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The Application of the Community Concept in Paleontology

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Introduction

The stimulus for this paper is twofold: First, at a recent symposium held by the Palaeontological Association of London entitled "Communities Through Time", we presented a paper (Brenchley and Pickerill, 1973) which made suggestions for a suitable terminology to be applied to the studies of ancient communities. Although the community concept has been widely used and applied in paleontology for nearly ten years, it became clear from the discussion that there were considerable differences in the utilization of some of the essential terminology; namely community, association and assemblage. Secondly, a series of papers on ancient benthic marine invertebrate communities have recently appeared (e.g. Thayer 1974, Watkins and Boucot 1975 etc.) which still utilize these terms with a considerable degree of variance. We therefore felt it useful to propose here a terminology which might be adopted by other workers or at least stimulate further discussion which might lead to an agreed terminology.

Discussion

Since the pioneer work of Petersen (1911, 1913) benthic marine communities have generally been considered to be real phenomena. This reality has on occasion been seriously contested (eg. Lindroth 1935, MacGinitie 1939, Muller 1958), in part because it is still not agreed whether or not a species is variously and complexly distributed, each according to its own physiological and biotic relations to the environment and other species (the "opportunistic species" of MacArthur 1960), or whether species are mutually interdependent and occupy non-overlapping niches in an equilibrium community (Whittaker and Fairbanks 1958, Speden 1966, Mills 1969). It is now generally accepted that benthonic organisms compete only to a small degree and occur together because of similar responses to a given physical environment (Neyman 1963, Johnson 1964) and that marine communities are natural units (Speden 1966). For a more detailed discussion of the nature and validity of benthic marine communities, the reader is referred to Allee (1934), Thorson (1957), Jones (1961), Raymont (1963), Johnson (1964) and Speden (1966).

In addition, it is generally accepted that community analysis is beset with many inherent problems, particularly with respect to the shortcomings of the geological record, but this should not preclude analysis. We assume, though this is not always clarified, that most paleontologists who have described fossil "communities" are expressing the experience that certain assemblages of fossils are recurrent and that the association of species represented is not a matter of chance but is related to specific environmental parameters. At

the outset there is a problem of relating this paleontological experience to the community concept, which embodies very different attitudes even amongst ecologists. Because there is not even agreement on the concept, Mills (1969) has suggested that the word community should have a practical meaning and has defined it as "a group of organisms occurring in a particular environment presumably interacting with one another and with the environment and separable by means of ecological survey from other groups". A limited and practical definition essentially similar to this has been adopted by other workers (e.g. Newell *et al.* 1959; Johnson 1972; Bretsky 1969, 1970; Boucot 1970; Walker and Laporte 1970). The recurrence concept has also formed an important part of some definitions of "community" (Petersen 1913, Johnson 1964, Speden 1966 and in the 'recurrent community' of Raup and Stanley 1971). Speden (1966) argues that the definition of a community as "a regularly recurring combination of certain types of animals as a rule strongly represented numerically" allows the recognition of empirical units at the present and in the sedimentary record.

The work of Petersen (1911, 1913), Thorson (1957) and Johnson (1972), amongst others, has suggested that ecological survey is capable of recognizing communities, as defined above, and that the communities are related to environmental parameters, some of which might be recognized by the geologist. Furthermore, there is some evidence that communities are recurrent in the sense that whenever a particular environment occurs a similar faunal composition can be expected. If the practical definition of community as used by ecologists is accepted by paleontologists, they are not usually describing communities because it is only where paleontologists can recognize ecological entities, such as bioherms, that the ecological definition can be applied. The essential point of the ecological definition is that the community is recognized at a given place and time by ecological survey while the paleontological community is recognized by recurrence. Usually the paleontologists' fossil assemblages come from different places at different times and cannot be subjected to a geographical ecological survey. A sample of a bedding plane with untransported fossils is a very limited reflection of a more widely distributed community. Most fossil assemblages on which fossil communities have been based have come from different bedding planes widely separated in space and time. Thus the method by which a paleontologist recognizes a "community" must be different from that of an ecologist and we therefore believe that this should be recognized in a separate paleontological definition or by using a definition which excludes the methodology of recognizing a community but which includes the recurrence concept. The problem of setting limits to a community which

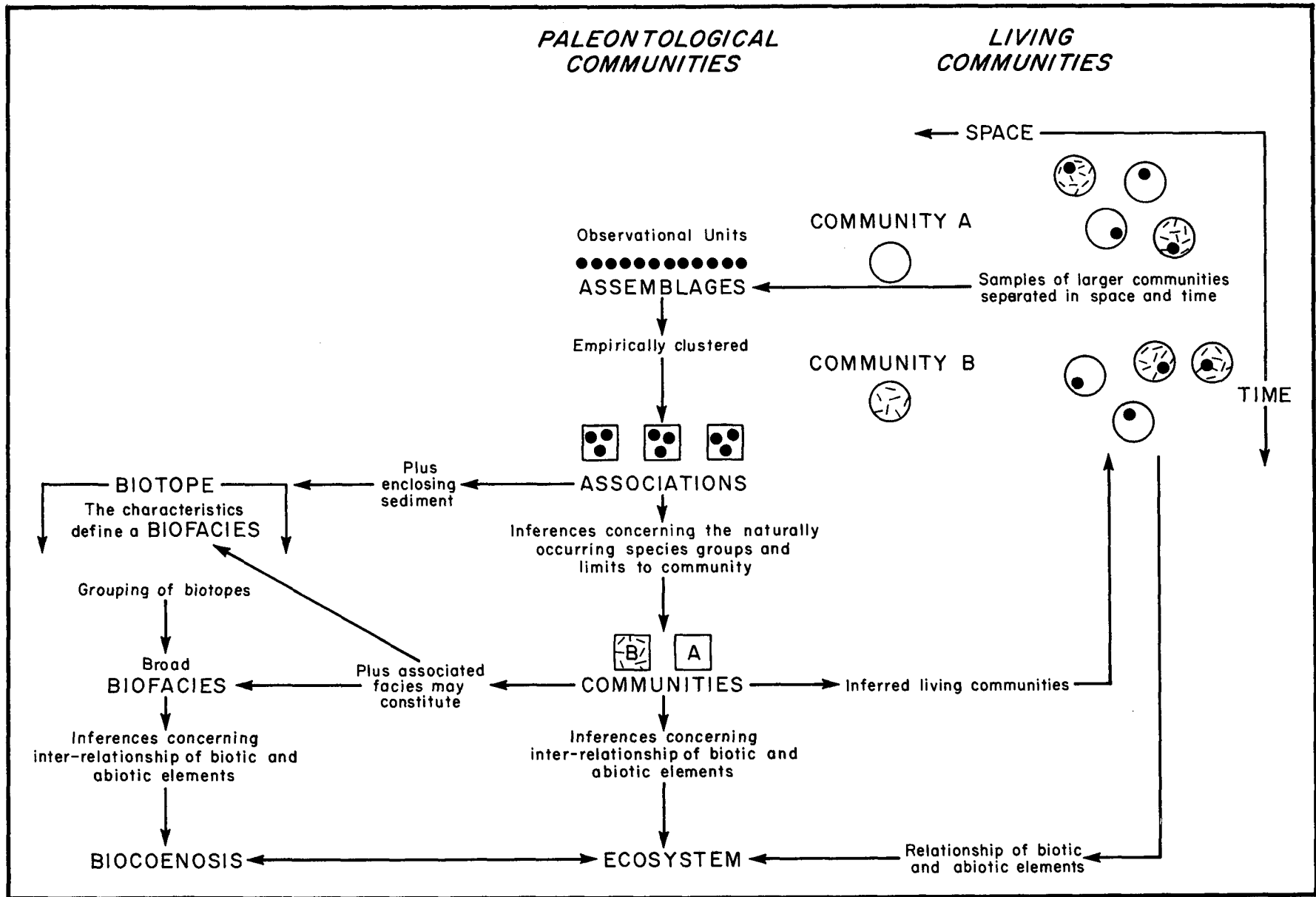


FIG. 1. The relationship between living and fossil communities.

besets the ecologist will be even more acute for the paleontologist. Not only are communities likely to be intergrading in space (Johnson 1972) but they will also intergrade through time. Because of this geographical and chronological intergradation, limits to a community will be arbitrary and it is important that they be as closely defined as possible.

The starting point for recognizing fossil communities is a number of fossil samples taken from rock units or bedding planes representing short-lived depositional events. These fossil samples are assemblages in our terminology. Assemblages commonly show recurrent associations of species which may be monospecific, paired or, more often, larger groups of species. Such associations can often be recognized qualitatively but should also be separable by numerical data handling, particularly by clustering techniques, provided that all associations are not totally intergrading. An excellent summary of the literature describing these techniques is given in Howard *et al.* (1971), p. 137). It is our experience that there is a polymodality in the distribution of species associations and we therefore believe that associations should be defined by grouping assemblages and that communities should be composed of one or more associations (Fig. 1). The ability to define or recognize communities is therefore determined, not only by the structural characteristics of the community being investigated, but also by the number and size of available samples. The community so constructed is arbitrarily delineated but it should reflect a reasonably coherent body of species. If the community is adequately defined on the basis of species associations it should be possible for other workers to allocate assemblages to particular communities.

It appears likely that in a given area communities may be more sharply separated than might be expected, because given the selective nature of the geological record only a small number of well-defined environments may well occur which yield associations which straddle the boundaries of the previously defined communities. This should give no cause for dismay. Generally, communities have been named either after their environment of occurrence (eg. Jones 1950, Buchanan 1958 etc., the *habitat community* of Newell *et al.* 1959) or more commonly after a genus which, in the sense of Johnson (1972), is dominant or characteristic (eg. Molander 1928, Sanders 1960, Fager 1963, Parker 1963, the *organism community* of Newell *et al.* 1959 *ibid.*). However, the paleontological community is recognized by certain associations of species, so that it is not necessary for the chosen genus to be present in every assemblage included in the community. This is as true of communities as it is of biozones!

An alternative approach to synecology (the study of the interrelations between two or more species and their environment) has been developed, largely in Germany, using the terms biocoenosis, biofacies and biotope (Schafer 1972). The term biocoenosis has been used to cover the biotic community and the inter-relationship of the biotic

and abiotic elements which give it its distinctive structure. As such it is similar to an ecosystem. Many elements of a biocoenosis are not preserved and elements of neighboring biocoenoses become partially intermixed and preserved in any body of sediment. The actual body of sediment with its preserved organic remains is the biotope (Schafer 1972 p. 471) and the sum total of lithological and organic characteristics define the biofacies. Communities will more or less coincide in their distribution with biofacies when the communities are closely related to a particular enclosing sediment, but where communities are not clearly related to substrate, as in the case of U. Llandovery communities of Ziegler *et al.* (1968), there is no clear relationship between communities and biofacies.

Schafer (*ibid*), using a combination of environmental and biotic characteristics, has defined five major biofacies. This approach has also been used by Seilacher (1963, 1964, 1967) in recognizing broadly defined biofacies based on the ichnofauna and the related sediment characteristics. It may well prove fruitful to define broad biofacies based on body fossils and environmental characteristics which have a broad applicability through time. It appears as though the recognition of communities and broad biofacies may prove complementary procedures.

The definitions of terms given below emphasize the difference in methodology used in recognizing recent and fossil communities. The concept of a 'recurrent community' is useful in embracing both ecological and paleoecological experience.

Definitions

An ASSEMBLAGE is defined as 'the collected sample' and is purely observational.

An ASSOCIATION is defined as the recurrent association of taxa in a group of assemblages.

A RECURRENT COMMUNITY is defined as a spatially repeated and/or temporally recurring group of organisms which show little variation in composition and is usually related to specific environmental parameters.

A community in the paleontological sense is usually a temporally recurrent community which is recognized by the occurrence of one or more associations.

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