Hermit Crabs as Taphonomic Agents

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Hermit crabs and their gastropod shell-using behavior have existed since the early Jurassic. Their fossil record is considered to be poor (based on occasional cheliped and carapace fragments). Consequently, their influence on gastropod taphonomy is often overlooked. This paper reinterprets the ecological and paleoecological literature, with additions from my own research, to provide a new synthetic framework illustrating the importance and ubiquity of hermit crabs as taphonomic agents. As secondary inhabitants of gastropod shells, hermit crabs physically modify the shells by breakage, or abrasion. They can also indirectly facilitate the settlement of encrusting and/or boring organisms (bionts) onto the shell or they can alter the molluscan shell assemblage as a whole, by transporting or maintaining shells in an anomalous habitat. These modifications are discussed in this paper under the rubric "anomalies" to provide a framework for future taphonomic studies on secondary inhabitants of shells.

Hermit crabs potentially produce numerous anomalies: 1) between-habitat anomalies (bathymetric, transport, and maintenance), 2) within-habitat anomalies (infaunal-epifaunal displacement), 3) abundance anomalies, 4) size-frequency anomalies, 5) shell species anomalies, 6) wear and destruction anomalies, and 7) temporal anomalies. Understanding the hermit crab's taphonomic role clarifies not only their poor fossil record but also their effects on fossil gastropod community structure and, concomitantly, their potential role in influencing the evolution of shell-inhabiting biota.

"After all, hermit crabs are exceeded only by modern executives in their frequency of entry into the real estate market."-Gould, 1982

INTRODUCTION

Physical processes leading to marine fossil accumulation and final deposition have traditionally been studied in more detail than have biological processes in taphonomy. Ocean currents, storm waves, rivers, and shore ice are noted for their abrasive effects on molluscan shells and their contribution to mixed fossil assemblages (e.g., Menard and Boucot, 1951; Valentine and Mallory, 1965; Driscoll, 1967; Clifton, 1971; Spjeldnaes, 1978).

In contrast, the taphonomic contributions of biological agents (e.g., invertebrates and vertebrates) have rarely been studied. These organisms can contribute to mixed fossil accumulations and/or alter the taphonomic information on fossils, including both physical and biological modifications. This process, whereby organisms affect the preservation of hardparts (e.g., molluscan shells), I call biological taphonomy (Walker, in press).

Many organisms can act as taphonomic agents and thereby affect the preservation of molluscan shells. Fungi, blue-green bacteria, and eukaryotic algae bore into mollusc shells (e.g., Perkins and Tsentas, 1976; Kobluk and Kahle, 1978; Tudhope and Risk, 1985) and consequently may accelerate the destruction of shells. Biological agents may also facilitate the preservation of shells by indirectly concentrating shells in burrows (Aller, 1982) or by accumulating shells for homes, camouflage, or other factors (Walker, in press). Because biological taphonomy is complex, with many interacting organisms, I have chosen to discuss the effects of one organism, the hermit crab, and its role in producing and modifying gastropod shell accumulations.

Hermit crabs offer excellent opportunities for studying biologically-induced preservational anomalies. In much the same way that predators and scavengers have a major taphonomic role in the destruction and alteration of articulated carcasses in Africa (Behrensmeyer et al., 1979), hermit crabs scavenge dead, unoccupied gastropod shells. Hermit crabs, then, provide an excellent system for studying taphonomic feedback processes (after Kidwell and Jablonski, 1983) in gastropod shell assemblages.

In this process, dead invertebrate hardparts (the gastropod shell resource) influence the living assemblage (the number and species of hermit crabs). In turn, the living assemblage (hermit crabs) modifies the death assemblage (the shells) either through physical damage or by facilitating biont (encrusting and boring organism) settlement onto the shell (e.g., Wright, 1973; Conover, 1975; Stachowitsch, 1977, 1979, 1980). Many of these bionts have a fossil record and therefore, are important for determining the hermit crab's presence in fossil gastropod assemblages (see Ehrenberg, 1931; Papp et al., 1947; Seilacher, 1969; Carlton, 1972; Taylor, 1981; Palmer and Hancock, 1973; Walker, 1988). Hence, hermit crabs influence the physical quality of the shell resource and can alter the taphonomic information on the shell.

Hermit crabs, until recently, have not been studied from a taphonomic perspective (e.g., Shimoyama, 1985; Walker, 1986, 1988; Frey, 1987). Previously, their contribution to mixed molluscan assemblages has been considered minor

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