PSEUDOPLANKTON

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ABSTRACT. All attached epifaunal species have the potential to colonize floating substrates such as driftwood, externally shelled cephalopods, *Sargassum*-like algae and marine vertebrates. Such pseudoplankton are preserved in a much wider range of facies than their benthic relatives. However, they are never as abundant as benthos due to the rarity of attachment sites. Pseudoplanktonic species utilize five attachment strategies: cemented, adpressed, pendent, boring and clinging. Overcrowding appears to be a common problem on floats and consequently the pendent strategy, with its limited attachment area relative to the size of the organism, appears to have been favoured by obligate pseudoplankton. However many species are facultatively pseudoplanktonic, making palaeoecological interpretations difficult. Most reported examples of pseudoplankton, particularly those from black shale facies, are too abundant to be attributed to this group and, in the majority of cases, a benthic mode of life is more plausible. The fossil record of pseudoplankton is thought to be considerably poorer than has hitherto been suggested. Evaluation of the literature reveals a low, although variable diversity of pseudoplanktonic populations through the Phanerozoic. High diversity in the mid-Palaeozoic is due to the presence of large orthoconic nautiloids which provided ideal floating substrates for a number of groups. Unexplained diversity minima occurred in the Permian and Cretaceous.

IN any palaeoecological work it is essential to distinguish between benthic and pelagic elements of the fauna since each provides evidence of their fundamentally different environments. In most instances it is relatively easy to discern the general mode of life of an organism from the morphology of the hardparts or from comparison with extant relatives. In particular, the constraints on morphology of benthic organisms differ greatly from those of free-swimming (nektonic) and drifting (planktonic) organisms. However, a few species have the morphological adaptations of epifaunal benthos yet they pursue a mode of life attached to floating objects (either organic or inorganic) in the water column and hence are effectively planktonic; these are termed pseudoplanktonic forms (alternatively known as epiplanktonic or pseudopelagic forms in some studies). Excluded from this definition are those organisms which secrete their own float, for these are more properly classified with the true plankton. The basic morphology of pseudoplankton means that, should they become detached from their floating substrate before burial, it may be difficult to deduce their original mode of life. As a result, conflicting palaeoecological interpretations have arisen frequently in the literature.

The aim of this paper is to provide criteria for the recognition of pseudoplankton in the fossil record and to discuss some of the biological constraints and consequences of this unusual mode of life. A tripartite classification scheme is then proposed for pseudoplanktonic forms. Finally the moderately diverse, though patchy, history of pseudoplankton in the Phanerozoic is reviewed.

A large proportion of fossil pseudoplankton described in the literature is recorded from black shales. The depositional conditions of this facies undoubtedly provide excellent potential conditions for the preservation of pseudoplankton, but in many cases the rationale behind such reports lies in the assumption that black shale environments are inimical to benthic life. Therefore, by default, any apparently benthic fossils are considered to have fallen on to the sea floor from floating substrates higher in the water column. Taphonomic and functional morphological evidence have rarely been cited to support such interpretations and, as will be discussed below, many examples of so-called black shale pseudoplankton were probably truly benthic.

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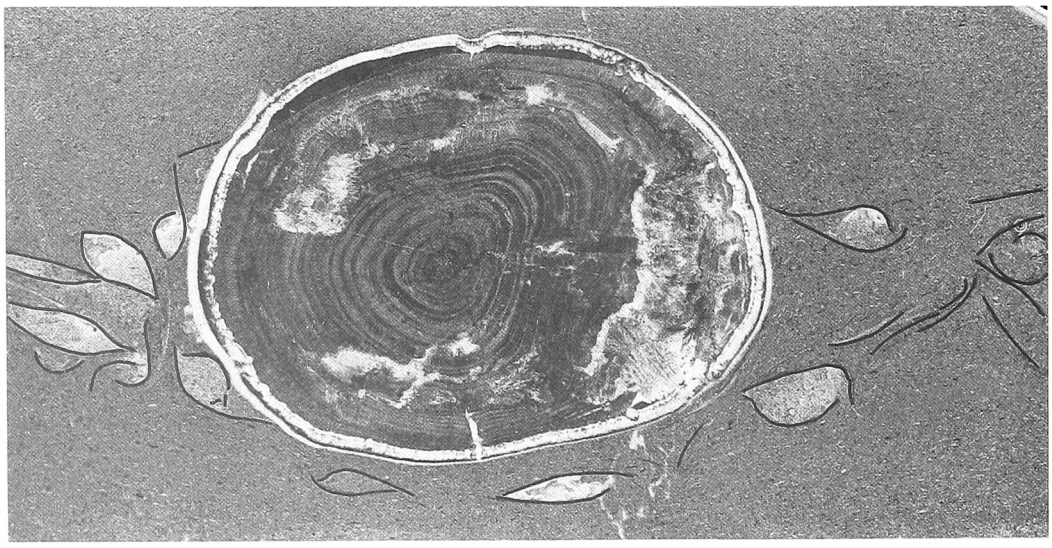
THE RECOGNITION OF FOSSIL PSEUDOPLANKTON

Virtually every aspect of the biology, taphonomy and facies distribution of pseudoplanktonic species differs from that of benthic species. Thus a number of features can be used to identify pseudoplankton in the fossil record.

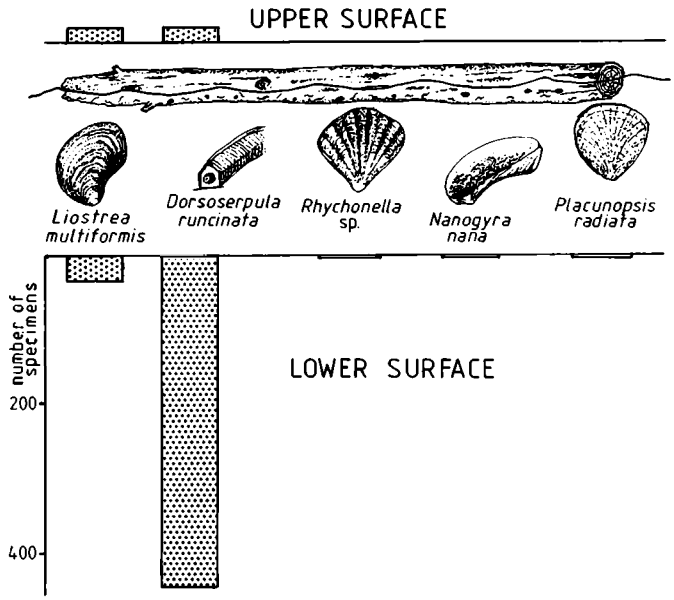
Association with floating objects

Pseudoplanktonic forms are most readily identified when they are preserved together with their floating substrate. The frequency with which this occurs is partially dependent on the style of attachment; for example, cemented bivalves are more likely to remain fixed than byssate forms which readily become dislodged after death. The energy of the depositional environment is also important – quiet conditions, such as those leading to organic-rich shale accumulation, are particularly favourable for the preservation of intact pseudoplanktonic colonies. A range of floating attachment sites was and is available in the marine realm.

Driftwood. Floating logs have been available for colonization by pseudoplankton since the appearance of trees in the late Devonian. Estimates for the maximum floating duration of driftwood range from less than one year (Kauffman 1981) to ten years or more (Simms 1986). The actual time will depend on a combination of factors, such as the nature of the wood, its size, and the influence of osmosis and bacterial sealing (Simms 1986). In general the carrying capacity of wood appears to be high. However, logs can become colonized both while they are afloat and after sinking to the substrate. Pseudoplanktonic colonies are generally found beneath driftwood or alongside the wood if it sank to the substrate at an oblique angle (e.g. Seilacher *et al.* 1968; text-fig. 1). Most pseudoplanktonic colonies on driftwood have been recorded from organic-rich shales (e.g. Withers 1928; McIntosh 1978; Simms 1986) but they are also known from more normal marine mudrocks. Thus Davis and Elliot (1958) record colonies from the Eocene London Clay, whilst a log with abundant epibionts on its lower surface has been examined from aerobic biofacies of the Kimmeridge Clay (text-fig. 2). Lepadomorph barnacles are the dominant driftwood colonizers in modern seas (Schäfer 1972).



TEXT-FIG. 1. Section through a nodule from the Obtusum Zone (Sinemurian, Lower Jurassic) of Stonebarrow Cliff, Charmouth, Dorset, illustrating driftwood, partially calcitized, with individuals of *Cuneigervillia* (outlined) occurring beneath and alongside the wood. Field of view is 100 mm wide.



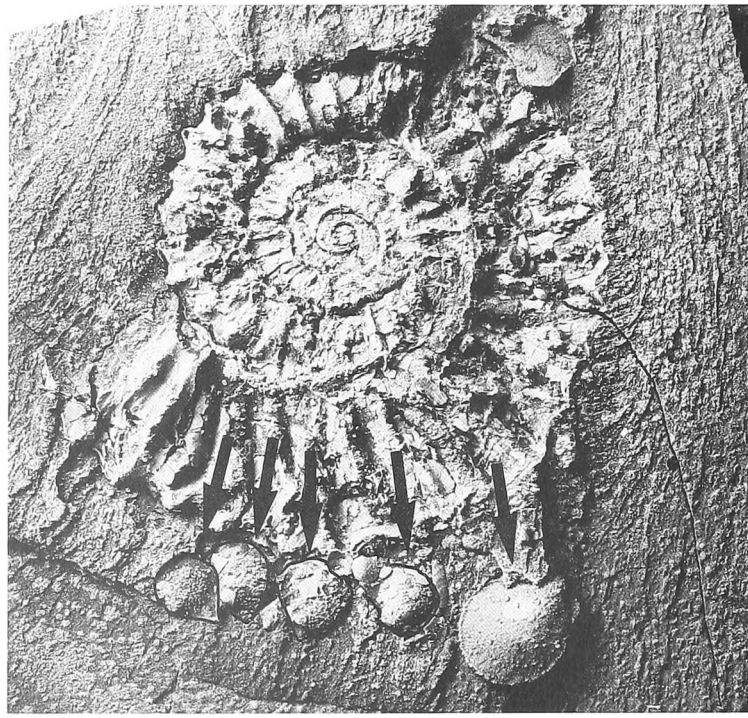
TEXT-FIG. 2. Epizoan abundance measured on a 3·5 m long piece of driftwood from the lower Mutabilis Zone (Lower Kimmeridge Clay, Upper Jurassic) at Wyke Regis, Weymouth, Dorset. The majority of encrusters is found beneath the wood whilst the specimens located towards the edges on the upper surface were probably originally on the flanks of the log. The occurrence of '*Rhynchonella*" *subvariabilis* beneath this log supports Ager's (1962) contention that this species was, at least occasionally, pseudoplanktonic. Several branches on the log would have inhibited it from rolling on the sea floor, thereby discounting the possibility that the log was overturned to cause the smothering of the epizoans.

Externally shelled cephalopods. Nektonic or nektobenthic cephalopods have been available as hosts for pseudoplankton since the Ordovician. The earliest colonizers were bryozoans and inarticulate brachiopods found on large orthoconic nautiloids in the Upper Ordovician (Havlíček 1972; Lockley and Antia 1980; Baird *et al.* 1989). Goniatites, the dominant Upper Palaeozoic cephalopods, were generally too small to support any significant epifauna although they may also have been able to defend themselves from colonization (Boston *et al.* 1988). Large ammonoids became common in the Mesozoic and many examples of oyster encrustation are known (e.g. Meischner 1968; Heptonstall 1970; Riccardi 1980; Seilacher 1982*a*; Tanabe 1983).

There has been considerable debate about whether ammonite colonization occurred during life (Seilacher 1982*a*, *b*), after death but whilst the ammonite was drifting (Palmer 1987; Tanabe 1983), or after the ammonite settled to the bottom to form a localized hard substrate (Kauffman 1981). In the last case, ammonites lying on the sea floor should be encrusted on the upper surface only, although this is not always easy to determine if aragonite dissolution has occurred at an early stage of burial. However, if the ammonite was overturned by foraging organisms then it would be possible for both sides to become encrusted while it lay on the sea floor. Other distinguishing criteria have been discussed by Seilacher (1982*a*). In-life colonization is thought to be characterized by orientated growth, commonly towards the aperture of the cephalopod. Individual ammonites may be heavily encrusted whilst other specimens, from the same horizon, totally lack epibionts. Typically the encrustation is host-specific with heavily ribbed ammonite species being preferentially colonized (Seilacher 1982*a*; Doyle and Whitham, in press). Such patterns are only likely to occur if infestation occurred in the water column where some ammonites may have defended themselves against infestation while others positively encouraged epibionts as a form of camouflage. This implies that most ammonite colonization occurred during life. Defence against unwanted epizoans may have been through active cleansing using tentacles. Alternatively, the possession of a thick

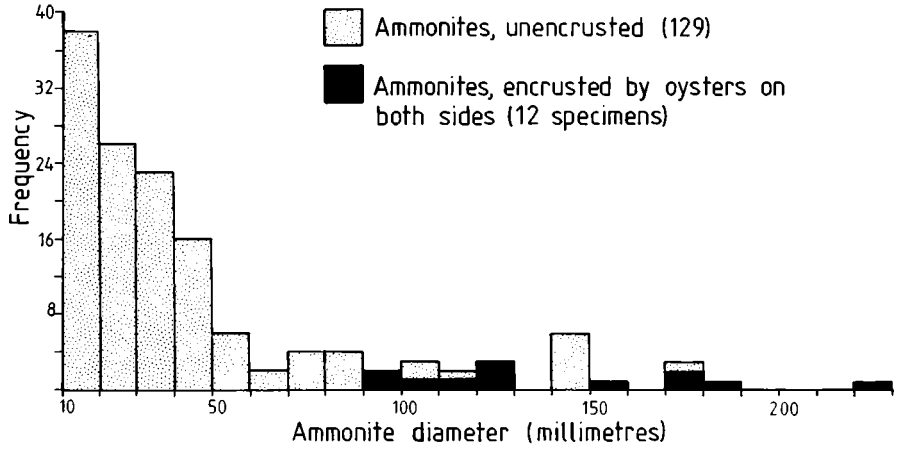
periostracum may inhibit boring and encrustation (Bottjer 1981). In rare cases ammonites have been observed to deviate from their normal planispiral growth pattern due to the presence of large oysters on one flank (Merkt 1966; Heptonstall 1970). Similarly, serpulids growing on the ventral margin of ammonites have been distally overgrown by the later whorls of the ammonite, providing unequivocal evidence of in-life colonization (Merkt 1966).

Nekroplanktonic colonization of dead ammonites floating at the surface cannot always be distinguished from in-life colonization. Diagnostic features include the presence of epibionts within the body chamber of ammonites. The uppermost flanks would project above the surface of the water after death and so these areas would be free of epizoans. Such distributions have rarely been recorded. Data from Recent *Nautilus* suggest that hydrostatic pressure rapidly fills the phragmocone with water following death and thus precludes significant nekroplanktonic drifting (Chamberlain *et al.* 1981). Ammonites were probably less robust than *Nautilus* and hence even less likely to remain afloat for long after death (Seilacher 1960). In general the majority of pseudoplankton associated with ammonites appears to have colonized the ammonite whilst it was alive. Ammonites with apparently *in situ* populations of byssally attached bivalves have been encountered in organic-rich facies from the Lower Jurassic. Seilacher (1982a, fig. 9) illustrated a colony of *Gervillia lanceolata* clustered around the venter of an ammonite close to the aperture. A similar distribution has been noted for specimens from the Sinemurian (Lower Jurassic) of Dorset; *Plagiostoma* has been found associated with *Arnioceras* from the Turneri Zone, *Cuneigervillia* with *Asteroceras* from the Obtusum Zone, and *Oxytoma inequivalve* attached to *Echioceras* from the Raricostatum Zone (text-fig. 3).



TEXT-FIG. 3. Five specimens of *Oxytoma* (arrowed) close to the apertural margin on the venter of a specimen of *Echioceras*. Collected from the Raricostatum Zone (Sinemurian, Lower Jurassic) of Charmouth, Dorset, by C. E. Savrda. The bivalves were probably suspended from beneath the ammonite during life. Benthic colonization would have been expected to produce a more random association. Ammonite is 19 mm in diameter.

In an unusual case of ammonite encrustation, documented by Cope (1968) from the Kimmeridge Clay, oysters were only found cemented to the lower side of ammonites, mainly in the umbilical region. This he attributed to a photonegative response of the oyster larvae settling under ammonite shells lying on the sea floor. However, extensive collecting from the same succession revealed that, of 20 oyster-encrusted ammonites, 14 had oysters on both flanks, 5 had oysters on the upper surface only and only a single specimen was found to have oysters restricted to its lower surface. These data suggest that most oyster-encrustation occurred while the ammonites were still in the water column. The five examples with colonization on the upper surface tended to have oyster nests nucleated anywhere on the shell with little preferred growth orientation. Examples with oysters on both sides of the ammonite tended to show a radial growth orientation centred on the umbilical region. This pattern may have been caused by the oyster spat seeking out the most sheltered region of the ammonite shell although it could also reflect the greater age of the umbilical region compared to the outer whorls. In support of this, all 14 of the Kimmeridge Clay ammonites with oysters on both flanks are large, old specimens greater than 90 mm in diameter (text-fig 4). Similarly, in-life encrustation of ammonites in the Lower Jurassic is mainly restricted to adult examples of large, presumably long-lived individuals. The radial orientation is caused by the competitive growth of the oysters with each individual being forced outwards from the umbilicus by the presence of its neighbours, causing the growth of wedge-shaped morphologies.



TEXT-FIG. 4. Size-frequency histogram illustrating the proportion and abundance of oyster-encrusted pectinatitid ammonites from the Upper Kimmeridge Clay (Upper Jurassic) of the Dorest coast. The over-representation of large and oyster-encrusted specimens in this sample is a collecting artifact. All specimens in the P. B. Wignall collection.

Vertebrates. For most marine vertebrates the presence of pseudoplankton is undesirable since it causes a drastic increase in drag. Precautions against such colonization include the ability to shed scales and the development of a skin surface unsuited to settlement. Only in large or slow moving vertebrates, such as whales and turtles, is the addition of large species of pseudoplankton unlikely to alter the hydrodynamic properties. Whales are commonly infested with large numbers of barnacles (*Xenobalanus* and *Coronula*), copepods and a diverse meiofauna including diatoms (e.g. Holmes 1985). Turtles are commonly host to an even greater range of epizoans, including gastropods, bivalves, hydroids, crabs and barnacles (Frazier *et al.* 1984). Due to the rarity of soft tissue preservation in the fossil record, no examples of pseudoplankton on vertebrates are known, though it is possible that suitably enlightened investigation of the immediate surrounds of large intact vertebrates in anoxic sediments may reveal their presence.

Conulariids. A diverse pseudoplanktonic fauna, including punctate brachiopods and bryozoans, has been found attached to conulariids in the Carboniferous, Bear Gulch Limestone of Montana (Williams 1983), whilst inarticulate brachiopods are considered to have attached to conulariids in the Ordovician (Havlíček 1972). Such occurrences are surprising considering the small, delicate nature of these organisms.

Chondrophorines. The fragile chitinous floats of these jellyfish-like organisms have only recently been identified in the fossil record, many examples previously having been misidentified as patellid gastropods (Stanley and Kanie 1985). As with conulariids, the chondrophorines were probably too fragile to support epizoans commonly, although an exception is the attached fauna found on chondrophorines in the early Devonian Hunsrückschiefer of Germany (Yochelson *et al.* 1983).

Algae. Vesicular algae, such as *Sargassum*, are one of the most common attachment substrates for pseudoplankton at the present day. Brown algae are commonly invoked as attachment sites for ancient epizoans, but such soft material has a very low preservation potential (see Jerzmanska and Kotlarczyk (1976) for an exception). Ruedemann (1934) has illustrated examples of so-called algae from Palaeozoic black shales. Many of these are probably trace fossils but a number of carbonaceous branching structures (e.g. Ruedemann 1934, pls. 2–3) remain unexplained. Rickards (1975) suggested that they may be the extrathecal tissue of graptolites.

Pumice. Pumice, which is probably the only naturally occurring non-organic substrate for pseudoplankton, has been available throughout the Phanerozoic. Its floating duration is dependent on size, initial density, temperature upon entering water and the size distribution and connectivity of the vesicles (Whitham and Sparks 1986). Their experiments showed that some pumice remained afloat for more than 18 months. Extrapolation from their observations suggested that large, low density masses up to 1 m across may remain afloat for more than 10 years. Jokiel (1984) also inferred, from the size of a coral colony attached to floating pumice, that pumice could remain afloat for two to three years at least. Despite such observations, examples of pseudoplankton attached to pumice are very rare in the fossil record, although Doyle and Whitham (in press) have recorded oxytomid bivalves associated with pumice from the Upper Jurassic.

Abundance and facies distribution

In many instances pseudoplankton may become detached from its floating substrate before burial or, in the case of epizoans attached to floating seaweed, their attachment site may not be preserved. In such situations less direct methods of taphonomic analysis must be used to determine their original mode of life.

Pseudoplankton today only constitutes a tiny fraction of the total abundance of epizoans due to the rarity of floating attachment sites compared to the abundant sites available in the benthic environment. Conditions are unlikely to have been significantly different in the past and consequently pseudoplanktonic species should generally be a rare component of fossil assemblages. For examples modern-day lepadomorph barnacles are an important pseudoplanktonic group but their plates are only found in very small numbers, scattered through a wide range of marine sediments (Schäfer 1972). Only under slow sedimentation rates, such as those commonly found in the depositional environments of organic-rich shale (Tyson 1987), will pseudoplankton ever occur in anything approaching moderate numbers. Even under such conditions, pseudoplanktonic forms should not occur as more than a few individuals scattered across bedding planes. Exceptionally slow sedimentation rates may lead to greater abundances although in these instances the pseudoplanktonic species should be accompanied by high concentrations of truly pelagic forms such as fish and marine vertebrates. Epizoans attached to brown algae may reach moderate abundances but do not contribute more than a few percent to the total skeletal carbonate content of modern sediments (Pestana 1985).

Pseudoplanktonic drifting causes species to be preserved in a wide range of benthic environments.

Examples of surprising facies distributions include the rare occurrence of sponges, crinoids and corals in organic-rich shales (e.g. Ruedemann 1934; Bulman 1964; Simms 1986, 1988*b*; Baird *et al.* 1989) where depositional conditions were oxygen-restricted. These groups are known to be particularly intolerant of such conditions at the present day (e.g. Webster 1975) and they are unlikely to have been true benthos in the ancient examples. This is not to say that all apparently benthic species in black shales were pseudoplanktonic, as has been tacitly assumed in many studies, for many groups of organisms, particularly molluscs, are able to live under conditions of very low oxygen (Sageman *et al.* in press).

Rafts of sunken *Sargassum* and their attached fauna have been recorded from modern benthic environments ranging from the intertidal zone down to abyssal depths (Schoener and Rowe 1970; Pestana 1985). Such a wide ranging facies distribution can also be expected for fossil pseudoplankton; indeed, a facies-crossing pattern is one of the most reliable, and widely used criteria for detecting ancient examples (e.g. Ager 1965; Tchoumatchenco 1972). Similarly, pseudoplanktonic species have a widespread geographic distribution when compared to their benthic relatives giving them a good potential for correlation (Schäfer 1972). For example, the pseudoplanktonic genera *Seirocrinus* and *Pentacrinites* are the only Lower Jurassic crinoids known from both the Boreal and Tethyan realms of the Lower Jurassic (Klikushin 1982).

Attachment Strategies

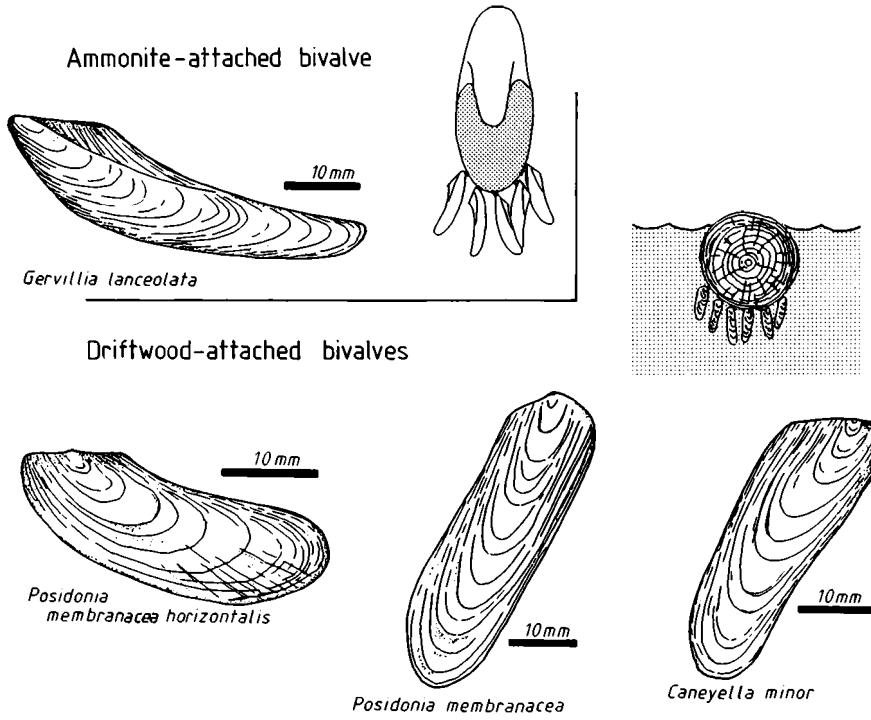
A precondition for all pseudoplanktonic species is the ability to attach to a floating substrate. Five attachment strategies can be recognized.

Cemented. Cementation provides one of the most secure means of attachment but it has the disadvantage that it requires a relatively large attachment area on a substrate where there might be intense competition for space. Oysters, bryozoans and serpulids are amongst the most frequently encountered cemented pseudoplankton in the fossil record, whilst acrothoracian barnacles are common cementers today (e.g. Landman *et al.* 1987); cnidarians and corals are less frequent cementers (Jokiel 1984).

Pendent. Pendent forms have a relatively small attachment area and dangle at some distance beneath their float. This strategy has the advantage of minimizing the area required for attachment on a floating substrate where crowding may be a serious problem. Crinoids (Simms 1986), certain lanceolate bivalves (text-fig. 5), lepadomorph barnacles (Moore 1867) and, more rarely, articulate brachiopods (text-fig. 2) all belong in this category.

The pseudoplanktonic adaptations of lanceolate bivalves include a short hinge line and weak dentition. Both factors tend to reduce the articulation strength, though this is not detrimental since the ligament does not have to operate against the confining pressure of the sediment such as is experienced by endobyssate bivalves. The byssus emerges ventrally to a sharp anterodorsal angle of an equivalve shell. Consequently the attachment area is effectively reduced to a point. In benthic epibyssate bivalves, such as *Mytilus*, the byssus emerges more centrally along the ventral margin and the contact area with the substrate is greater. The lanceolate bivalve morphology is also adapted to a reefal environment (Fürsich and Wendt 1977) where such forms may be able to hang beneath crevices or from branching corals. However, such reef dwellers are typically much thicker-shelled than their thin, fragile pseudoplanktonic relatives.

Few generalizations can be made about the morphology of pseudoplanktonic crinoids since very few are considered to have adopted this mode of life. Both the early Jurassic Pentacrinitidae and the late Devonian *Melocrinites* have an endotomous pattern of arm branching (Simms 1986), though this is by no means unique and is also found in many benthic taxa. The stem of pentacrinitids differs from other articulates in showing an apparent increase in flexibility distally, as might be expected for a pseudoplanktonic crinoid (Seilacher *et al.* 1968), but this has not been documented for melocrinitids. The dense spacing of cirri on the proximal and distal parts of pentacrinitid stems may also be specifically adaptated for a pseudoplanktonic mode of life, though



TEXT-FIG. 5. Lanceolate bivalve genera inferred to have been pseudoplanktonic. *Gervillia lanceolata* is from the Lower Toarcian and is commonly associated with ammonites. The species of *Posidonia* and *Caneyella* are from the lower Namurian of northern England and are inferred to have attached to driftwood which was fairly common at this time.

again this cannot be confirmed from observation of melocrinitids which have a cemented type of attachment at the base of the stem.

Adpressed. Adpressed forms attach themselves by organic tissue or threads and hold tight to the substrate. This has the advantage over the pendant strategy of reducing the chances of dislodgement but, as in cementing forms, the attachment area is relatively large. This mode of life is common in many benthic groups such as mytiliform bivalves, including many inoceramids, and the inarticulate brachiopod genera *Discinisca* and *Orbiculoidea*, of which some individuals may have been pseudoplanktonic (e.g. Tanabe 1983; Seilacher 1982*a*, *b*).

Boring. Tunnelling into the floating substrate is the most secure strategy against dislodgement but has the detrimental effect of reducing its floating properties. Boring bryozoans and acrothoracian barnacles have been reported from belemnites and *Nautilus* (Landman *et al.* 1987; Seilacher 1968). Seilacher (1968) argued that the consistent orientation of barnacle borings in the distal portion of a belemnite guard indicated that such infestation occurred during life. The majority of belemnite encrustation and boring is, however, random and probably occurred after death. Wood is commonly bored by isopods and, more importantly for the fossil record, teredinid bivalves. Boring bivalves appear to utilize wood either as a dwelling, from which to filter feed, or as the source of food itself (Kelly 1988*b*). The latter strategy severely reduces floating duration; consequently wood-eating bivalves are unlikely to be pseudoplanktonic for long.

Clingers. These are species which are able to move about their float, often in search of prey;

Friedrich (1969) referred to them as haptic forms. Only Recent examples are known with certainty. They include pycnogonids, flatworms and gastropods attached to *Sargassum* (Morris and Mogelberg 1973), gastropods and crabs attached to turtles (Frazier *et al.* 1984) and an isopod, *Idotea metallica*, which clings to blobs of crude oil (Herring 1969). The possibility that ancient, vagrant epifaunal forms, such as gastropods, may represent pseudoplankton does not appear to have been appreciated, although they are never likely to be common.

A number of supposed pseudoplanktonic forms from the fossil record cannot be assigned to any of the above five categories. These examples all occur in finely laminated shales of mid-Palaeozoic age and include the praecardioid bivalve genera *Manulicula*, *Butovicella*, *Cardiola*, *Slava* and *Dualina* (Watkins and Berry 1977; Watkins 1978) and lingulid brachiopods (Barron and Ettensohn 1981). *Butovicella* possibly utilized an epibyssate, adpressed strategy (Kriz 1969) but the remaining bivalves are all endobyssate forms (Pojeta *et al.* 1976) which are unlikely to have been able to attach to floating objects. Lingulids are infaunal benthic forms which could not have led a pseudoplanktonic life.

BIOLOGICAL CONSTRAINTS ON A PSEUDOPLANKTONIC LIFESTYLE

The biology of pseudoplankton is severely constrained by a number of ecological features unique to this mode of life. As well as an ability to attach to the float, discussed above, the great rarity of floating substrates necessitates a rapid response when such a site is encountered. Species which produce large numbers of planktonic larvae will clearly have the greatest potential for exploiting floating objects. This can be achieved by large adults producing a large number of offspring at one time or by small adults producing fewer larvae but at more frequent intervals (Jablonski and Lutz 1983). Increasing size of individuals in the former case and continuing recruitment onto the original float in both cases results in a population of large biomass which will rapidly overload the floating attachment site, possibly before the epizoans can reach sexual maturity. Even before the float becomes overloaded it may run aground and cause the premature demise of its occupants. Thus two counteracting selective pressures can be seen to operate on pseudoplanktonic species. A solution to this problem includes the rapid attainment of maturity. This may be achieved by maturation at a relatively small size or by accelerating the growth rate to reach a large size in a short time. The former can be attained relatively easily through heterochrony, in particular paedomorphosis (McNamara 1986), although such forms will be restricted by their small size of producing relatively few larvae at a time. Accelerating growth rates is, perhaps, less straightforward since it requires considerable extra expenditure of both energy and materials. Amongst the pseudoplankton only crinoids appear to have adopted this latter strategy of rapid growth to large size but this required specialized adaptations to increase feeding efficiency. In both the Devonian camerate *Melocrinites* and the early Jurassic articulates *Pentacrinites* and *Seirocrinus*, the arms branch endotomously beyond the second division, an unusual arrangement amongst crinoids generally. This is interpreted as the most efficient filtering arrangement possible for the most economical outlay of materials, comparable with the ideal arrangement of roads on a banana plantation (Cowen 1981). The early Jurassic pentacrinitids further enhanced the efficiency of their filtration fan by the suppression of syzygial articulations in the arms, resulting in the attainment of almost complete pinnulation, a feature peculiar to this group (Simms 1986).

A further strategy which increases the likelihood of colonizing rare attachment sites includes the delay of larval metamorphosis, thereby prolonging the time spent in the water column and thus the time available for encountering attachment sites. Lockley and Antia (1980) documented a probable example of delayed larval metamorphosis in *Schizocrania*, an inarticulate brachiopod attached to orthoconic nautiloids in the Ordovician. There is strong evidence to suggest that the presence of adults may also encourage larval settlement, possibly by a chemoautotrophic response (Crisp 1979; Grosberg and Quinn 1986). The ability of adults to attract larvae probably accounts for the often observed pattern of 'all-or-nothing' pseudoplanktonic colonization. Thus, once a few epizoans are established, their presence can rapidly induce large numbers of other individuals to colonize. For

example, the heavily encrusted log in text-figure 2 occurred with several other large logs which were totally devoid of epizoans. Similarly, Baird *et al.* (1989) noted all-or-nothing encrustation of orthocones.

The development of a relatively lightweight body plan and the reduction of any skeletal components is a further strategy which is likely to prolong the floating duration of attachment sites. Thus, the pseudoplanktonic bakevelliid bivalves of the Lower Jurassic are considerably thinner-shelled than their benthic relatives (Seilacher 1984; text-fig. 5).

Many of the biological constraints on marine wood-borers are very similar to those acting on pseudoplankton as both exploit generally rare resources. It is thus interesting that wood-boring bivalves exhibit many of the life strategies found in pseudoplanktonic species; indeed many such bivalves are also pseudoplanktonic due to the nature of their substrate! Turner (1973) noted that such bivalves tended to be 'r'-strategists.

THE CLASSIFICATION OF PSEUDOPLANKTON

It is clear from an examination of the Recent and ancient record that pseudoplanktonic species can be readily classified on the basis of the relative frequency with which they adopt this mode of life and their dependence upon it.

Obligate Pseudoplankton

This group encompasses forms which have an exclusively pseudoplanktonic adult stage. The biological constraints, discussed above, require highly specialized adaptations which may inhibit them from returning to a benthic existence. Ancient examples include two independent crinoid groups, the Melocrinitidae and Pentacrinitidae (Wells 1941; Simms 1986) and probably many of the thin-shelled, lanceolate bivalve genera of the Palaeozoic and Mesozoic (text-fig. 5). Certain genera of lepadomorph barnacles constitute the most important group of obligate pseudoplankton at the present day with cosmopolitan genera such as *Conchoderma* and *Coronula* occurring attached to a wide range of substrates including whales, turtles and sea snakes (Friedrich 1969). Other genera, such as *Lepas* itself, occur on driftwood (Schäfer 1972). In the past many apparently obligate pseudoplanktonic species appear to have been substrate-specific; for example in the Posidonienschiefer *Gervillia* is restricted to ammonites (Seilacher 1982*a*).

It is noteworthy that many obligate pseudoplankton utilize the pendent strategy which suggests that a limited attachment area is a strong selective advantage. A rather more diverse range of attachment strategies is illustrated by the obligate pseudoplankton associated with *Sargassum* (Morris and Mogelberg 1973).

Facultative Pseudoplankton

The morphology and physiology of many benthic epifaunal species are pre-adapted to enable a limited number of these forms to settle successfully on floating objects. This chance colonization, by normally benthic species, considerably confuses their ecology, particularly in the fossil record, for it misleadingly suggests tolerance of a wide range of facies. For example all the pseudoplanktonic species recorded in text-figure 2 were probably also benthic, for other specimens of these species occur in greater abundance in other Kimmeridge Clay horizons where they are not associated with driftwood. *Pseudomytiloides dubius* is frequently associated with driftwood in the Posidonienschiefer (Seilacher 1982*a*), but in many horizons this bivalve is too abundant for all specimens to have been derived from the relatively rare examples of driftwood (Kauffman 1981). The discovery of a colony of pseudoplanktonic species, associated with a float such as driftwood, does not indicate that all individuals of that species led such an existence.

Accidental Pseudoplankton

This category includes very rare occurrences where benthic species are unintentionally cast adrift. Examples include forams attached to blades of seagrass which become detached (Brasier 1975), the

gastropods found on turtles which are thought to have attached whilst the turtles were at rest on the sea floor (Frazier *et al.* 1984) and possibly an early Jurassic crinoid (Simms 1988*b*). Whilst such chance occurrences are highly unlikely to be preserved in the fossil record, they are of great importance in palaeobiogeography as they vastly increase the dispersal ability of a huge range of benthic species across wide oceans (Ekman 1953; Hallam 1973; Jokiel 1984).

The classification of pseudoplankton is complicated by those species which are able to survive once the floating object has sunk to the substrate. For example ammonites have been observed encrusted by oysters, nucleated in the umbilical region, which have grown-over the outer whorls and across the substrate (Clausen and Wignall, 1990, plate 6d). In such examples initial colonization probably occurred whilst the ammonite was alive and floating in the water column, but they subsequently became 'facultative benthos' after the ammonite had died and settled to the sea floor.

The ability to distinguish between obligate and facultative pseudoplankton is of great importance both in evolutionary and ecological studies. The biological constraints, discussed above, only apply to obligate pseudoplankton. For the facultative species the evolutionary pressures are basically those experienced by the benthic population which contains the majority of individuals of that species. In palaeoecological studies the discovery of a colony of facultative pseudoplankton may be incorrectly extrapolated to assume that all populations of the species pursued this mode of life. The distinguishing features between obligate and facultative pseudoplankton are given in table 1.

TABLE 1. Criteria used to distinguish obligate from facultative pseudoplankton in the fossil record.

	Obligate	Facultative
Abundance and facies distribution	Always rare, found in a wide range of facies.	Occur in a wide range of facies but they reach a peak abundance in one facies type.
Occurrence	Nearly always associated with a floating object.	Very rarely associated with floating objects.
	Commonly found with a particular type of float (host specific)	Found with a range of floating objects.
Morphology	Normally thin-shelled, commonly pendent.	Broad range of morphologies, e.g. cemented, adpressed.
Lifestyle	In comparison to their nearest benthic relatives, they may illustrate delayed larval metamorphosis followed by rapid growth rates.	No unusual adaptations.

EVOLUTION IN OBLIGATE PSEUDOPLANKTON

The profound ecological constraints which influence the biology and morphology of obligate pseudoplankton exert a considerable influence on the evolution of pseudoplanktonic taxa. Once the two basic problems of attachment and reproductive success have been overcome by such taxa, further evolution is likely to be restricted largely to 'fine tuning' of the original strategy. However, opportunities to investigate this hypothesis are severely limited as relatively few supraspecific taxa have a fossil record that is sufficiently good to document evolutionary lineages. This problem is compounded in obligate pseudoplankton due to the rarity of such groups, both in numbers of individuals and taxonomic diversity.

The Mesozoic crinoid family Pentacrinitidae is the only group of obligate pseudoplankton for which an evolutionary lineage has been recognized and documented. The two closely related genera, *Pentacrinites* and *Seirocrinus*, were already quite distinct when first recorded in the late Triassic. Thereafter the two lineages underwent very little morphological change through time and individual species showed unusual longevity by comparison with contemporaneous benthic crinoids. They also showed apparent immunity to the benthic hypoxic event which caused a major faunal turnover in the early Toarcian (Hallam 1986; Simms 1986, 1988*a*), a feature perhaps to be anticipated in pseudoplanktonic taxa. *Seirocrinus subangularis*, a Carixian to Toarcian (Lower Jurassic) species, differs from the Norian (Upper Triassic) *S. klikushini* only in having slightly fewer brachials in each brachitaxis and in the development of a slightly more complex pattern of endotomous arm branching than is seen in other pentacrinitids (Simms 1988*a*, 1990). The two earlier species of *Pentacrinites*, *P. doreckae* (Hettangian to lower Sinemurian) and *P. fossilis* (upper Sinemurian) show an almost parallel change in the number of brachials per brachitaxis (Simms 1988*a*). These changes relate to an increased food-gathering capability in the later species.

In the four described species of *Pentacrinites* there are several marked changes between the earlier *Pentacrinites doreckae-fossilis* part of the lineage and the succeeding *P. dichotomus-dargniesi* lineage. In the latter group the stem is very much shorter with densely-spaced cirri, while the arms have a more poorly developed pattern of endotomous branching and contain syzygial articulations at one or two points, interrupting the pinnule spacing. Furthermore, although *S. subangularis*, *P. doreckae* and *P. fossilis* are very frequently found attached to driftwood (data on this are not available for *S. klikushini*), there are no records of the *P. dichotomus-dargniesi* group having been found in association with driftwood or any other float, yet *P. dichotomus*, at least, otherwise conforms to all the criteria used to identify pseudoplankton. The obvious assumption here is that a fundamental change in life strategy occurred between *P. fossilis* and *P. dichotomus*. The morphological changes suggest that the latter group were no longer subject to the severe selection pressures which operated on the earlier, definitely pseudoplanktonic, taxa. The implication of this is that they either exploited an unusually stable floating substrate, not preserved in the fossil record, or became either truly planktonic, which seems unlikely, or benthic. The latter strategy certainly seems to apply to *P. dargniesi*, but the mode of life of *P. dichotomus* remains unclear.

Evolutionary case histories are less well documented for other pseudoplanktonic groups. *Gervillia lanceolata*, a probable obligate pseudoplanktonic bivalve from the Lower Jurassic, has a long fossil record extending from the Hettangian to the Lower Toarcian (Hallam 1976), although this is not exceptional for a bivalve. Unlike the pentacrinitids, *G. lanceolata* did not survive the early Toarcian hypoxic event (Hallam 1986). The species duration for the mid-Carboniferous homeomorphs (text-fig. 5) is considerably shorter (P. B. Wignall, unpublished data). In all cases the pseudoplanktonic bivalves appear to be species derived from benthic ancestors rather than part of a pseudoplanktonic lineage, implying that this mode of life was, in many cases, an evolutionary 'dead-end'.

BLACK SHALE PSEUDOPLANKTON

The previous review of pseudoplankton in the fossil record has revealed that the majority of examples are reported from finely laminated black shale facies. This may be due to the favourable preservational conditions that occur in black shale depositional environments. The generally low sedimentation rates allow relatively large numbers of pseudoplankton to accumulate whilst the low energy conditions and lack of scavengers in such oxygen-restricted environments are further factors which increase the preservational potential of commonly fragile pseudoplanktonic species.

In the mid and late Palaeozoic the most commonly reported pseudoplankton in black shales are thin-shelled brachiopods belonging to the chonetids, plectambonitids, strophomenids and *Leiorhynchus* (Havlíček 1967; Bergstrom 1968; Thayer 1974), and praecardioid bivalves (Krebs 1979; Watkins 1978), which are inferred to have attached to algae. These groups are widespread spatially within a deep-water, fine grained facies, but they do not occur in other facies. This argues against a pseudoplanktonic lifestyle. Their distribution within the sediment is similarly suggestive

of a benthic existence for they are common on certain bedding planes and absent in the intervening strata; a distribution typical of frequent, opportunistic colonization (Wignall and Myers 1988). Floating algal communities in Recent oceans are characterized by high diversity assemblages dominated by bryozoa. However, the Palaeozoic assemblages are generally mono- or paucispecific. The combined evidence of low diversity, facies restriction and large numbers restricted to individual horizons strongly suggests that the brachiopods and praecardioids were benthic forms in black shales (Thompson and Newton 1987; Sheehan 1977). This has important implications for the depositional conditions of this facies as it indicates that benthic oxygen was available for at least short periods of time.

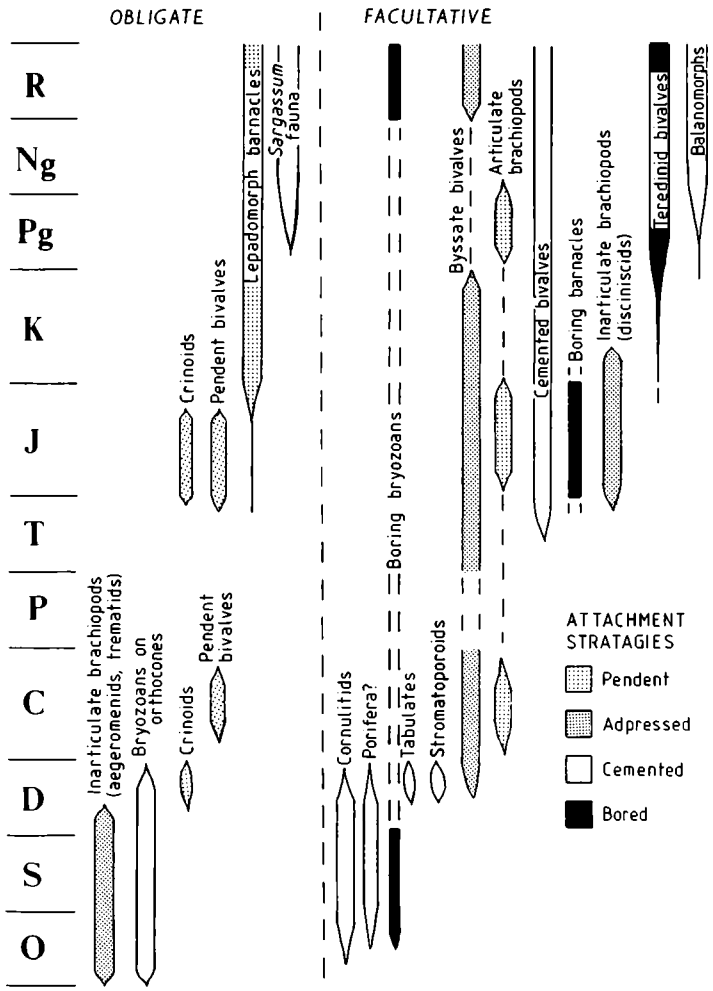
An even larger volume of literature on pseudoplankton relates to a diverse group of pterioid bivalves which occur in black shales from the Devonian to the Cretaceous (Hudson and Cotton 1943; Ichikawa 1958; Hayami 1969). The group includes the posidoniids, halobiids and some of the monotids, buchiids and inoceramids. The functional morphology of these bivalves is far from clearly understood and opinions have changed markedly over the past hundred years. Initially they were thought to be benthic, reclining forms but, with the interpretation of black shale as hostile, anoxic depositional environments, inimical to benthic life, they were reinterpreted as pseudoplankton (e.g. Paul 1939; Hudson and Cotton 1943); a view still widely held today (Hayami 1969; Krebs 1979; Rieber 1982; Campbell 1985; Schumann 1988). Jefferies and Minton (1965) proposed the interesting alternative of a free-swimming lifestyle for some posidoniids. Other recent studies of Carboniferous and Lower Jurassic black shales have concluded that pterioids were probably truly benthic (Antia and Wood 1977; Kauffman 1981; Wignall 1987) with a few, specialized, pendent exceptions (text-fig. 5). The evidence for a pseudoplanktonic existence is slightly more compelling for these pterioids than for the Palaeozoic brachiopods and praecardioids. Many pterioids occur in a greater range of facies than just black shales, although they are nearly always in fine-grained facies. Also, examples of driftwood and other floating objects colonized by such bivalves are relatively common (e.g. Paul 1939; Hauff and Hauff 1981; Tanabe 1983), but these may only be facultative occurrences. However, it is their distribution within the sediment which provides the strongest evidence of a benthic lifestyle. Like the brachiopods discussed above, the pterioids tend to be abundant in thin horizons and absent in the intervening sediment, suggesting brief benthic opportunistic colonization.

Thus, it appears that many of the reported occurrences of pseudoplankton may be more realistically interpreted as true benthos. This considerably increases the diversity of benthic life recorded from black shales whilst substantially reducing the diversity of the pseudoplanktonic record. Many of these occurrences owe their interpretation to the tacit assumption that black shale depositional environments are permanently anoxic, and thus fail to appreciate the highly dynamic nature of many such environments (Sageman *et al.* in press) where even transient improvements in benthic oxygen levels are rapidly exploited by benthic opportunists.

THE PHANEROZOIC HISTORY OF PSEUDOPLANKTON

Having re-interpreted a large number of 'pseudoplanktonic' occurrences as benthic, the remaining record is relatively sparse and weighted towards cementing forms which are the least likely to become detached from their float. The data have been divided into obligate and facultative pseudoplankton (table 1 and text-fig. 6), thus distinguishing between relatively rare, specialized forms specifically adapted to this lifestyle and the more common benthic forms which have occasionally exploited a chance encounter with a floating object.

The potential floating attachment sites in the Cambrian were pumice and possibly algae, but no organisms have been inferred to have adopted a pseudoplanktonic lifestyle during this interval. The appearance of large cephalopods, particularly the orthoconic nautiloids, in the Ordovician was exploited by bryozoans and inarticulate brachiopods (text-fig. 6). Nearly all of these appear to have been host-specific suggesting that they were commensal forms and obligate pseudoplankton (Havlíček 1972; Lockley and Antia 1980; Baird *et al.* 1989). Drifting graptolites also appeared



TEXT-FIG. 6. Changes in the composition of pseudoplankton through the Phanerozoic with obligate and facultative occurrences distinguished. Variation in attachment strategies is also illustrated. The majority of obligate forms appears to have been pendent.

at this time but are considered to be true plankton (Rickards 1975) and are thus beyond the scope of our study. Pseudoplanktonic diversity reached new heights in the Devonian with the first appearance of driftwood which was rapidly exploited by both crinoids (Wells 1941; McIntosh 1978) and bivalves (Nye *et al.* 1975). Curiously, the Carboniferous marked a decline in the fortunes of pseudoplankton despite the increase in driftwood in the world's oceans. However, a number of lanceolate bivalves may have attached to driftwood (text-fig. 5). The main cause of the low diversity is the rarity of cephalopod encrustation. A review by Boston *et al.* (1988) revealed that less than 2% of shells were colonized by epizoans in the Carboniferous and some of these examples may have occurred on the sea floor. This low value was attributed to the success of the cephalopods at defending themselves against unwanted infestation either by physical or chemical means. But this apparent 'success', on the part of the cephalopods, may also be due to the rarity of large forms at this time as the dominant group, the goniatites, were typically small.

Diversity of pseudoplankton appears to have declined to zero in the Permian. The thick sequence of organic-rich shales in the Upper Permian Phosphoria Formation of the United States would have provided good preservational conditions but no pseudoplanktonic forms have been recorded, despite detailed study (e.g. Yochelson 1963).

The Triassic was marked by the appearance of several groups able to exploit a pseudoplanktonic

lifestyle. These include lepadomorph barnacles, cementing bivalves, the reappearance of the lanceolate bivalve morphotype in the bakevelliid lineage, and pseudoplanktonic crinoids (text-fig. 6). Pseudoplanktonic diversity rose to an all time high in the Lower Jurassic with crinoids, inoceramids and lepadomorphs occurring on driftwood (Moore 1867; Tanabe 1983; Simms 1986). Ammonites were infested by an equally diverse range of epizoans including bryozoans, inarticulate brachiopods, oysters and a range of byssate bivalves (Seilacher 1982*a*). A number of Jurassic articulate brachiopod genera also may have attached to floating algae (Ager 1962, 1965; Tchoumatchenco 1972), although, as in many supposed ancient algal colonies, associated fauna such as bryozoans curiously are absent.

Towards the end of the Lower Jurassic the first wood-boring, teredinid bivalves appeared (Kelly 1988*b*). However these Jurassic forms appear to have been exclusively benthic colonizers because, as Kelly (1988*a*) noted for the Upper Jurassic, bored wood is only found in shallow marine arenaceous sediments. Driftwood from contemporary deeper water, muddier facies was not bored. Such a strong facies control upon boring could only occur if the bivalves colonized after the wood had reached the sea floor. During the Cretaceous the frequency of bored wood appears to have increased considerably in all facies, suggesting that the bivalves were able to settle on floating driftwood. This may have had serious consequences for other pseudoplanktonic species as the activity of boring bivalves greatly shortens the floating duration of driftwood.

Faunal changes amongst driftwood faunas in the Upper Jurassic may be at least partially driven by the rise of wood-borers. Obligate, pendent, pseudoplanktonic crinoids and lanceolate bivalves both occur for the last time in the late Jurassic (text-fig. 6). The pseudoplanktonic driftwood colony recorded from the Upper Jurassic in text-figure 2 contains an unusual fauna dominated by encrusting forms (serpulids and oysters) in contrast to the adpressed and pendent strategies of earlier Jurassic driftwood colonies (Hauff and Hauff 1981) and coeval colonies of Antarctica (Doyle and Whitham, in press). By the Cretaceous driftwood is rarely associated with any epizoans apart from boring bivalves (E. G. Kauffman, pers. comm.).

The Cretaceous, like the Carboniferous, marked a low point in pseudoplanktonic diversity primarily due to the virtual absence of cephalopod epizoans, except for some examples from the Maastrichtian (Dunbar 1928; Riccardi 1980). This may have been due to a widespread ability amongst all cephalopod groups to defend themselves against colonization (cf. Boston *et al.* 1988). It also testifies to the likelihood that such infestation occurred during life, for nekroplanktonic infestation would produce a more uniform record through the Phanerozoic. However, preservational factors may also have a major influence on the record. Cretaceous and Carboniferous ammonoids are commonly collected as composite moulds produced by aragonite dissolution. Hence any encrusters may remain embedded in the matrix following collection of the ammonoid.

A few examples of Lower Tertiary pseudoplankton are known (Davis and Elliot 1958; Lindqvist 1986). Associated with many logs of driftwood in the Eocene London Clay of south east England are crinoids (*Isselicrinus subbasaltiformis*) and pendent bivalves (*Pteria papyracea*) – an assemblage strongly reminiscent of Lower Jurassic pseudoplanktonic driftwood colonies, although the Eocene examples more probably colonized the wood after it sank to the sea floor (Taylor 1978). The Eocene also marks the first appearance of a genuine *Sargassum*-like fish fauna (Jerzmanska and Kotlarczyk 1976), but without any associated invertebrate fauna.

The *Sargassum* fauna constitutes the most diverse pseudoplanktonic community in the modern oceans with over 70 species recorded (Fine 1970; Morris and Mogelberg 1973). The majority are small forms, a strategy to reduce weight and the possibility of overloading the brown algae to which they were attached. The bryozoan *Membranipora* is the dominant form and, along with the co-occurring annelid, *Spirorbis*, and the gastropod *Litiopa*, has a fairly high preservation potential. Thus the absence of a pre-Eocene occurrence of these faunas strongly suggests that *Sargassum* is a relatively recent innovation of the Cenozoic. Diverse pseudoplanktonic communities are also known from recent studies of *Nautilus* (Landman *et al.* 1987) and turtles (Frazier *et al.* 1984). Indeed, pseudoplankton is probably more abundant today than at any time in the past due to the large amounts of man-made flotsam found in the oceans, such as hollow plastic, glass and metal

containers. In particular, the use of expanded polymers has created flotsam of very extended floating duration thus increasing the time available for colonization. Boats and ships theoretically provide even more ideal attachment sites since, not only do they have very extended floating durations, they are able deliberately to avoid being cast ashore, thus eliminating one of the major hazards of the pseudoplanktonic lifestyle. Consequently, a wide range of organisms attach to ships (Carlton 1985), much to the chagrin of their owners. Lepadomorph barnacles appear, from personal observations, to be the main group exploiting this new diversity of attachment sites.

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