) regarding the nature of the hardground horizons. Amongst the bivalves, *Aucellina*, *Chlamys*, some *Inoceramus*, *Pseudolimea*, *Septifer*, *Barbatia* and *Limopsis* are all forms whose morphology (and living relatives) suggest a life habit attached to hard bottom, or nestling in crevices. Associated animals include abundant benthic gastropods (*Cerithium*, *Scalaria*, *Calliostoma*, *Emarginula*, “*Trochus*” and “*Turbo*”), cephalopods (*Turritites*), brachiopods, corals, bryozoa and echinoids. Whereas the general absence from the “typical” chalk of the infaunal part of the *reussianum* fauna may be due to preservation, most of the forms listed above are only likely to be collected on, or near, true hard-bottom horizons.

SOFT-BOTTOM EPIFAUNA

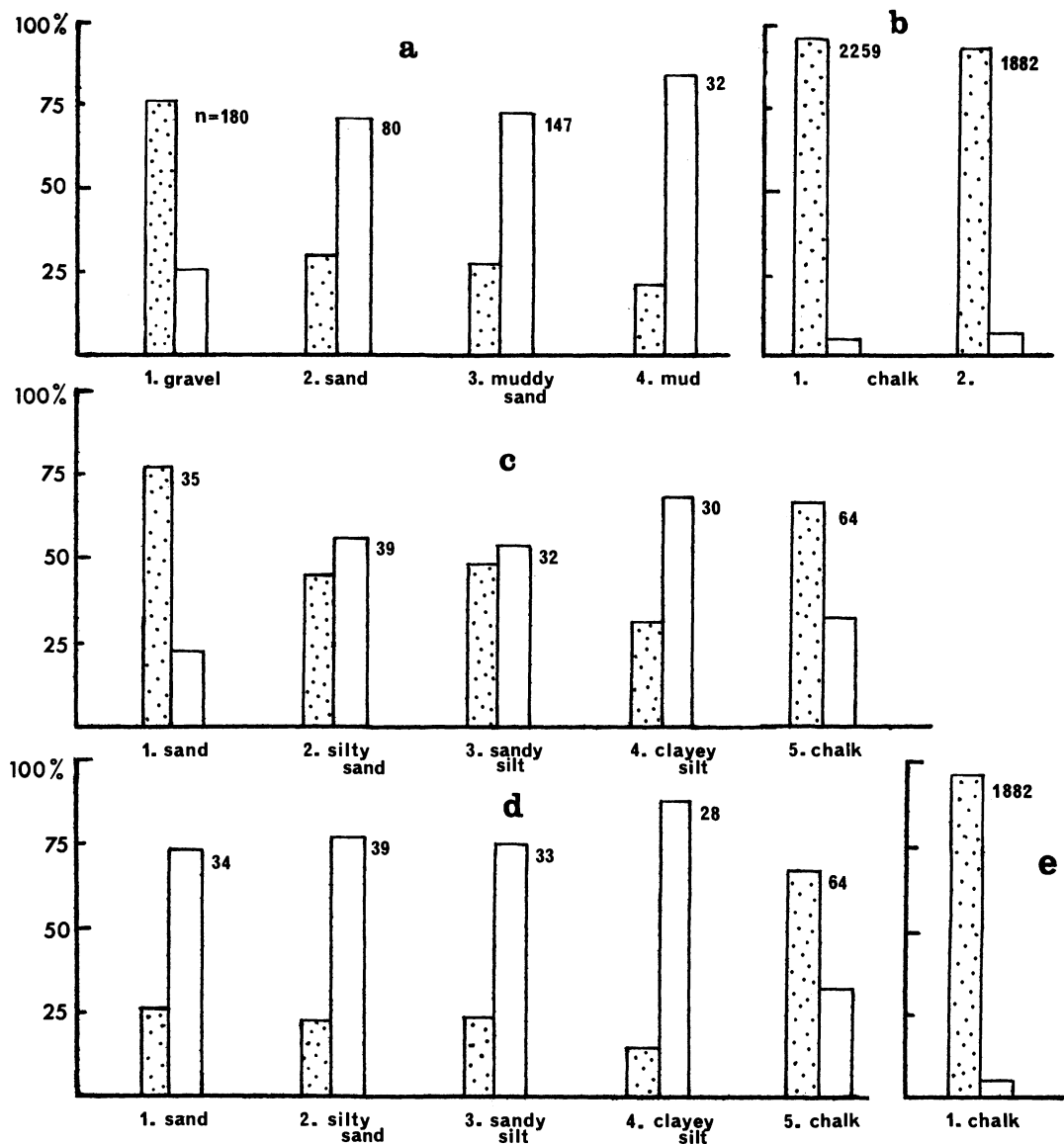
Notwithstanding the widespread occurrence of hardground horizons, by far the greater part of the Chalk represents sediments that accumulated as a series of soft sea-floors (see,

e.g., Nichols, 1959), yet the overwhelming majority of museum specimens collected from “typical” Chalk (as judged by adhering or infilling chalk matrix) represent epifaunal animals. Unfortunately, little quantitative work has been published, but Text-figure 2 (prepared from data in Kennedy, 1969) illustrates the predominance of epifauna amongst both the bivalves and the whole fauna.

Considerable interest has been shown lately (e.g. Sanders, 1956; Purdy, 1964; Driscoll, 1968) in the broader ecologic and trophic aspects of various benthic invertebrate faunas as correlated with the substrate they inhabit. There is widespread agreement that deposit-feeding infaunal bivalves characterise argillaceous low-energy substrates, whereas suspension-feeding infaunal bivalves are typical of higher energy, medium-grained clastic substrates, and suspension-feeding epifaunal bivalves are commonest on coarse-grained clastic (generally with abundant dead shell), or true hard, substrates. Such generalisations are not only based on data from the Recent (e.g., Craig and Jones, 1966), but can also be substantiated by palaeoecological observations (e.g., Driscoll, 1969; a New Zealand example is provided in figure 2 for comparison with the Chalk data). The scarcity of Chalk infauna relative to epifauna (as judged from museum collections)—if not entirely an artifact of the dissolution of aragonitic shells—is therefore of considerable biotic significance, for it provides an example of a rich epifaunal assemblage that lived on a fine-grained, probably low energy, substrate. However, detailed field studies are required to clarify the important and unresolved diagenetic problem.

Additional evidence that the relative lack of infauna is not entirely diagenetic comes from consideration of faunas from other (extra-European) Cretaceous formations with chalky lithology. For instance, in the Gingin Chalk of Western Australia, all 16 species in the originally described fauna are epifaunal (Etheridge, 1913); and Stephenson (1936) reports that by far the dominant fossils in the Austin Chalk of Texas belong to the epifaunal genera *Ostrea*, *Gryphaea* and *Inoceramus* (see also Reeside, 1957).

One might anticipate that epifaunal bivalves inhabiting a typical soft Chalk substrate would require special adaptations, for there is the dual danger of being buried (dependent upon the sedimentation rate), or of sinking into the soft oozy bottom, each of which is correlated with the serious threat of a general clogging of respiratory and feeding organs.



TEXT-FIG. 2.—*A*, percentage distribution of infaunal (unshaded) and epifaunal (stippled) invertebrate species on different sediments in the Irish Sea. *B*, percentage distribution of number of individuals of invertebrate infauna (unshaded) and epifauna (stippled) in the Chalk; (1) all invertebrates except cephalopods; (2) bivalve fauna only. *C*, percentage distribution of infaunal (unshaded) and epifaunal (stippled) bivalve species on different sediments of Miocene age at Clifden, Southland, New Zealand, and in the Chalk: (1) Lill Sand; (2) Calamity Point Sandstone; (3) Long Beach Shellbed; (4) Fouraye Siltstone; (5) Chalk. *D*, percentage distribution of number of species of Pterioda (stippled) relative to number of species of all other bivalves (unshaded): 1–5, localities as in *C*, above. *E*, percentage distribution of number of individuals of Pterioda (stippled) relative to all other bivalves (unshaded) in the Chalk. In all cases, n = total number of species or individuals. Data for Irish Sea from Craig and Jones (1966, fig. 1); for Chalk, from Kennedy (1969, p. 532–545); for Clifden, from Fleming (p. 82–95, in Wood, 1969.)

Obvious adaptations “available” in the Bivalvia, and represented in the Chalk fauna, include swimming on and above the substrate, byssally attached or cemented to hard objects

on and above the bottom, and the secretion of specialised structures (e.g., spines, or a gryphaeate lower valve) that would ensure stability on soft substrate. None of these adaptations

is unique in the Bivalvia, and probably none of them appeared for the first time in the Chalk, but in no other fauna documented to date are a set of basic bivalvian adaptations so clearly and consistently displayed. It is convenient to discuss these adaptations, summarized in Appendix 2, under five different headings:

Active Epifauna.—Amongst Recent Pectinidae known to be efficient swimmers there are several structural correlatives associated with the habit. Kauffman (1969, p. N160-1) and Stanley (1970, p. 37-43) suggest these include (a) a smooth streamlined shape, (b) a relatively light shell, (c) an equivalve shell (with some obvious exceptions), (d) the possession of gapes on the anterior and posterior dorsal margins to allow the ejection of propulsive current jets, (e) a large umbonal angle; and to these one might add (f) the presence of a straight hinge line, often coupled with sub-equal anterior and posterior ears (related to the absence of a functional byssus in the adult), (g) the possession of two calcareous lugs (auricular crurae of authors) on the inside of the shell distal to the anterior and posterior dorsal gapes (Pl. 1, fig. 4), and (h) the presence of a relatively large adductor muscle and strong ligament. Generally, no one genus possesses all these attributes, and the morphology of different forms obviously represents a compromise between differing structural demands. Nonetheless, the presence of many of these structural correlatives enables swimming to be inferred in species possibly as old as *Pernopecten ohioensis* (Newell) (Permian), almost certainly for *Entolium subdemissum* (Munster) (Triassic), and suggests that the habit evolved fairly early in pectinacean history.

Of all members of the benthos it is the active biota that might be expected to have the least trouble in coping with a chalk sedimentation regime, for they are to a certain extent independent of the substratum for the basic processes of feeding and reproducing. Indeed some of the most efficient Recent swimming pectinids preferentially inhabit fine-grained substrates (e.g., Kauffman, 1969, p. N160 hypothesises that "the lightweight shell and active swimming of *Chlamys radiata* is ... adaptive to the preferred soft-mud habitat of this species, preventing it from sinking into the substrate"). *Entolium orbiculare* (Sowerby), occasionally present in the Chalk "by the thousand" (Kennedy, 1969, p. 482), possesses many of the swimmers' structural adaptations, and a further species probably having the same mode of life is the large *Aequipecten*

beaveri (J. Sowerby), which for its size has a conspicuously light and fragile shell. It would seem likely that these two species at least lived, right valve undermost, on the floor of the Chalk sea, and that they were initially able to counter adverse sedimentation or turbid conditions by vigorous flapping of the valves, resulting in sediment dispersal and/or swimming. Concomitant physiological adaptations, such as increased rate of pumping and increased efficiency of pseudo-faeces dispersal, (see Yonge, 1936), are also likely to have been present.

Some Recent species of *Lima* also swim (Jeffries, 1960), and the broadly homoeomorphic Chalk *Plagiostoma* is a candidate for the possession of similar abilities.

Byssally attached epifauna.—Many species of Recent Bivalvia possess an early ontogenetic stage of byssal attachment; indeed it may even be universal in the post-larval stage (Yonge, 1962). However, fewer species retain a byssus as a permanent adult feature. Under soft sedimentation conditions a byssus would have great survival value if it enabled the adoption of life above the substrate, attached to rooted fauna such as crinoids or Bryozoa.

Fortunately the life habit of byssal attachment may be inferred with some degree of confidence in most fossil pectinids because of its correlation in living species with a deep byssal notch in the ear of the right valve (usually the undermost valve), and with a small umbonal angle (Stanley, 1970). Many species of Chalk *Chlamys*, including *C. fissicosta* (Etheridge), *C. britannica* (Woods) (Pl. 2, fig. 1), *C. elongata* (Lamarck), *C. cretosa* (Defrance), and *C. mantelliana* (d'Orbigny), possess well defined byssal notches and narrow umbonal angles, and can be assumed to have been byssally attached in the adult.

One unusual variety of byssal attachment is the specialised habit of living embedded in sponges. The common New Zealand Recent *Chlamys dieffenbachii* (Reeve), is often collected completely enclosed in sponges, to which it is strongly attached by its short recurved spines (Pl. 2, fig. 4) (Beu, 1966). There is also a marked byssal notch, and ctenolium, corresponding to the strong byssal attachment dorsally (Pl. 2, fig. 3). Morphologically similar short spines are known in the Pectinacea at many stratigraphic horizons. While it would not be reasonable to suggest that these spines always reflect life embedded in sponges, it is probable that some fossil species possessed such a mode of life. In the Chalk, *Aequipecten*

pexatus (Woods) (Pl. 2, fig. 2), and *Lima granulata* (Nilsson), are two species that may have possessed this life habit.

Cemented epifauna.—There was a wealth of cemented epifauna in the Chalk (Appendix 2). The Bivalvia in this category include small species of *Plicatula* and *Spondylus* together with innumerable oysters of several species (Pl. 1, fig. 3) and *Atreta nilssoni* (Hagenow) (Pl. 1, fig. 11). It is especially noteworthy that three common species, which as adults lay free on the substrate, all possessed an initial phase of cementation early in ontogeny (*Spondylus spinosus* (J. Sowerby), *Arctostrea colubrina* (Lamarck) and *Plicatula inflata* J. de C. Sowerby, see Spinose epifauna below). The spat of many Recent Bivalvia exercise considerable powers of selection of a suitable substrate for settlement (e.g., Thorson, 1966), and the closest Recent relatives of these species require suitable attachment areas for settlement and do not metamorphose successfully on soft, muddy substrates. It is not difficult to imagine the fate of spat of any species that were eventually forced to touch down directly on the soft Chalk ooze, after an unsuccessful search for a suitable hard attachment site.

Striking evidence for similarity of mode of life (and hence probably of environment) between a Chalk and Recent species comes from the small spondylids. *Spondylus latus* (J. Sowerby) is a small strongly cemented species that is especially common in the Middle and Upper Chalk; it is often attached to dead

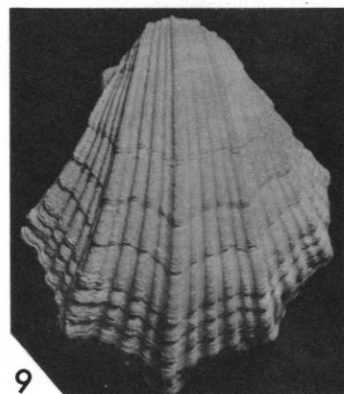
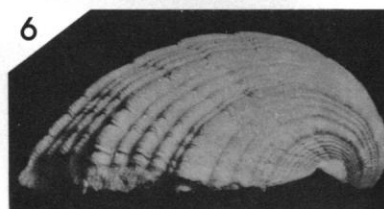
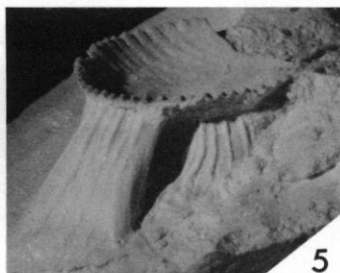
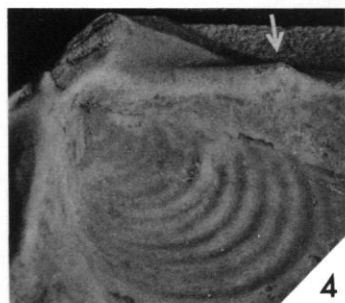
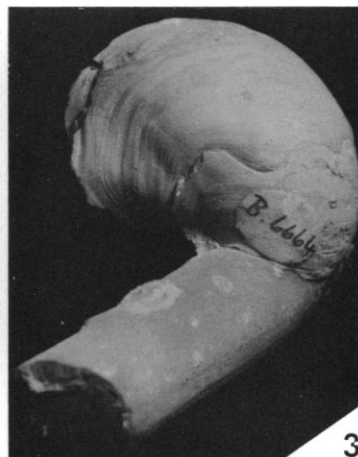
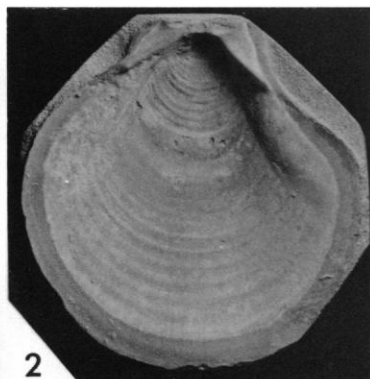
echinoid (*Echinocorys*) tests, and some specimens were apparently attached to locally exposed pieces of compacted substrate (Pl. 1, fig. 5). However, one specimen from the British Museum presents an extraordinary similarity in its habitat to *S. gussoni* O. G. Costa, a Recent species from deep water in the Atlantic. The specimen of *S. latus* (Pl. 2, fig. 5) is attached to a flat piece of sponge in association with pieces of serpulid worm tube; specimens of the Recent *gussoni* (Pl. 2, fig. 6) are cemented to a thin slab of compacted Tertiary mudstone lying on a bottom of soft foraminiferal ooze (dredged by DISCOVERY (station 5951) in 1120 m on the Galicia Bank, western Atlantic). The slab carries an abundant epifauna including worms, brachiopods, Bryozoa, corals and other bivalves.

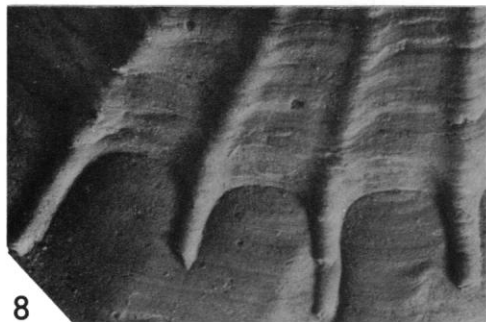
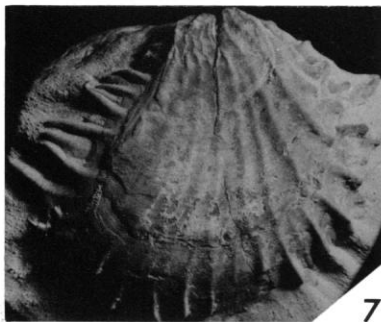
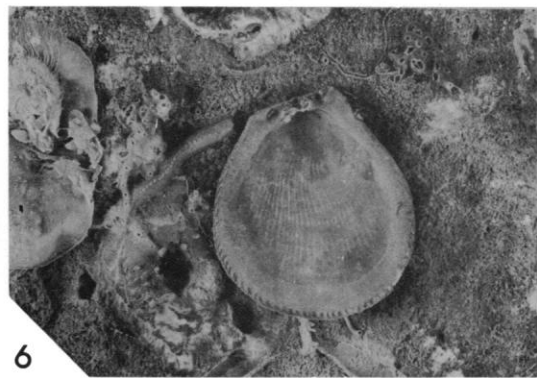
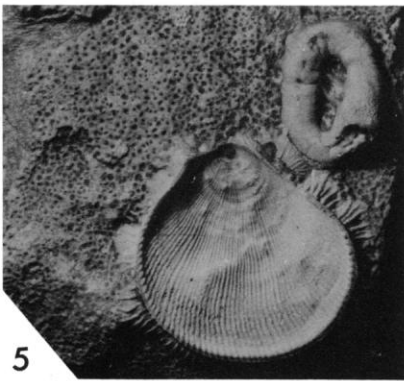
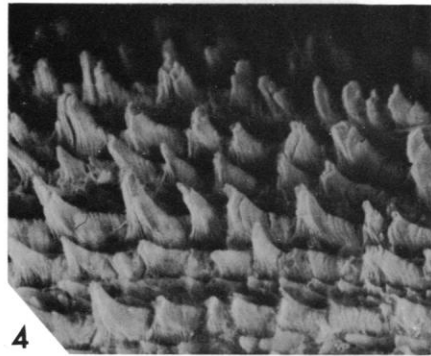
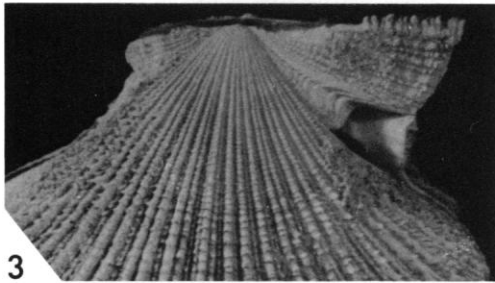
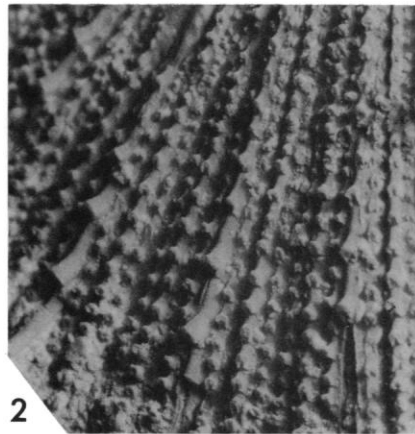
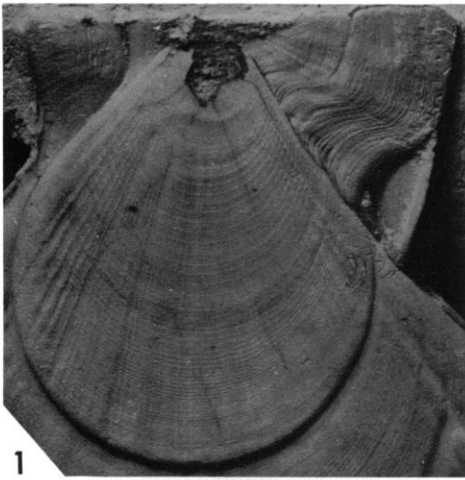
Gryphaeate epifauna.—Amongst bivalves that live free on the sea floor with their commissure horizontal, there is a recurrent tendency for the lower valve to become deeply cupped. This trend is exemplified by the Jurassic oyster *Gryphaea* (which is cemented in the juvenile, but generally free-living in the adult), and is so widespread amongst Bivalvia that the informal term gryphaeate is used to describe it. Amidst the voluminous literature on *Gryphaea* are occasional suggestions as to the functional significance of a deeply cupped lower valve. The commonest of these is that a gryphaeate shape is advantageous in that it enables its possessor to sink into a soft substrate in such a way as to minimise the chance of having the commissure smothered

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EXPLANATION OF PLATE 1

- FIG. 1—*Entolium orbiculare* J. Sowerby. Lower Chalk, Burwell, Cambridgeshire. S.M. B.6153. Right valve, $\times 1\frac{1}{2}$.
 2—*Entolium orbiculare* J. Sowerby. Lower Chalk, Burwell, Cambridgeshire. S.M. B.6154. Right valve, $\times 1\frac{1}{2}$.
 3—*Pycnodonte vesicularis* Lamarck. Upper Chalk, Norwich. S.M. B.6664. Right valve, $\times 1\frac{1}{2}$. Attached to a specimen of *Belemnitella mucronata* Schlotheim.
 4—*Entolium orbiculare* J. Sowerby. Same specimen as Fig. 2. $\times 4$. Note the well developed calcareous lugs situated latero-ventrally on the interior of the valves beneath the ears.
 5—*Spondylus latus* J. Sowerby. Upper Chalk, Charlton, Kent. S.M. B.5875. Right valve, $\times 3$. Note expanded attachment frills apparently cemented onto compacted ooze.
 6, 9—*Neitheia quinquecostata* J. Sowerby. Upper Chalk, Sutton Scotney, Hants. S.M. B.65387. Right valve, $\times 1\frac{1}{2}$; 6, to show the inflation of the right valve (though the left valve is *in situ* on this specimen, it is so flat that it is not visible in strict lateral view); 9, view normal to commissure.
 7—*Plicatula inflata* J. de C. Sowerby. Lower Chalk, Reach, Cambridgeshire. S.M. B.275. Right valve, $\times 1\frac{1}{2}$. Figured by Woods, Plate 26, Fig. 7.
 8, 10—*Inoceramus lamarcki* Parkinson. Upper Chalk, Newmarket. S.M. B.632. Left valve below, $\times 1$. Figured by Woods, Plate 52, Fig. 4. Note the very inflated under (left) valve.
 11—*Atreta nilssoni* Hagenow. Upper Chalk, Gravesend, Kent. S.M. 6132. Right valves, $\times 1\frac{1}{2}$. Two specimens cemented to a fragment of *Inoceramus* shell.





(Kauffman, 1969, p. N157). Though there has never been any rigorous demonstration that this is true, such a suggestion is intuitively very feasible, and there is some supporting evidence. For instance, MacLennan and Trueman (1942) observed that adult animals of *Ostrea edulis* Linnaeus transferred from normal substrate to a soft muddy bottom, all phenotypically developed a gryphaeate lower valve; and in a thorough comparative study of Recent species of *Ostrea* and *Crassostrea*, Menzel (1955) makes it plain that he considers the cupped lower valve of *Crassostrea* to be one of many interlinked adaptations suiting the genus for life in soft substrate turbid environments (see also Yonge, 1960, and Galtsoff, 1964, for full discussions of the physiological adaptations present in *Crassostrea* that suit it for life in turbid environments).

Hallam (1968, p. 119-122) has undertaken flume experiments with *Gryphaea*, and shown that in most cases increasing curvature of the lower valve results in increased stability on a current-swept substrate. However, the critical current velocities (at which the "unstable" forms are tipped over) are generally 20 cm/sec or greater, and seem extremely high. As Hallam notes, "such high velocities would have been intolerable to the great majority of, if not all, *gryphaeas*", and therefore "it is... arguable whether or not these results are relevant to natural conditions...". Though it is pleasant (cf. Rudwick, 1961) to see some experimental rigour being introduced to the generally speculative field of functional morphology, these experiments surely demonstrate that stability is *not* likely to have been the

prime function of a gryphaeate lower valve. At 20 cm/sec current velocity, the medium sand in Hallam's flume was being moulded into ripples, and the argillaceous substrates that *Gryphaea* is usually associated with would surely have been in turbid suspension.

Most previous writers have assumed that a gryphaeate lower valve always represents a stable, genetically fixed, adaptation. However, the observation of MacLennan and Trueman (quoted above) that a gryphaeate valve can be phenotypically induced in Recent *Ostrea*, suggests that many cases of gryphaeate form may represent immediate phenotypic reactions to a turbid or soft substrate environment. Orton (1928) was one of the first writers to point out clearly that the overall shape of an oyster shell is basically a result of the orientation of the mantle edge during shell secretion. One may develop this train of thought by suggesting that, in the Ostreidae at least, a gryphaeate shell form is an *inevitable* result of adult growth on a soft substrate (or in a turbid environment). An animal inhabiting such a substrate is forced to hold its mantle edge more vertical than is usual in order to avoid encroaching sediment; provided shell secretion continues unchecked, such a posture of the mantle edge will inevitably lead to the secretion of a relatively gryphaeate shell (cf. Carter, 1967). The consistent and repeated evolution of gryphaeate shell shapes in Bivalvia that live with commissure horizontal is appealing evidence for the basic correctness of this suggestion; and what was initially a phenotypic curiosity could have rapidly become a genetic necessity on a substrate such as soft ooze.

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EXPLANATION OF PLATE 2

- FIG. 1—*Chlamys britannica* Woods. Upper Chalk, Bromley, Kent. S.M. B.831. Right valve above, $\times 6$. Figured by Woods, Plate 61, Fig. 18. Note the well developed byssal notch.
- 2—*Aequipecten pexatus* Woods. Upper Chalk, Cheveley, Cambridgeshire. S.M. B.664., $\times 6$. Specimen figured by Woods as syntype, Plate 36, Fig. 6. Note the presence of well developed short, sharp spines, similar to those of *C. dieffenbachi*, and probably associated with a comparable mode of life.
- 3—4—*Chlamys dieffenbachi* Reeve. Recent, Dunedin, New Zealand. S.M. D.20867; 3, right valve above, $\times 2$; 4, right valve, $\times 8$. Specimen collected embedded deeply in a sponge; note well developed byssal notch, and sharp recurved spines.
- 5—*Spondylus latus* J. Sowerby. Chalk, Gravesend. B.M.N.H. 73333. Right valve, $\times 1\frac{1}{2}$.
- 6—*Spondylus gussoni* O. G. Costa. Recent, Galicia Bank (Discovery Station 5951), 1120 m. S.M. D.20920. Right valve, $\times 2$. (Photograph Dr. R. Cowen).
- 7—*Plicatula inflata* J. de C. Sowerby. Lower Chalk, Burwell, Cambridgeshire. S.M. B.6061. Right valve, $\times 1$.
- 8—*Plicatula inflata* J. de C. Sowerby. Chalk Marl, Saxon Cement Works, Cambridge. S.M. B.6065. Right valve, $\times 6$. To show the development of snowshoe spines, subparallel to the valve surface (and hence to the plane of the commissure), along a major growth pause.

Predictably, then, the Chalk fauna demonstrates several examples of gryphaeate shell form. Perhaps *Neitheia* (Pl. 1, fig. 6, 9) and various species of *Inoceramus* (Pl. 1, fig. 8, 10) illustrate it best, and a study of the gradual change in *Inoceramus* faunas through the Chalk might well reveal that in some lineages there was a continued trend towards life embedded in a soft substrate. The remarkable *I. involutus* J. de C. Sowerby of the Upper Chalk must certainly have lain free in the adult, with its very convex left valve buried in the substrate—for the shell presents a gross homeomorphy with both *Exogyra* (in its coiled 'operculate' upper valve) and *Gryphaea* (in its deeply cupped lower valve), and epifauna is commonly concentrated on the 'operculate' valve. Other species possibly possessing this mode of life include *I. inconstans* Woods and *I. lamarcki* Parkinson (Pl. 1, fig. 8, 10).

Spinose epifauna.—The Appendix presents a functional analysis of two Chalk bivalves (*Spondylus spinosus* (J. Sowerby) and *Plicatula inflata* J. de C. Sowerby) that were free-living in the adult, and are inferred to have been stabilised and supported on the substrate by a set of "snowshoe" spines. Details of the morphology of *Arctostrea colubrina ricordiana* (d'Orbigny), a third such species, may be found in Carter (1968). *Arctostrea* and *Spondylus* represent a striking example of parallel evolution. The parallelism is less striking in the case of *Plicatula*, for the spinose adaptation had already evolved in pre-Chalk times (see *P. gurgitis* Pictet and Roux, of the Gault), and was also combined with a gryphaeate lower valve.

GENERAL IMPLICATIONS

The competition for space, often an important factor amongst benthic faunal associations, was of a somewhat unusual type in the Chalk sea. Except at certain horizons, infaunal Bivalvia are conspicuous only by their absence and the fauna is usually totally composed of epifaunal species. Available hard attachment sites were strictly limited in number, and consequently there must have been intense competition for their occupation. Museum collections contain innumerable specimens of litter from the bottom of the Chalk sea, mainly fragments of dead shells and tests, and these are invariably smothered with epifaunal species. Though such specimens were undoubtedly selectively collected, they equally undoubtedly give some indication of the relative abundance of the Chalk epifauna.

Korringa (1952) has reported that a large part of an oyster's staple food consists of minute bacteria and small flagellates of much less than the usual size of the gill ostia (about 30–60 microns wide). This is likely to hold true for many other bivalves, especially those of the Pterioidea that so dominate the Chalk fauna (see Text-fig. 2). As coccoliths are so common, it may be suggested that there was a super-abundance of food available on the Chalk bottom, a conclusion already reached by Nichols (1959), and from this point of view at least the Chalk sea was a very suitable habitat for microphagous animals, both deposit and suspension feeders. However, and as outlined above, the price to be paid for exploiting such a food supply was the possession of physiologic and structural adaptations enabling their owners to cope with the physical problems of life on a soft, fine-grained substrate. In this respect it is surely significant that the Pterioidea are so common in the Chalk, for their Recent representatives all possess very sophisticated and powerful ctenidia. The other major group of Chalk Bivalvia, the inoceramids, are also dominant members of overseas "chalk" faunas, and one would suspect that this genus too had a highly developed gill-palp complex, in order to deal effectively with the feeding and cleansing problems associated with life on a Chalk substrate.

Allowing the division of the Chalk epifauna into permanently attached species and those that were only attached in their young stages, it is clear that competition for settling space was initially the same for all Chalk bivalves, but was continued into adult life only by those of the permanently attached group. Though I have not seen specimens that demonstrate it for *Entolium*, *Plagiostoma* and *Neitheia*, it would seem likely that all Chalk Bivalvia possessed an early stage in ontogeny when they were either cemented directly to hard attachment objects, or else attached by a byssus to other epifauna such as branching sponges or Bryozoa. Some species contrived to avoid the competition for adult living space by being, or becoming, adapted to free living on the bottom, either by swimming, or by secreting a gryphaeate ventral valve, or by secreting specialised supporting structures. Yet it seems likely that even these adaptations were often only temporarily expedient, and ultimately unsuccessful measures. Though it is dangerous to speculate on the basis of known stratigraphic range, the more spectacularly adapted forms were apparently relatively unsuccessful (see Text-fig. 1). For example, the swimming

pectinid *Entolium orbiculare*, though a common member of faunas back to the Lower Greensand, fails to outlast the Lower Chalk sedimentation. It is especially instructive to compare the stratigraphic ranges of the spinose forms *Plicatula inflata* J. de C. Sowerby, *Spondylus spinosus* (J. Sowerby), and *Arcostrea colubrina ricordeana* (d'Orbigny).

The immediate predecessor of *P. inflata*, *P. gurgitis*, was itself a spinose form, presumably already adapted to the soft bottom of the Gault in Albian times. Indeed, one is forced to this conclusion, for the morphology of the two species is so close that it would be ridiculous to attribute different functions to the spines of each. Thus, compared with *S. spinosus*, *P. inflata* possessed a reasonable "genetic start" in the race for adaptation in the Chalk sea. One might expect it to have benefited from this, but in fact *P. inflata* is not known from above the *subglobosus* zone of the Chalk; and this in spite of its remarkable phenotypic plasticity which enabled the species to combine its spine secreting powers, and its ability to form a gryphaeate lower valve. The fact that both *Plicatula* and *Entolium* last only through the basal "Chalk Marls", and their previous presence in such argillaceous sediments as the Gault, suggests that though well adapted to cope with muddy clastic conditions, these genera were ill-fitted for survival on a true Chalk bottom.

Though it is known quite commonly before the Cretaceous, pre-Chalk *Spondylus* was not a particularly widespread or abundant genus, and it did not possess long spines on the right valve. There can be little doubt that the spines of *S. spinosus* were a specific adaptation to Chalk conditions; and, in this case, the adaptation was relatively successful for *S. spinosus* is a common and typical member of the Chalk fauna ranging from the zone of *Inoceramus labiatus* up to the top of the English Chalk.

The ability to form spines is widespread in ostreids throughout the stratigraphic column, though such spines are generally either for subsidiary attachment purposes, or else perhaps connected with feeding currents. In only one place, and at one time, in the Cenomanian Chalk Marl of Western Europe, was this ability utilized for the construction of long snowshoe spines. Yet the attempt was apparently in vain, for *ricordeana* failed to outlast the basal Chalk zone of *Schloenbachia varians*. By way of contrast, another species of *Arcostrea* that assumed a competitive life amongst the permanently cemented epifauna was strik-

ingly successful. The small cemented *A. pusilla* (Nilsson) (see Carter, 1968, pl. 90) is very rarely found in Albian and Cenomanian rocks, but in the Upper Chalk seas this species group is one of the dominants in the rich epifauna.

ACKNOWLEDGMENTS

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APPENDIX 1

Functional Analysis of *Spondylus spinosus* (Sowerby) and *Plicatula inflata* (Sowerby)

SPONDYLUS SPINOSUS (J. Sowerby)

There are three common forms of *Spondylus* known from the Chalk. Two of these (*S. latus* (J. Sowerby) and *S. dutempleanus* d'Orbigny) appear to intergrade morphologically, and are hence doubtfully distinct; they are small species that live amongst the permanently attached epifauna, and are not considered further. The third species (*S. spinosus*) comprises moderately large spondylids that possess striking spines on their right valve. Large specimens may reach a height of almost 100 mm, though 50–60 mm is a more normal adult size. Although the dentition is missing (being aragonitic it is universally removed in Chalk specimens), the shell is unmistakably a *Spondylus*. An individual valve is bilaterally symmetrical, with well developed radial ribbing. The right valve is little inflated and carries the set of long well developed spines that give the species its name; the left valve is generally well inflated, and usually without spines (Pl. 3, fig. 7).

Life attitude.—Recent *Spondylus* generally live with the right valve beneath. An attempt was made to check this orientation for *S. spinosus* by analysing the distribution of epifauna preserved on the valve surfaces. Of 230 specimens examined that have conjoined valves (and can hence be inferred to have been fossilised close to their actual living site), 90 have epifauna confined to the left valve, 32 specimens have epifauna on both valves, and only 12 specimens have epifauna confined to the right valve. The remaining 96 specimens carry no epifauna. It should be added that of the 32 specimens carrying epifauna on both valves, many have only small amounts on either the umbonal or ventral

margins of the right valve. Both these regions could be exposed under normal conditions were the right valve underneath, and hence the analysis of epifaunal distribution strongly supports this assumption. The rich epifauna preserved on these animals includes Bryozoa, worm tubes, sponges, bivalve spat of all types, and small bivalve species such as *Atrreta*; further signs of the contemporaneous biota are the presence of rare (?gastropod) borings.

Early ontogeny.—Though the umbones of the left valve are quite frequently found intact, it is extremely rare to find a specimen in which the right umbo is preserved. The removal by solution of the internal shell layer means that there is only a very thin skin of ectostracum left over the umbonal area of both valves, hence the common hole in place of the umbones in so many specimens of *S. spinosus*. In one specimen only, out of several hundred examined, is the umbo of the right valve preserved intact (Pl. 3, fig. 2); about 9 further specimens retain more or less recognisable fragments of the right valve umbo.

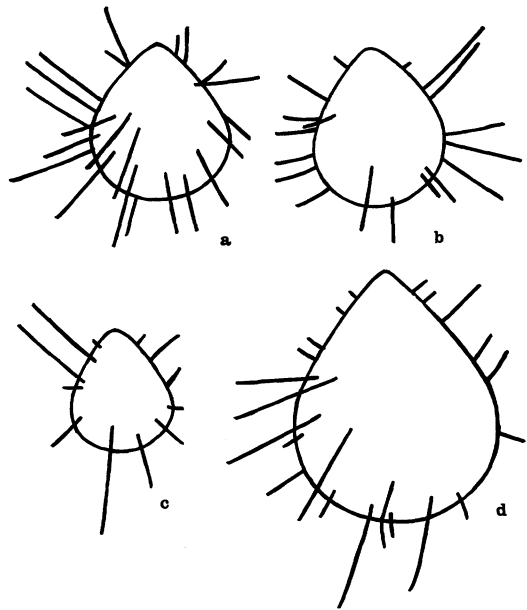
These specimens demonstrate clearly that the spat of *S. spinosus* were cemented to hard attachment objects. The area of cementation was usually small (perhaps 4 mm high), hence its rare fossilisation (the specimen of Plate 3, fig. 2 possesses an unusually large attachment scar). However, even the usual small attachment area would have served to keep the whole animal firmly cemented until the shell had grown large enough (say 5–10 mm high) to stand some chance of survival on the substrate; at this stage the weight of the shell and contained body would cause it to heel over, or possibly to break free, if attached to a large shell or hard substrate.

During the juvenile attached phase, the morphology of the right valve broadly reflected that of the object to which the animal was cemented (Pl. 3, fig. 2). This attachment, as is usual in cemented species of *Spondylus*, was by means of irregular concentric frills, which must have been secreted by a local concentric zone of mantle tissue extended outside of the shell. The attachment area of the right valve is reflected in the left by a sharply delimited juvenile stage (Pl. 3, fig. 6). The juvenile left valve is well inflated and possesses strong radial ribs; it differs from the adult in its possession of low, tuberculate spines on the rib crests. These spines are probably homologous with the small spinous structures of the left valve of adults of the contemporaneous species *S. duteupleanus*; their function is unknown. The attached phase ends when the shell is between 3 and 6 mm high.

Adult ontogeny.—The moment of breaking free of the attachment area, or of heeling over, may usefully be taken to mark the start of adult life lying free on the sea floor. Spines are secreted on the right valve from the very beginning of the adult phase of life, as displayed on a well preserved specimen only 18 mm high (Pl. 3, fig. 3). Even at this early stage the spines are strong and structurally well developed with all the characteristics of those of much larger specimens.

In general, the spines are not secreted according to any strict morphological pattern, but the following generalisations may be made:

1. It is generally the two lateral spine rows situated on the most lateral interlocking radial ribs that are the most conspicuously developed.
2. The individual spines are long and tapering, with a groove on their upper surface (Pl. 3, fig.



TEXT-FIG. 3.—Shell outlines of *Spondylus spinosus* J. Sowerby, to show the disposition of spines on the right valve with respect to the over-all shape of the shell; specimens viewed from beneath. Note especially the disposition of the spines at right angles to the shell margins. All specimens in British Museum (Natural History): a, BM 84767; b, BM 4907; c, BM 44510; d, BM unregistered.

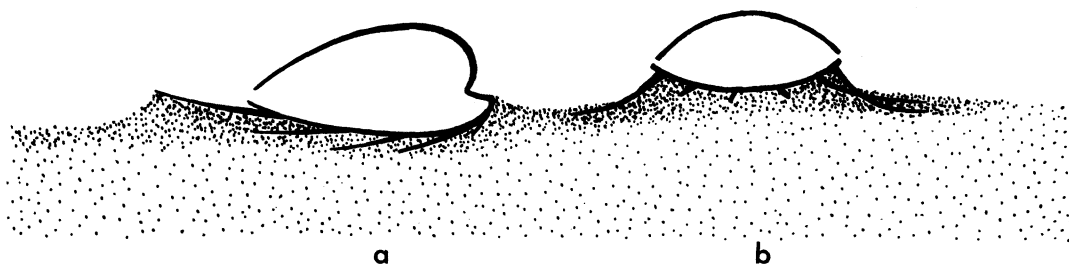
5, 7). They project initially beyond the edge of the shell at an angle of up to 40° with the shell surface (Pl. 3, fig. 4, 5), but distally from the shell edge they bend to become sub-parallel to the plane of the commissure (Pl. 3, fig. 5). The spines always project at approximately 90° to the outline of the shell, no matter where they are situated on the commissure (Pl. 3, fig. 1, 7; Text-fig. 3).

3. The spines are often very long; not infrequently as long as the shell is high.

4. The spines are introduced at spaced intervals on certain radial ribs, evenly spaced around the commissure; commonly there are 6 or 7 such radial spine rows (Pl. 3, fig. 1). There is a tendency for spines to be introduced in concentric sets on these different radial ribs; sometimes spines may be secreted simultaneously, or at very close time intervals, on 3 or 4 separate radial ribs (Pl. 3, fig. 3).

5. When a spine is broken whilst at the growing edge, the mantle may expand again under the broken portion to re-secrete the end of the same spine.

The morphology of the adult left valve requires little explanation; it is relatively well inflated, and possesses strong radial ribs. Very occasionally the presence of a broken spine stump testifies to the existence of rare and inconsistent spines on this morphologically upper valve. In such cases the spine base clearly shows that the spine was initially directed upwards at a high angle to the plane of the commissure. Whilst these rare spines might not have had functional significance, their presence



TEXT-FIG. 4—Reconstructed life position of adult *Spondylus spinosus* J. Sowerby: a, lateral view; b, ventral view. Approximately $\times \frac{1}{2}$.

merits mention because of the widespread occurrence of spondylids with spines on both valves in Eocene and later faunas.

Functional interpretation.—By its possession of an early cemented stage *S. spinosus* was forced to compete with most other Chalk epifauna for attachment space in early ontogeny. The mortality rate amongst newly settled bivalvian spat must have been enormous; even in Recent seas, where attachment space is generally very much commoner than it can have been in the Chalk, the mortality rate amongst oyster spat in the first week of settling may be as high as 98% (Andrews, 1948). But amongst those individuals of *S. spinosus* that successfully survived this initial test and achieved a foothold on the bottom, competition for space would have been very much reduced by the assumption of the adult free-living habit. Most of the functions usually suggested for molluscan spines are obviously inapplicable to those of *S. spinosus*, though the possibility of non-functionality is eliminated by the observation that spines broken at the growing edge are immediately repaired. By virtue of their confinement to the lower valve, the spines are unlikely to have served either as camouflage or as a protection against predators. Since they must have been lined with mantle tissue when actually at the growing edge, this mantle tissue (but not necessarily the spines themselves) must inevitably have provided a certain amount of information to the animal as to its external environment. By virtue of their exposed position external to the shell, these epithelial outposts would be particularly well situated to garner information on the turbidity of the water, or to estimate how much material was falling from suspension at any given time. It is impossible to estimate how much of this type of information was in fact made available to the animal by its exposed mantle tissues. Such an estimate would be dependant upon properties of the mantle at the cellular level, of which we have little knowledge in Recent species and no direct evidence for any fossil species.

However, it is extremely unlikely that the superbly moulded spines are merely an incidental effect, being secreted as 'support' structures for epithelial tentacles. Recent *Lima* for example has a highly tentaculate mantle edge, yet there is no "inevitable" secretion of covering or supporting spines for these tentacles. Indeed, it is obvious that in *Lima* the secretion of any such structures would be positively disadvantageous in view of the importance of the tentacles in the swimming process. It is clear, therefore, that there is a strong *a priori* case for expecting the spines themselves, as discrete from

the epithelial extensions that once occupied them, to possess a definable function.

The common occurrence of adult specimens of *S. spinosus* with conjoined valves and delicate spines intact implies that the animal lived where it is usually preserved (i.e., free on the soft oozy bottom of the Chalk sea), and the obvious functional significance of the spines of *S. spinosus* is that they helped to anchor the animal and so to prevent it from sinking into the soft substrate (a sort of "snowshoe" effect, cf. Grant 1966; see Pl. 3, figs. 4, 7; Text-fig. 4). The angle the spines make with the plane of the commissure, their relative length, their relatively even spacing intervals round the commissure, their concentration on the anterior and posterior flanks where the shell is narrowest and most prone to sink in, their being situated on a relatively flat lower valve—all might be expected in a paradigmatic snowshoe structure.

It is fair to conclude, then, that the spines were secreted as sets around the commissure in order to help stabilise the animal, and prevent it from sinking into the substrate. An inevitable, but probably incidental, result of this is that the mantle tissue secreting any given spine was in a position to convey a certain amount of information about the state of the external environment to the animal; it is unlikely that this was in any way a primary function particularly as the tips of the spines would probably have been buried (cf. Text-fig. 4).

PLICATULA INFLATA J. de C. Sowerby

This species exhibits an interesting development of "snowshoe" type spines, coupled with a tendency to gryphaeate form.

A large specimen of *P. inflata* is about 40 mm high, and is of roughly triangular shape (Pl. 1, fig. 7). Well preserved specimens have an attachment scar on the umbo of the right valve demonstrating clearly that the immediate post-larval stage was one of attachment to a hard substrate. The adult animal was almost certainly too big and heavy to have remained attached by the small attachment scars observed (average height of scar is about 5 mm), and we may infer that it became free living in the adult.

The right valve of *P. inflata* is marked by a number of very strong periodic growth lines (Pl. 1, fig. 7). The commissure represented by any one of these marked growth lines has a number of spaced radial spines (between 7 and 13 in number) distributed evenly around it (Pl. 2, fig. 7). Finer growth lines (Pl. 2, fig. 8) clearly display that these spines were built during a growth pause represented by the

marked periodic growth line; during normal shell growth between such periodic pauses, no spines were built. However, the point on the mantle responsible for secreting any given spine during a major growth pause can be traced across the shell between two successive pauses as a faintly marked "radial rib," formed by slight ventral deflections in the mantle edge at a single homologous point throughout ontogeny (Pl. 2, fig. 7).

Similar sets of spines are secreted on all major growth pause commissures up to about five in number; throughout this part of ontogeny the valve is very flattened. When a valve height of about 20 mm is reached, many (though not all) specimens undergo a further ontogenetic change. This rate of shell secretion relative to the rate of mantle expansion is increased (see Carter, 1967) inevitably resulting in a more deeply cupped lower valve of gryphaeate shape; concomitant with this there is a cessation of secretion of spines around the commissure.

Functional interpretation.—This entire ontogenetic sequence is readily explicable in terms of functional morphology. The initial attached stage is one that seems to have been essential for successful survival of all spat in the Chalk sea. After detachment of the shell to lie on the surface of the substrate there would have been an ever increasing danger of the shell sinking into the ooze as its weight gradually increased relative to area. The spines were an attempt to counter this tendency. Details of their morphology (regular spacing, flattened blade shape, concentration on the lateral shell flanks, etc.) are similar to the spines of *S. spinosus*, and it is apparent that they served the similar purpose of "snow-shoe" type support on the substrate. However, a noteworthy feature of the morphology of *inflata* is that the spines are of relatively constant length on successive growth-pause commissures, and it is

certain that the length of the spines was not increasing proportionately with the size of the shell. The obvious corollary is that the spines must have been increasingly less efficient as supporting structures as shell size continued to increase, and there must have been a tendency for the shell to become submerged in the substrate at a certain stage of ontogeny. That this was a very real danger is suggested by the fact that many specimens never grow beyond this spinous stage. However, of those specimens that do grow larger, an appreciable percentage had recourse to the further adaptation of secreting a gryphaeate lower valve. But allowing the shell to sink into the substrate up to a certain level, this adaptation both stabilised the animal on the bottom and kept the actual commissure clear of the sediment/water interface.

It is probable that these various adaptations were at least partly phenotypic, for there is a tendency for those individuals that are cemented for an abnormally long juvenile phase (as judged from the size of the attachment scar) to miss out the spinose ontogenetic stage altogether; and conversely, those specimens that have a relatively short attachment phase are commonly the specimens that reach a gryphaeate stage late in adult life.

Very few specimens of left valves of this species are extant in current museum collections. Because of its thinness and general fragility, it is presumably generally destroyed on fossilisation. The few preserved specimens are flat, and have short, semi-cylindrical spines (with sutures facing ventrally) arranged in concentric sets along radial lines. These spines are directed at a high angle to the valve surface, and may either reflect tubular sheaths of mantle tissue that reached away from the shell edge in an attempt to increase the efficiency of the inhalant current (cf. Carter, 1968, p. 477-9), or may alternatively have been sensory in function.

APPENDIX 2

A. Quantitative faunal list of Chalk Bivalve species (from Kennedy, 1969), with inferred life-habits.

	number	epifauna/ infauna	adult life habit
<i>Anomia papyracea</i> (d'Orbigny)	5	e	c
<i>Arca</i> spp.	3	e	b
<i>Arctostrea colubrina ricordeana</i> (d'Orbigny)	4	e	sp
<i>Atrreta nilssoni</i> (Hagenow)	1	e	c
<i>Aucellina gryphaeoides</i> (J. de C. Sowerby)	1	e	?b
<i>Barbatia gallieni</i> (d'Orbigny)	19	e	b
<i>Cardita cottaldina</i> (d'Orbigny)	13	i	(bu)
<i>Chlamys aspera</i> (Lamarck)	3	e	b
<i>Chlamys fissicostata</i> (Etheridge)	1	e	b
<i>Crassatellites</i> sp.	3	i	(bu)
<i>Cucullaea obesa</i> (Pictet & Roux)	65	i	(bu)
<i>Cyprina quadrata</i> d'Orbigny	2	i	(bu)
<i>Entolium orbiculare</i> (J. Sowerby)	253	e	sw
<i>Inoceramus crippi</i> Mantell	1019	e	b
<i>Inoceramus etheridgei</i> Woods	2	e	b
<i>Isoarca obesa</i> (Pictet & Roux)	3	e	b
<i>Lima</i> (<i>Plagiostoma</i>) <i>globosa</i> (J. de C. Sowerby)	40	e	?b
<i>Lima</i> (<i>Mantellum</i>) <i>elongata</i> (J. de C. Sowerby)	17	e	?b/?sw
<i>Lima subovalis</i> J. de C. Sowerby	1	e	sw
<i>Lopha semiplana</i> (J. de C. Sowerby)	1	e	c
<i>Neithea gibbosa</i> (Pulteney)	1	e	g/?sw
<i>Neithea sexcostata</i> (S. Woodward)	11	e	g/?sw
<i>Nucula</i> sp.	6	i	(bu)

APPENDIX 2 (Continued)

	number	epifauna/ infauna	adult life habit
<i>Oxytoma seminudum</i> Dames	11	e	b
<i>Panopea mandibula</i> (J. Sowerby)	2	i	(bu)
<i>Pecten beaveri</i> J. Sowerby	8	e	sw
<i>Plicatula inflata</i> J. de C. Sowerby	88	e	sp/g
<i>Pholadomya decussata</i> (Mantell)	1	i	(bu)
<i>Pycnodonte vesicularis</i> (Lamarck)	282	e	c
<i>Spondylus striatus</i> (J. Sowerby)	2	e	c
<i>Spondylus latus</i> (J. Sowerby)	1	e	c
<i>Tellina</i> sp.	1	i	(bu)
<i>Teredo amphibaena</i> (Goldfuss)	2	i	(bo)
<i>Unicardium ringmeriense</i> (Mantell)	10	i	(bu)

n = 1882

% epifauna (individuals) = 94%
 % epifauna (species) = 71%
 % Pterioda (individuals) = 93%
 % Pterioda (species) = 65%

KEY

b, bysally attached
 c, cemented
 g, gryphaeate
 sp, spinose
 sw, swimmer
 (bo), borer
 (bu), burrower

B. Other important bivalve species known from the Chalk (quantitative data not available), with inferred life-habits.

	epifauna/ fauna	adult life habit
<i>Inoceramus cordiformis</i> J. de C. Sowerby	e	?b
<i>Inoceramus costellatus</i> Woods	e	?b
<i>Inoceramus cuvieri</i> J. Sowerby	e	?b
<i>Inoceramus inconstans</i> Woods	e	?b
<i>Inoceramus involutus</i> J. Sowerby	e	g
<i>Inoceramus labiatus</i> (Schlotheim)	e	?b
<i>Inoceramus lamarcki</i> Parkinson	e	?b/?g
<i>Inoceramus pictus</i> J. Sowerby	e	?b
<i>Spondylus spinosus</i> (J. Sowerby)	e	sp

REFERENCES

- Beu, A. G. 1965. Ecological variation of *Chlamys dieffenbachi* (Reeve) (Mollusca, Lamellibranchia). Roy. Soc. N.Z., Trans. (Zool.) 7(5):93-96.
- Black, M. 1953. The constitution of the Chalk. Geol. Soc. Lond., Proc. 1499:lxvii-ii, lxxxv-vi.
- Bromley, R. G. 1967. Some observations on burrows of thalassinidean Crustacea in Chalk hardgrounds. Geol. Soc. Lond., Quart. J. 123:157-182.
- Burnaby, T. P. 1961. The palaeoecology of the foraminifera of the Chalk Marl. Palaeontology 4:599-608.
- Carter, R. M. 1967. On Lison's model of bivalve shell form and its biological interpretation. Malacol. Soc. Lond., Proc. 37:265-278.
- . 1968. The functional morphology of *Arctostrea*, Pervinquier, 1910. Palaeontology 11:458-85.
- Cox, L. R. 1962. British Mesozoic Fossils. British Museum (Natural History), 205 pp.
- Craig, G. Y., and N. S. Jones. 1966. Marine benthos, substrate and palaeoecology. Palaeontology 9:30-8.
- Davis, A. G. 1926. Notes on some Chalk sections in N.E. Surrey. Geol. Assoc. U. K., Proc. 37: 211-220.
- Driscoll, E. G. 1968. Attached epifauna-substrate relations. Limnol. Oceanogr. 12:633-41.
- . 1969. Animal-sediment relationships of the Coldwater and Marshall Formations of Michigan. In Stratigraphy and Palaeontology (ed. K.S.W. Campbell), p. 337-352.
- Etheridge, R. 1913. Palaeontological contributions to the geology of Western Australia. Geol. Surv. W. Aust., Bull. 55.
- Galtsoff, P. 1964. The American oyster *Crassostrea virginica* Gmelin. U. S. Dept. Interior, Fish and Wildlife Service Fishery Bull. 64:480 pp.
- Grant, R. E. 1966. Spine arrangement and life habits of the productoid brachiopod *Waagenoconcha*. J. Paleontology 40:1063-9.
- Hallam, A. 1968. Morphology, palaeoecology and evolution of the genus *Gryphaea* in the British Lias. Roy. Soc. Lond., Phil. Trans. B254:91-128.
- Hancock, J. M. 1963. The hardness of the Irish Chalk. Irish Nat. J. 14:157-64.
- Hofker, J. 1959. Les foraminifères du Crétacé Supérieur de Harmignies, Bassin de Mons. Soc. géol. Belg., Ann. 82:319-33.
- Hudson, J. D. 1967. Speculations on the depth relations of calcium carbonate solution in Recent and ancient seas. Marine Geol. 5:473-480.
- Jefferies, R. P. S. 1960. Photonegative young in the Triassic lamellibranch *Lima lineata* (Schlotheim). Palaeontology 3:362-9.
- . 1961. The palaeoecology of the *Actinocamax plenus* subzone (lowest Turonian) in the Anglo-Paris basin. Palaeontology 4:609-647.
- Jukes-Brown, A. J. 1904. The Cretaceous rocks of Britain. Vol. III. The Upper Chalk of England. Geol. Surv. U.K. Mem.

- Kauffman, E. G. 1969. Form, function and evolution. In Moore, R. C. (ed.). Treatise on Invertebrate Palaeontology. Part N, Mollusca 6, Bivalvia, p. N129-N205. Geol. Soc. Amer. and University of Kansas.
- Kennedy, W. J. 1969. The correlation of the Lower Chalk of south-east England. Geol. Assoc. U.K., Proc. 80(4):459-560.
- Kennedy, W. J., and A. Hall. 1967. The influence of organic matter on the preservation of aragonite in fossils. Geol. Soc. Lond., Proc. 1643:253-5.
- Korringa, P. 1952. Recent advances in oyster biology. Quart. Rev. Biol. 27:266-308, 339-365.
- Lombard, A. 1956. Géologie sédimentaire: les séries marines. Paris and Liège.
- Lowenstam, H. A., and S. Epstein. 1954. Paleotemperatures of the post-Aptian Cretaceous as determined by the oxygen isotope method. J. Geol. 62:207-48.
- Maclean, R. M., and A. E. Trueman. 1942. Variation in *Gryphaea incurva* (Sow.) from the Lower Lias of Loch Aline, Argyll. Roy. Soc. Edinburgh, Proc. B 61:211-232.
- Majewske, O. P. 1969. Recognition of invertebrate fossil fragments in rocks and thin sections. Brill, Leiden, 101 pp., 106 pls.
- Menzel, R. W. 1955. Some phases of the biology of *Ostrea equestris* Say and a comparison with *Crassostrea virginica* (Gmelin). Inst. Marine Sci. (Texas), Publ. 4:1-53.
- Nichols, D. 1959. Changes in the Chalk heart-urchin *Micraster* interpreted in relation to living forms. Roy. Soc. Lond., Phil. Trans. B 242:347-437.
- Orton, J. H. 1928. On rhythmic periods in shell-growth in *O. edulis* with a note on fattening. Marine Biol. Assoc. U.K., J. 15:365-427.
- Purdy, E. G. 1964. Sediments as substrates. In Approaches to Paleoeology (J. Imbrie and N. D. Newell, eds.), John Wiley, p. 238-271.
- Rayner, D. H. 1967. The stratigraphy of the British Isles. C.U.P., 453 pp.
- Reeside, J. B., Jr. 1957. Paleoeology of the Cretaceous seas of the western interior of the United States. Geol. Soc. Amer. Mem. 67:505-42.
- Reid, E. H. 1962. Sponges and the Chalk Rock. Geol. Mag. 99:273-8.
- Rudwick, M. J. S. 1961. The feeding mechanism of the Permian brachiopod *Prorichthofenia*. Palaeontology 3(4):450-71.
- Sanders, H. L. 1956. Oceanography of Long Island Sound, 1952-1954. X. The biology of marine bottom communities. Bingham Oceanogr. Coll., Bull. 15:345-414.
- Shinn, E. A. 1969. Submarine lithification of Holocene carbonate sediments in the Persian Gulf. Sedimentology 12:109-144.
- Smart, J. G. D., G. Bisson, and B. C. Worssam. 1966. Geology of the country around Canterbury and Folkestone. Geol. Surv. U.K. Mem.
- Smith, W. E. 1957. The Cenomanian limestone of the Beer District, South Devon. Geol. Assoc. U.K., Proc. 68:115-135.
- Stanley, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Geol. Soc. Amer. Mem. 125.
- Stephenson, L. W. 1936. Stratigraphic relations of the Austin, Taylor, and equivalent formations in Texas. U.S. Geol. Surv., Prof. Paper 186-G.
- Taylor, J. D., W. J. Kennedy, and A. Hall. 1969. The shell structure and mineralogy of the Bivalvia. Brit. Mus. (Nat. Hist.), Bull. (Zool.) Suppl. 3.
- Thorson, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3(2):267-93.
- Voigt, E. 1959. Die ökologische Bedeutung der Hartgründe ("Hardgrounds") in der oberen Kreide. Paläont. Z. 33:129-47.
- Woods, H. 1897. The Mollusca of the Chalk Rock: Part II. Geol. Soc. Lond., Quart. J. 53:377-404.
- . 1899-1913. A monograph of the Cretaceous Lamellibranchia of England. 2 Vols. Paleont. Soc.
- Worssam, B. C., and J. H. Taylor. 1969. Geology of the country around Cambridge. Geol. Surv. U.K. Mem.
- Wright, C. W. 1935. The Chalk Rock Fauna in East Yorkshire. Geol. Mag. 72:441-2.
- Yonge, C. M. 1936. The evolution of the swimming habit in the Lamellibranchia. Mus. Roy. d'hist. Nat. Belgique, Mem., ser. 2, fasc. 3, pp. 77-100.
- . 1960. Oysters. Collins, 209 pp.
- . 1962. On the primitive significance of the byssus in the Bivalvia and its effects in evolution. Mar. Biol. Assoc. U.K., J. 42:113-125.

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EXPLANATION OF PLATE 3

All Figures of *Spondylus spinosus* J. Sowerby.

- FIG. 1—Upper Chalk, Cheveley, Cambridge. S.M. B.5943. Right valve, $\times 1$.
- 2—Chalk, unlocated. B.M.N.H. LL26834. Right valve, $\times 6$. A specimen of great rarity preserving the umbo of the right valve intact; note the clearly defined attachment scar.
- 3—Chalk, unlocated. B.M.N.H. L.80591. Right valve, $\times 2$. A juvenile specimen showing the early secretion of well developed spines; note the eroded hole in place of the umbo.
- 4-5, 7—Upper Chalk, Cheveley. S.M. B.5944. Left valve above, $\times 1$; 4, umbonal view of the two valves, note the distal flattening of the spines; 5, lateral view; 7, viewed from above, showing the high angle at which the spines meet the outline of the valve edges.
- 6—Upper Chalk. B.M.N.H. L.80536. Left valve, $\times 6$. Very small juvenile upper left valve displaying clearly the early growth stage corresponding to the attached phase of the under valve. Note the spinose ribs on this early growth stage, and the inception of several new radial ribs by bifurcation of previous ribs.

