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Preservation of soft tissues in the fossil record

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ABSTRACT

Soft bodied fossils are a vital yet under exploited source of palaeontological data. A full understanding of their taphonomy is essential to ensure that the evidence they provide is correctly interpreted. This is being pursued using two complementary approaches, experimental and field based.

RESUME

Les fossiles à corps mous représentent une source d'information paléontologique vitale, mais encore sous-exploitée. Une bonne compréhension de leur taphonomie est essentielle afin de vérifier que les données qu'ils nous permettent d'observer sont correctement interprétées. Les études se poursuivent actuellement en employant deux approches complémentaires, à savoir des données expérimentales obtenues en laboratoire et des études sur le terrain.

1. The importance of soft-bodied fossils

The term Konservat-Lagerstätten refers to occurrences of extraordinarily preserved fossils, where the emphasis is on the quality rather than the quantity of preservation (Seilacher 1970). This category includes, for example, deposits which yield fully articulated skeletons of vertebrates and echinoderms. The most important group of Konservat-Lagerstätten, however, are those that preserve non-biomineralized or 'soft' tissues. They represent a unique source of palaeontological data in a number of areas:

1. *They provide a much more complete record of the diversity and palaeoecology of ancient communities than does the shelly fossil record.* This is nowhere better illustrated than by studies of the soft-bodied faunas of the Cambrian, like the Burgess Shale of British Columbia. Conway Morris (1986) calculated that up to 86% of genera and maybe as many as 98% of individuals in the Burgess Shale deposit would not have been preserved in a 'normal' shelly assemblage.
2. *They represent the only evidence of many extinct types of organism, thus adding to the spectrum of morphologies (and consequently character combinations for cladistic analysis) known from the present day biota.* Inevitably the Cambrian provides some of the classic examples like *Anomalocaris* and *Opabinia* (see Briggs et al. 1994). There are later forms, however – such as *Typhloesus* from the Bear Gulch Limestone of Montana, and *Tullimonstrum* from Mazon Creek, both Carboniferous in age.

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3. *They reveal the morphology of the soft and lightly sclerotized tissues of extinct animals known otherwise only as mineralized skeletons.* Here a good example is provided by the discovery of the soft parts of conodonts, originally in the Carboniferous of Scotland (Aldridge et al. 1993), most recently in the Ordovician Soom Shale of South Africa (Gabbott et al. 1995). A second example is *Archaeopteryx,* the earliest bird from the Jurassic Solnhofen Limestone. Some of the specimens were first interpreted as examples of a small dinosaur until the feather impressions were observed.
4. *They have the potential to provide insights into the factors controlling the growth of authigenic minerals in sediments.* Many of the minerals that form in the early stages of sediment diagenesis do so under the influence of microbial processes involved in the decay of organic matter. Experiments can reveal the controls on mineral growth in association with decaying carcasses (e.g. Briggs & Kear 1994) and, by implication, in soft-bodied fossils. The results can be extrapolated, in turn, to the formation of minerals in sediments.
5. *They provide a target for the discovery of ancient biomolecules.* The most obvious example is the discovery of fragments of deoxyribonucleic acid in soft-bodied fossils trapped in amber. Amber, however, is a special case, and the search for ancient biomolecules in fossils has otherwise focused mainly on plants (which are, of course, soft-bodied fossils in that they lack biomineralized tissues). It has already been demonstrated, for example, that diagnostic chemical signatures are preserved in the structural tissues of a variety of fossil plants (e.g. seed coats of water plants: Van Bergen et al. 1994a; Carboniferous pteridosperm cuticles: Van Bergen et al. 1994b).

It is clear, therefore, that soft-bodied fossils are a very important source of palaeontological data. To understand the biases in these data we need to investigate the processes and controls involved in decay inhibition, the diagenesis of organic material, and the fossilization of soft tissues through authigenic mineralization.

2. The preservation of soft-bodied fossils

Non-biomineralized ('soft') tissues display a range of susceptibility to decay. The most labile, like muscle, are degraded very rapidly, normally within days. In order to be fossilized such tissues must be replicated by authigenic minerals (commonly calcium phosphate) early enough to avoid the loss of morphological detail. This process is finely balanced because some decay is necessary to promote the conditions required for mineralization. In contrast, more decay resistant material, like the sclerotised or tanned (but not originally biomineralized) cuticles of some arthropods, the periderm of graptolites, and the cuticles of plants, may survive and become fossilized as organic material, albeit diagenetically altered. Both these types of soft-tissue preservation may occur in the same fossil assemblage, even in the same fossil.

The preservation of soft tissues is investigated by means of two complementary types of approach: through decay experiments on a range of organisms to explore the early stages of the fossilization process, and through description and analysis of the fossils themselves. The relative resistance of different tissues to decay, and the morphological configurations observed in experiments, can resolve the interpretation of extinct animals. Simple decay experiments on the lancelet *Branchiostoma* (Briggs & Kear 1994a) assisted in the interpretation of the soft-tissues of conodonts (Aldridge et al. 1993). The notochord, for example, is much more decay resistant than the gut, and can be confidently interpreted as represented by the axial lines in the fossils. The rapid decay of the ventral tissue in the head region of *Branchiostoma* provides an explanation for the apparent lack of support for the conodont elements in the fossils.

Replication of labile tissues in calcium phosphate has been induced within two to four weeks in experiments on decaying shrimps (Briggs & Kear 1993). The detail of muscle tissues preserved is comparable to that in examples reported from the fossil record, such as the Cretaceous Santana Formation of Brazil (Martill 1988; Briggs et al. 1993). The experiments indicate that pH is a major control determining whether preservation of soft-tissues in calcium phosphate occurs, or morphological details are lost accompanied by the precipitation of crystal bundles of calcium carbonate (Briggs & Kear 1994b). pH values fall most where the system is closed and diffusion in and out of the decaying carcass is limited. This inhibits the precipitation of calcium carbonate, allowing calcium phosphate to form. Alternatively where the system is open to diffusion pH remains higher and precipitation of crystal bundles of calcium carbonate dominates; they take a range of forms, including discs, rods and dumbbells. Both these minerals may form in different parts of the same decaying carcass. Phosphatized soft-tissues and crystal bundles of calcium carbonate have since been discovered in association in the same fossil, in specimens from the Solnhofen Limestone, for example, indicating that the processes operating in the experiments are similar to those involved in fossilization. The closed conditions that promote soft tissue preservation may be the result, for example, of rapid burial or the formation of a microbial film over the carcass or on the sediment surface.

Histological details of phosphatized soft tissues in fossils have the potential to yield important phylogenetic information. Specimens of the squid *Mastigophora* from the Oxford Clay of Christian Malford, U.K., for example, preserve a continuous series of tissues from the outer tunic, through the mantle and gladius, to the muscular sheath of the digestive gland (Kear et al. 1995). The mantle morphology found in *Mastigophora* and *Belemnotheutis* corresponds to that found in living coleoid cephalopods and indicates that this structure had evolved by the Lower Jurassic. This calls into question the systematic position of *Belemnotheutis* as a member of Belemnitida. A second example is provided by the preservation of extrinsic eye muscles in conodonts (Gabbott et al. 1995), which indicates a degree of encephalization comparable with that of petromyzontids (lampreys).

Field based studies may also throw important light on the factors influencing the preservation of soft-tissues. Investigations of deposits yielding pyritized soft-tissues, such as Beecher's Trilobite Bed (Ordovician, New York State) and the Hunsrück Slate (Devonian, Germany), indicate that the sediments generally contain low concentrations of organic matter and pyrite sulphur, but unusually high concentrations of iron (Briggs et al. in review). Isotopic studies show that pyritization persisted longer in the carcasses than in the adjacent sediment (Briggs et al. 1991; Briggs et al. in review). However pyrite, unlike phosphate, does not replicate the detailed structure of the tissues. The appendages of arthropods, for example, are preserved as an infill. Pyrite grows in the space enclosed by the cuticle that was formerly occupied by muscle. Some indication of the rate of these processes is provided by experiments. Pyrite must grow rapidly to provide evidence of the soft tissues. In shrimps, for example, only structural tissues like cuticle are likely to survive normal decay beyond 30 days. Cuticles, however, may be preserved as an organic trace. Analyses of decaying shrimps show that in the short term (8 weeks) the chitin of the cuticle is preferentially preserved. The cuticle of fossil shrimp, however, is composed of a homologous series of alkanes and alkenes (Baas et al. 1995), and includes no trace of the original chitin. Thus the long term survival of even decay resistant tissues may involve diagenesis to complex biomacromolecules.

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