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Application of Ichnology to the Study of Ancient Marine Benthic Community Paleoeology

A Discussion and Case Example

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Introduction

A major goal of marine paleoecology is the description of community structure and evolution over long periods of geologic time and the ultimate development of general models relating them to controlling environmental parameters. Indeed, attempts have been made to trace the evolution of certain communities, for example Bretsky (1969), Anderson (1971), Watkins and Boucot (1975) and Boucot (1975), though as Thayer (1974) points out, such efforts must be regarded with some caution until a sufficient number of detailed regional paleoecologic investigations have been completed. It is generally recognized that community analysis and reconstruction is beset with many problems, particularly with respect to the shortcomings of the geologic record, and Johnson (1960) and Lawrence (1968), for example, have discussed at length the problem of deriving from fossil assemblages an understanding of the original community. However, paleoecology has become perhaps overly concerned about many of these problems, which are inherent in any community study and about which little can be resolved. Ecologists and zoologists too have serious problems, even though they work in modern situations, but they are not deterred. As Boucot (1975, p. 377) points out, "How many communities defined for living materials represent the entire biota?". In a similar manner many of the problems facing paleoecologists should give no cause for dismay!

One problem that is of concern, however, is that many ancient communities are recognized and defined without reference to the soft-bodied elements within the particular community. This concern is related to the fact that many organisms in Recent marine communities are soft-bodied and hence are subject to destruction, decay, and non-preservation after death. Lawrence (1968) for example, based on his own studies of Recent oyster communities in North Carolina and calculated estimates of potential loss by Johnson (1964) and Craig and Jones (1966), stated that a minimum of 7 to 67% of a marine communities' species could be expected to leave no direct record of their existence. That soft-bodied elements constitute an integral and important part of a marine community cannot, therefore, be over-emphasized.

One method of approaching this taphonomic problem, in spite of the numerous inherent problems, is to make a direct study of the trace fossils produced by these soft-bodied organisms. It is perhaps still somewhat enigmatic that in fact many trace fossils are found in sequences otherwise devoid of body fossils. Probably the most classical example of this is afforded by the many *Cruziana*-bearing unfossiliferous shallow water sandstones of Paleozoic age described from many parts of the

world (Seilacher 1970). The absence of body fossils in such sequences is attributed to the fact that sands favoring the preservation of trace fossils are usually too permeable to retain their shelly fossils during diagenesis. Similarly, many sequences formed in outer shelf environments contain trace fossils but are generally devoid of body fossils. This has been related to the fact that soft-bodied annelids are generally more tolerant of low and fluctuating dissolved oxygen concentrations (Rhoads and Morse 1971, Bowen *et al* 1974). Nevertheless, there are also many examples where body fossils and ichnofossils occur in association within the same geological horizon. The purpose of this paper, therefore, is firstly to point out some of the limitations and hazards associated with analysis of trace fossils and secondly to briefly examine and document an example of their application in the context of community paleoecology from the upper Ordovician (Caradoc) rocks of Central Wales, Great Britain.

Some preservational and other hazards

As with body fossils, the detailed observation and sampling of trace fossils depends to a large extent on the size, quality and kind of outcrop and ideally, before any attempt at analysis is made, large three-dimensional exposures are required. Even with seemingly ideal sampling conditions there still remains several difficulties in the application of ichnology to community paleoecology. It has been argued that because they represent a true biocoenosis trace fossils present few problems in terms of analysis. Indeed, ichnologists are certainly not faced with many of the post-mortem taphonomic problems inherent to the analysis of shelly faunas (such problems have been discussed at length by many authors and because they are beyond the scope of this paper the reader is referred to Johnson 1960, 1962, 1964 and Lawrence 1968, 1971). However, there are many preservational hazards unique to trace fossils, particularly those formed at the sediment-water interface, which present important difficulties to their analysis. The more important of these preservational hazards may be summarized as follows:

1. Surface tracks and trails require a change in lithology for their preservation as epi- or hypo-reliefs. Thus, thickly bedded monolithologic sequences will have a lower preservation potential than, for example, a thinly bedded sequence of sands and muds.
2. In many cases a lining or the nature of a sediment fill determine whether burrows remain visible after diagenesis. For example, burrows with mucous-covered bacterial-rich walls will be preserved even with the presence of a lithologically identical casting medium, whereas other traces would perhaps remain unobserved (Pickerill 1974).

3. Preservation of surface traces is dependant on the mass properties of the sediment. In muds, for example, sedimentary parameters which prevent any animal sinking or the walls of the trace collapsing (e.g. shear strength, cohesion and high angle of internal friction) will also favour the preservation of the trace during deposition of the casting medium (see Crimes 1975). Preservation may also be related to water content, for example thixotropic muds are easily resuspended and preservation potential will therefore be lower than in muds containing less water.

4. Taxonomic recognition of the traces is possible when burrow density is low. However, with increasing bioturbation successive generations of burrows may be destroyed and the end product may even be a completely mottled sediment (cf. Moore and Scruton 1957), making the recognition of any characteristic trace fossils impossible.

5. As Fursich (1975) points out, deeper burrows are less likely to be destroyed by wave action or erosion than shallower ones or surface traces and therefore the fossil record is biased towards the former.

In addition to these preservational problems, another difficulty concerning the application of ichnology to community paleoecology is that a single organism can produce more than one trace. This again is particularly critical when attempting to handle quantitatively tracks and trails formed at the sediment-water interface and unfortunately there is little the paleoecologist can do to resolve such a problem. Fortunately, however, ichnofaunas, produced by many soft-bodied organisms are dwelling burrows and it can often be assumed that each organism produces a single trace. In spite of the inherent difficulties associated with the study of ichnofaunas, careful and detailed sedimentological analysis should enable an assessment of the importance of many of these problems to be made. Admittedly some will be impossible to resolve, but to assess the bias presented by them, the problems should be considered as carefully as possible.

Upper Ordovician communities from Wales - a case example

The Upper Ordovician (Caradoc) rocks of Central Wales, Great Britain, contain an abundantly rich shelly fauna and a moderately diverse but less abundant ichnofaunal suite. The dominant ichnogenera are *Skolithos* cf. *linearis*, *Planolites* cf. *beverleyensis*, *Teichichnus* and *Vermiforichnus*. These forms, together with *Diplocraterion parallelum*, *Arenicolites*, *Gyrochorte* and *Palaeophycus* are all produced by organisms of debatable affinity, most of which were probably soft-bodied filter-feeding and deposit-feeding polychaete and oligochaete annelids (Pickerill 1975; 1976, in press). Less frequent ichnospecies are all related to trilobites, for example *Cruziana pudica*, *Cruziana* aff. *petraea*, *Rusophycus jenningsi*; *Rusophycus*, *Trichophycus*, *Monomorphichnus* and *Dimorphichnus* bivalves, for example *Lockeia siliquaria*, and gastropods. Because they were not formed by soft-bodied organisms this latter group of ichnospecies is n

not considered in the ensuing discussion.

Fortunately the collection of ichnofaunal data from the succession did not prove too difficult and many of the preservational problems mentioned previously could be critically assessed. For example, the sediments consist of a thinly interbedded sequence of muds and silts or sands which show little evidence of secondary modification by wave action or erosion and consequently conditions for preservation must have been extremely favorable. In addition, many of the traces produced by the soft-bodied organisms were dwelling burrows (Pickerill 1976, in press) which, as modern studies demonstrate, invariably possess mucous-covered walls to prevent burrow collapse and would therefore be preserved with relative ease. Furthermore, as stated previously, it can be assumed that each dwelling burrow represented a single individual. The major problem, in fact, was that of ichnofaunal recognition in sediments that were moderately bioturbated. This was approached by studying in detail oriented polished specimens and thin sections of these sediments.

Based on recurrent genera and species associations of the shelly faunas, four low-grade benthic communities have been recognized within the sequence, these being the *Dinorthis*, *Howellites*, *Nicolella* and *Onniella* Communities, each being named after its most characteristic component (see Pickerill 1973, Brenchley and Pickerill 1973; Pickerill and Brenchley 1975). A detailed analysis of the hard-shelled elements constituting these communities is beyond the scope of this paper but essentially they are all controlled by physical (particularly substrate) as opposed to biotic parameters. This is hardly surprising as physical control is likely to have been extremely pronounced in the Paleozoic, before taxa had become specialized for the occupancy of narrowly divided niches (Valentine 1969), a condition which involved increased competitive exclusion between taxa. In brief, the communities tend to be intergrading without sharp transitions and natural breaks. Thus, species characteristic of one community can occur in adjacent coexisting communities, the actual species composition within an individual community fluctuating in response to environmental fluctuations and the order of appearance or disappearance tending to follow the local order of ecological succession or regression. The general patterns exhibited by the hard-shelled elements within these communities, i.e. the direct relation to substrate type and the intergradation between adjacent communities, are also illustrated by several of the ichnogenera.

Figures 1 and 2 illustrate the distribution, in terms of communities, of the ichnogenera produced by soft-bodied organisms. The ichnogenera *Arenicolites* and *Vermiforichnus* form an integral part of the *Dinorthis* Community and are directly associated with sand and coarse silt substrates. Furthermore, they may be regarded as community and substrate specific as they are restricted to the *Dinorthis* Community and do not intergrade with adjacent communities. Diagnostic ichnogeneric elements within the *Howellites* Community, which inhabited muddy silt substrates, include *Skolithos*,

COMMUNITY	DINORTHIS	HOWELLITES	ONNIELLA	NICOLELLA
SUBSTRATE	Sands and silts	Muddy silts	Muds	Calcareous muds and sands
DIAGNOSTIC HARD-SHELLED ELEMENTS	<i>Dinorthis</i> <i>Macrocoelia</i> <i>Leptaena</i> <i>Dalmanella</i> <i>Salopia</i> <i>Oxoplecia</i> <i>Kiaeromena</i>	<i>Howellites</i> <i>Sowerbyella</i> <i>Paracraniops</i> <i>Reuschella</i>	<i>Onniella</i> <i>Sericoidea</i> <i>Paracraniops</i> <i>Modiolopsis</i> <i>Ctenodonta</i> <i>Cyrtodonta</i> <i>Ostracodes</i>	<i>Nicolella</i> <i>Platystrophia</i> <i>Dolerorthis</i> <i>Eoplectodonta</i> <i>Skenidiodes</i> <i>Cremnorthis</i> <i>Leptestina</i>
RELATIVE DIVERSITY	High	Low	Medium	High
ENVIRONMENT	Inshore inner-outer sublittoral	Offshore outer sublittoral	Varied inshore-offshore sublittoral	Varied inshore-offshore sublittoral
DIAGNOSTIC (SOFT-BODIED) ICHNOGENERA	<i>Arenicolites</i> <i>Vermiforichnus</i>	<i>Skolithos</i> <i>Diplocraterion</i> <i>Teichichnus</i> <i>Planolites</i> ? <i>Gyrochorte</i> ? <i>Palaeophycus</i>	---	---
INTERGRADING (SOFT-BODIED) ICHNOGENERA	<i>Skolithos</i> <i>Planolites</i> <i>Teichichnus</i>	---	<i>Skolithos</i> <i>Planolites</i> <i>Teichichnus</i>	<i>Skolithos</i> <i>Planolites</i>

Fig. 1. Structure, composition and ichnofaunal distribution within the Caradocian marine benthic communities of the Berwyn Hills.

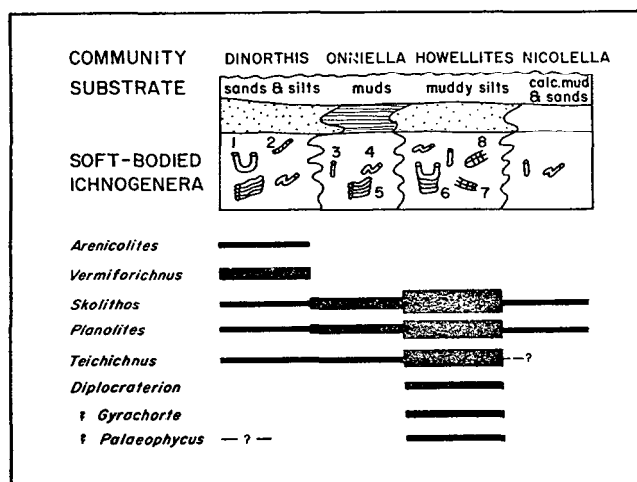


Fig. 2. Distribution of ichnogenera produced by soft-bodied organisms in relation to communities. Bar width expresses the relative abundance of each ichnogenera within different communities.

1 - *Arenicolites*; 2 - *Vermiforichnus*; 3 - *Skolithos*; 4 - *Planolites*; 5 - *Teichichnus*; 6 - *Diplocraterion*; 7 - ?*Gyrochorte*; 8 - ?*Palaeophycus*

Diplocraterion, *Teichichnus*, *Planolites*, *Gyrochorte* and *Palaeophycus*. Several of these elements are community and substrate specific, for example *Diplocraterion*, *Gyrochorte* and *Palaeophycus*, and yet several intergrade with adjacent communities, where they are found with considerably less frequency and in variable combinations. Thus, *Teichichnus*, *Planolites* and *Skolithos*, in particular, may be found as part of the *Dinorthis* Community and *Skolithos* and *Planolites* within the *Onniella* and *Nicolella* Communities. The *Onniella* and *Nicolella* Communities, which inhabited muds and calcareous muds and sands respectively, did not contain any diagnostic ichnogenera but instead contained low numbers of intergrading elements from the *Howellites* Community, in particular *Planolites* and *Skolithos*.

As a corollary, it is also notable that the relative diversity of each community (Fig. 1), a diversity based on the number of hard-shelled elements within each community, is only apparent. Instead, in fact, there would appear to be an inverse relationship between the number of hard-shelled elements within a particular community and the number of related soft-bodied elements. Thus, for example, the *Howellites* Community, which has the lowest relative diversity, contains the most diverse and abundant ichnofaunas and the *Nicolella* Community, which has the highest relative diversity, the least abundant and diverse ichnofaunas.

In conclusion, therefore, it is hoped that this example from Central Wales has served to illustrate some of the dangers in omitting soft-bodied organisms, via the study of trace fossils, in studies of community paleoecology. It must be emphasized that conclusions based on taxonomic diversity as a criterion for paleoecological and evolutionary studies (e.g. Bretsky and Lorenz 1970), conclusions which are often made with complete disregard for soft-bodied elements, must necessarily be regarded with some degree of caution. Hopefully, future community studies will, wherever possible, take into account any associated ichnofaunas so that more meaningful and realistic models on community paleoecology will eventually be realized.

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