

TUBE-BUILDING SYMBIONTS OF HERMIT CRABS: PALAEOECOLOGY AND MACROEVOLUTIONARY PATTERNS

TAYLOR, Paul D., Department of Palaeontology, The Natural History Museum, London SW7 5BD, U.K.

Modern hermit crabs usually inhabit the shells of dead gastropods. Many share these homes with a variety of other organisms that encrust or bore into the shell, or cohabit within the chamber of the shell. Sometimes these associations are dominated by a single encrusting species which envelops the entire surface of the shell and constructs a tubular prolongation outwards from the shell aperture, thus enlarging the chamber occupied by the crab. Such massive tube-building symbionts include bryozoans, sponges and cnidarians. Comparatively little is known about the biology of these symbioses, despite the considerable interest in hermit crab behaviour. They are presumed to be mutualistic symbioses but there is no available data on the relative fitness or population growth rates of the two symbionts in and out of association.

The sparse body fossil record of hermit crabs begins in the Early Jurassic. By the Mid Jurassic tube-building bryozoans inferred with confidence to have been symbiotic with hermit crabs make their appearance. Like all subsequent fossil examples of such symbiotic associations, the hermit crab itself is not fossilized but the characteristic tubular form of the symbiont is diagnostic of the former presence of a crab. Unfortunately, loss of the hermit crabs in fossil symbioses restricts analysis of obligacy levels to those of the tube-builder alone, and degrees of species specificity are unobtainable.

The fossil record does, however, allow the distribution of symbiotic associations through geological time to be tracked, and provides a minimum estimate of the time of origin of particular groups of tube-building symbionts. Fossil evidence also increases the diversity of groups known to form such symbioses. For example, there are no tube-building scleractinian corals at the present day but *Septastrea marylandica* is a common tube-building symbiont of hermit crabs in the Pliocene Pinecrest Beds of Florida.

A detailed study of bryozoans symbiotic with hermit crabs has revealed a surprisingly wide diversity of species almost randomly distributed through the taxonomy of the phylum. Seventeen bryozoan families contain tube-building symbionts but in only one of these families (Hippoporidridae) do tube-builders comprise a high proportion of the constituent species. Tube-building symbioses are very rare in the Mesozoic and do not become particularly common until the Neogene. The evolutionary pattern of the bryozoan-hermit crab symbiosis can be summarized as one of multiple origins of symbiotic associations which are seldom obligate and never species specific, with little indication of coadaptation and no evidence of coevolution. This pattern contrasts with the prevailing model of obligate, species specific, coadapted and tightly co-evolved symbioses.