

of these studies had experiments with tagged hermitted shells to conclusively deduce shell transport between habitats.

Hermit crab shell transport between habitats may not be limited to shallow water. For example, hermit crabs were found in the Oxygen Minimum Zone (700 m water depth) off Point Sur, California, inhabiting gastropod shells not represented by the living species in that area (Thompson et al., 1985). The only epifaunal organisms found in this zone were hermit crabs and no physical downslope shell transport was found. Thompson et al. (1985) suggested that hermit crabs actively transport, recycle, and concentrate gastropod shells in this zone. Consequently, they conclude that if these shells were preserved in the fossil record, the assemblage might be misinterpreted as a well-oxygenated environment when in fact it represented an anoxic environment. Hazlett (1966) and Schembri (1988) also document behavior and bathymetric distributions of deep-water hermit crabs but do not discuss gastropod shell dynamics within these assemblages.

Marine hermit crabs migrate *en masse*, potentially bringing many deep-water shells shoreward during their seasonal forays. Observing migrating hermit crabs and the shells they inhabit would be an important taphonomic study. Migrating hermit crabs and the shells they import into or export out of habitats would especially affect gastropod shell temporal dynamics. Many hermit crabs migrate from shallow to deeper water during winter months on the east coast of North America (Hazlett, 1981; Scully, 1979) and during the spring on the south coast (Wright, 1973). For example, *Pagurus longicarpus* Say is subtidal in winter and migrates to the intertidal zone of Naragansett Bay on the east coast in spring (Rebach, 1974). *Clibanarius vittatus* migrates seasonally between intertidal and subtidal areas in Texas (Fotheringham, 1976). Migrating marine hermit crabs have also been studied in Japan (Asakura and Kikuchi, 1984; Shimoyama, 1979).

In contrast to marine hermit crabs, land hermit crabs may be easily studied because they transport shells on land. Land hermit crabs make seasonal forays to the sea to mate and exchange shells (see Burggren and McMahon, 1988; de Wilde, 1973). These crabs move several hundred meters a day (Hazlett, 1981; de Wilde, 1973) and are found many miles from shore carrying marine snail shells (Burggren and McMahon, 1988, p. 393-384; Hazlett, 1981; A. Bauer, pers. comm., 1986, New Caledonia; de Wilde, 1973). Thus, these abundant crabs provide the potential for anomalous marine shell deposits on land. Tagging experiments and mark-recapture experiments with land hermit crabs would shed light on this little-studied area and the effect these crabs have on tropical shell assemblages.

#### Maintenance of Shells

Empty shells, carried inshore by currents or other factors, can be maintained in the intertidal zone by hermit crabs. These hermitted shells may represent different habitats than those of the original snail. For example, the sandy habitat snail, *Olivella biplicata*, is one of the most abundant California Pleistocene gastropods. It occurs in an anomalous "habitat": rocky intertidal deposits (Valentine, 1961). Did hermit crabs maintain the shells represented in these fossil deposits?

Valentine (1961) suggested that the anomalous occurrence of the sandy habitat *O. biplicata* in Pleistocene rocky intertidal sites resulted from hermit crabs (based on his Recent observations). However, he had no direct method to deduce whether the shells were in fact occupied by hermit crabs. Using biont trace fossils, Walker (1988) determined that many Pleistocene *O. biplicata* from rocky intertidal sites in California (e.g., Los Angeles County Museum of Invertebrate Paleontology (LACMIP) Loc. 1305, LACMIP Loc. 1307; LACMIP Loc. 1308) were used by hermit crabs.

Low-intertidal to subtidal temperate zone rocky intertidal shells (e.g., *Calliostoma ligatum*, *Tegula brunnea*, *Nucella lamellosa*, *Oceanebra lurida*, *Erato vellitina*, and *Trivia* sp.) are maintained in the high intertidal zone by hermit crabs (Carlton, pers. comm., 1985; Walker, pers. obs.). Conversely, intertidal shells, such as *Tegula funebris*, are maintained subtidally by hermit crabs (A. Kuris, pers. comm., 1986). Walters and Griffiths (1987) discovered that the abundant hermit crab *Diogenes brevisirostris* occupied 20 species of gastropod shells in Langebann Lagoon, near Cape Town, South Africa. Living snails represented only five of the shell types occupied by the crab in the habitat. Thus, 75% of the shell species used and at least 54% of the actual shells occupied appeared to have been imported from other habitats (Walters and Griffiths, 1987, p. 270).

How would one determine whether a fossil shell had been occupied by a marine or terrestrial hermit crab? Land hermit crabs physically modify their shells by removing the columella (Mead, 1961; Kuris and Brody, 1976; Abrams, 1978; Vermeij, 1987). Marine hermit crabs are recognized by biont body fossils (e.g., bryozoan exoskeletons) and/or trace fossils (e.g., borings or etchings) (Ehrenberg, 1931; Boekschoten, 1966; Carlton, 1972; Palmer, 1972; Taylor, 1981; Walker, 1988).

#### Within-Habitat Anomalies

Within-habitat anomalies occur if infaunal gastropods have a postmortem existence as a shell carried by an epifaunal hermit crab. Shell surfaces, left exposed after the snail's death, become available for biont settlement. For example, living infaunal *Olivella biplicata* has a highly polished and mostly biont-free shell (Walker, 1985, 1988). Upon death, an epifaunal hermit crab uses the shell and exposes the shell surface to biont settlement.

Secondary inhabitants of shells are usually overlooked in paleoecological studies. Consequently, biont taphonomic overprints are usually attributed to the living snails or to postmortem settlement on empty shells. For example, Arua (1982, p. 272) inferred that an Eocene gastropod (*Cyrtulotibia unidigitata*) was epifaunal based on the occurrence and distribution of calcareous serpulid polychaete tubes (on the callus and within the aperture). However, within-aperture dwelling organisms are postmortem events. The location of the serpulids on the shell indicates that a secondary inhabitant of the shell, most likely a hermit crab, occupied the shell.

A Recent analogue to this Eocene example is Stachowitsch's (1980) work that describes aggregations of filter-feeding serpulid polychaetes, within and surrounding shell apertures, as characteristic of hermitted shells and not living snails or empty

**TABLE 3**—*Crepidula perforans* in gastropod apertures from Point Cabrillo (Hopkins Marine Station) Pacific Grove, California (Walker unpublished data, August 1985); numbers in parentheses represent the percentage of *C. perforans* per sample size.

GASTROPOD SPECIES	LIVING SNAIL	HERMIT CRAB	N	NUMBER OF SHELLS WITH CREPIDULA PERFORANS
<i>Tegula funebris</i> (Adams, 1855)	+	—	52	0
<i>Tegula brunnea</i> (Philippi, 1848)	+	—	6	0
<i>Calliostoma ligatum</i> (Gould, 1849)	+	—	3	0
<i>T. funebris</i>	—	Pgran	106	17 (.16)
<i>T. funebris</i>	—	Psam	4	3 (.75)
<i>T. brunnea</i>	—	Pgran	106	11 (.10)
<i>C. ligatum</i>	—	Pgran	6	1 (.17)
<i>Olivella biplicata</i> (Sowerby, 1825)	—	Pgran	4	1 (.25)
<i>Nucella emarginata</i> (Deshayes, 1839)	—	Psam	3	1 (.33)
<i>Acanthina spirata</i> (Blainville, 1832)	—	Pgran	7	0
<i>Ceratostoma foliatum</i> (Gmelin, 1791)	—	Pgran	1	0

KEY: + = present; — = not applicable; Pgran = *Pagurus granosimanus* (Stimpson, 1859); Psam = *Pagurus samuelis* (Stimpson, 1857); N = sample size. Living snails and hermit crabs collected from two mid-intertidal tidepools with a search time of one half hour.

shells. He found that bionts could not settle in areas covered by the mantle of the living snail but could settle posthumously in shell areas exposed by the hermit crab. Thus, it is more likely, given the location of the serpulid polychaetes on the Eocene gastropod shell described by Arua, that a hermit crab occupied the shell.

A second example of a potentially erroneous interpretation of life mode concerns slipper limpets (*Crepidula* spp.) that inhabit the interiors of gastropod shells. Pits on large Eocene gastropod steinkerns from West Germany appear to be external casts of the slipper limpet *Crepidula* (Baluk and Radwanski, 1985). Similar aperture-inhabiting *Crepidula* occur abundantly from the Middle Miocene Korytnica Basin in central Poland (Baluk and Radwanski, 1977). These filter-feeding limpets were thought to have settled within empty gastropod shells that had been lying on, or partially buried in, marine soft-bottom sediments. Several reasons for this interpretation were given: shells were corroded, subjected to bioerosion and/or epibionts, or damaged on shell parts exposed above the sediment surface.

A mobile hermit crab that prevented shell burial, enhanced bioerosion, and facilitated the settlement of *Crepidula* is a more plausible paleoecological interpretation for these Eocene *Crepidula*. Slipper-limpets of the genus *Crepidula* (e.g., *Crepidula perforans*, *C. plana* and *C. unguiformis*) are aperture-inhabiting species associated with hermit crabs (Stachowitsch, 1980; Conover, 1979; Fotheringham, 1976; Carlton and Roth, 1975).

Modern studies indicate that *Crepidula plana* occurs on 3-8% of hermitted shells (east coast of North America: Con-

over, 1979; Scully, 1979). Another species, *Crepidula unguiformis*, occurred in 38% of hermitted shells (North Adriatic Sea; Stachowitsch, 1980). *Crepidula perforans* occupied 50% of hermitted *Tegula funebris* at Point Cabrillo, Pacific Grove, California (Baxter, pers. comm., 1985). For the same area, I found that the frequency of occurrence of *C. perforans* was low (Table 3). It appeared that the frequency of *Crepidula* was patchy, depending on the microhabitat sampled (Walker, pers. obs.). Recent and Pleistocene *Crepidula* have also been reported from hermitted shells from Coal Oil Point, Goleta, California (Walker, 1988).

In Recent soft-bottom habitats, empty shells are rapidly buried and bionts attached to the shell either die or sediment prevents their settlement (Conover, 1975; Stachowitsch, 1977, 1979, 1980). Conover (1975) and Stachowitsch (1977, 1979, 1980) present strong evidence that hermit crabs keep the shell above the sediment surface allowing bionts to settle on a sediment-free substrate. For these reasons, it is probable that the *Crepidula* cited in Baluk and Radwanski (1985) settled on hermit crab inhabited shells and not on shells lying partially buried in soft sediment. However, biological dynamics of empty gastropod shells in various soft-bottom habitats needs further taphonomic study.

#### Abundance Anomalies

Abundance anomalies result from hermit crabs that occupy the same species of snail shell side-by-side with the living snail.

Valentine (1961) suggested that overestimates of fossil snail abundance could result from hermit crabs using similar shells in the same habitat as the snail.

This "hermit crab in snail clothing" hypothesis has been tested, in part, by Walker (1988). Using biont body and trace fossils present in Pleistocene *Olivella biplicata* from California, I found that hermit crabs were more ubiquitous (and more numerous) than their reported body fossil record. I extended their paleobiogeographical range from five Cenozoic body fossil localities in California (Rathbun, 1926) to 36 Pleistocene localities using biont fossils. Within each locality, hermit crabs occupied an average of 40% of the shells studied (up to 70% for some localities).

For many of these California Pleistocene communities, the hermit crab number is probably an underestimate of the actual amount of shells used because not all hermitted shells have bionts (Walker, 1988). Consequently, it is highly probable that almost all the Pleistocene *Olivella* were occupied by hermit crabs and not the living snail, especially in localities where the "pagurization potential" was 30% or more.

Abundance anomalies also result from removal of shells by hermit crabs from a habitat. Determination of shell removal from a fossil perspective is difficult to assess, but demonstrating that a fossil assemblage is biased for certain species or lack of species in different localities may indicate that hermit crabs have tampered with the shell resource. Terrestrial hermit crabs (i.e., coenobitids) can remove shells from tropical intertidal zones after storms (Hazlett, 1981). Because land hermit crabs form a large part of terrestrial fauna on tropical islands, they could contribute significantly to fossil shell abundance anomalies. Coenobitids have a fossil record, based on chelipeds, dating from the Miocene (recorded from Java; Glaessner, 1969), and they also remove the columella of gastropod shells (as discussed before). Therefore, it might not be difficult to trace their taphonomic occurrence in fossil gastropod communities.

#### Size-Frequency Anomalies

Size-frequency distributions are commonly used in paleontology to determine if a fossil assemblage has been modified by either physical (i.e., currents) or biological transport (Fagerstrom, 1964; Hallam, 1967; Shimoyama, 1985; Cummins et al., 1986). Shimoyama (1985) suggested that size-frequency distribution of dead shells is influenced by hermit crabs. He found that two species of hermit crabs (*Pagurus dubius* Ortman and *Diogenes nitidimanus* Terao) were selecting a specific size range (7-18 mm) of *Umbonium* (*Suchium*) *moniliferum*. This size range was not transported by currents nor could the shells be passively transported through a seagrass bed. He therefore concluded that hermit crabs caused the size-specific sorting of *Umbonium* shells.

Shimoyama (1985) then applied his Recent size-frequency observations to a Quaternary fossil deposit, with many of the same gastropod species, near Arato, Fukuoka City, Japan. The fossils had a similar size-frequency distribution like his hermit crab-modified Recent assemblage. He concluded that hermit crabs play an important taphonomic role in concentrating shells of a particular size within a habitat.

Shimoyama (1985) further suggested that embayment fossil gastropods should not be used for detailed paleoenvironmental reconstruction because of the potential for hermit crab modification. Although he did not report biont fossils associated with *U. moniliferum*, such an examination would have provided direct evidence that the fossil gastropod shells had been inhabited by hermit crabs.

#### Shell Species Anomalies

Hermit crabs are known for their shell selection capabilities (e.g., Reese, 1962; Orians and King, 1964; Grant and Ulmer, 1974; Mitchell, 1975; Hazlett, 1981). Although shell selection (experimentally shown shell preference) and shell use are sometimes conflated, both are important in formulating taphonomic hypotheses on the range of shells that may be affected by hermit crabs. For example, one hypothetical prediction could be made that shells of trochid gastropods may be consistently occupied by hermit crabs through time. Or perhaps a "guild" of fossil gastropod shells, identified as preferred species from Recent analogues, could be studied through time. In an empirical example, Frey (1987) suggested hermit crabs modify Recent detrital shell accumulations by using a particular subset of shells, which he attributed to shell selection, and concluded hermit crabs would have a taphonomic affect on the resultant gastropod fossil record.

Hermit crabs may select shells for many reasons, such as shell shape, shell weight, presence of certain shell-inhabiting bionts, and shell internal volume (Reese, 1962; Kuris and Brody, 1976; Conover, 1976, 1978; Hazlett, 1981). Hermit crab shell preference differs within and between species and may also reflect different biogeographical provinces (Hazlett, 1981).

Displaying specific preference for shells indicates that hermit crabs may affect the type of shell that is represented in the fossil record. This "gastropod species selection" may have taken place for over 200 million years since the hermit crab's inception (Glaessner, 1969) as result of the culling of shells by hermit crabs.

Shells selected may also reflect predation pressure or physical stress on hermit crabs. For example, in a Bay of Panama study, *Anachis* and *Cerithium* shells were preferred by hermit crabs over *Nerita* shells, despite the greater abundance of *Nerita* shells (Bertness, 1981a,b). The lower intertidal hermit crab, *Pagurus* spp., preferred heavier *Anachis* shells presumably because these shells afforded protection from predation. In the high intertidal zone, two other hermit crabs (*Calcinus obscurus* and *Clibanarius albidigitus*) preferred high-spired *Cerithium* shells, possibly because these shells hold more water and therefore prevent desiccation. Bertness (1981a,b) suggested that *Nerita* provided little protection from predators or physical stresses in the environment. Thus, fossil assemblages containing particular gastropod species could well have been accumulated and deposited by hermit crabs reflecting predation and/or environmental pressures they experienced in the paleoenvironment.

#### Anomalous Wear and Destruction

Recycled shells inhabited by hermit crabs provide post-mortem opportunities for taphonomic information (bionts and

physical damage) to accumulate on the shell. In turn, these taphonomic overprints either contribute to the destruction of the shell or aid in its preservation. For instance, Stachowitsch (1980) observed that numerous bionts associated with hermit shells have constructive or destructive effects. He suggests that calcium carbonate-secreting bionts (coralline algae and the tube worm, *Dodecaceria concharum*) provide shell-protecting support by strengthening the shell. A biomechanical test to determine if the shells were actually stronger with these bionts has not been done. If Stachowitsch's observation is correct, shells with large encrusting bionts, like *Dodecaceria*, would be preferentially preserved in the fossil record.

In contrast, boring clionid sponges and boring polydroid polychaete worms may weaken the hermit crab shell (Stachowitsch, 1980). Frequently, Stachowitsch found only fragments of the original gastropod shell under a thick cover of boring sponges. Thus, the action of boring sponges (and/or polydroid worms) predisposes the shell to fragmentation, and may severely decrease the shell's chances of representation in the fossil record.

How long does a pristine shell last in a rocky intertidal zone once the shell is occupied by hermit crabs? Kuris et al. (1979, in press) released 1000 experimental shells (freshly killed *Tegula gallina* re-occupied with hermit crabs) in the rocky intertidal at Bodega Bay, Sonoma County, California. The released shells showed signs of physical wear in less than three months, and by nine months, the shells were physically and biologically damaged (shells at this stage were abandoned by the crabs). Their results suggest that intertidal snail shells (e.g., *Tegula gallina* and *Tegula funebris*) last a short time within a hermit crab guild before they are discarded. Shells, at any time in their "life," can become part of the fossil record. However, hermit crabs can facilitate damage to the shells such that the fossil record, at least from the early Jurassic, may be biased towards damaged shells or seriously biased shell assemblages.

Modern observations of hermit crabs at gastropod kill sites (areas where predatory gastropods prey on other living gastropods; *sensu* McLean, 1974) indicate that discarded hermit crab shells present at those sites are all damaged (McLean, 1974). These damaged shells are likely to accumulate in those areas, potentially creating a modern "fossil" deposit at gastropod kill sites. However, the ecological studies available do not provide the type and abundance of discarded shells in the habitat and the ultimate fate of the shells. This information is important to the understanding of biologically-induced shell accumulations.

#### Temporal Anomalies

Temporal anomalies may result from fossil shells that are removed from strata directly by hermit crabs or passively picked up by hermit crabs after the fossil has weathered out of a nearby fossil formation. Fossil localities adjacent to modern intertidal habitats are susceptible to temporal reworking by hermit crabs.

A few paleontological studies have suggested that hermit crabs contribute to the reworking of fossil gastropods. Valentine (1980) suggested that the Miocene gastropod *Nucella*

*trancosana*, present in a Pleistocene marine terrace deposit in Baja California, was probably the result of a Pleistocene hermit crab wearing the Miocene shell.

The land hermit crab *Coenobita diogenes* uses shells of the Pleistocene gastropod *Cittarium* as its primary abode on Bermuda (Verrill, 1907; Haas, 1950; see also Gould, 1982). In the Pleistocene of Bermuda, *Cittarium* were deposited on land, presumably by coenobitids. The living snail went extinct in the mid- to late 1800s because of human exploitation. Since that time, the fossil *Cittarium* "real estate" has been used up and, consequently, the coenobitid populations have dwindled (S. Cook, pers. comm., 1987; Gould, 1982).

#### GASTROPOD TAPHONOMIC SCENARIO WITH HERMIT CRABS

Many alternative taphonomic histories are possible for a gastropod shell. A simplified diagram based on the infaunal snail *Olivella biplicata* study by Walker (1988) will summarize the numerous ways the hermit crab influences gastropod taphonomy (Fig. 5).

In Figure 5, the shells of living snails (i.e., *Olivella biplicata*) are relatively pristine (see Walker, 1985, 1988). When the snails die, their empty shells may be immediately buried. If burial is immediate, the shells presumably retain the taphonomic information of the snail and perhaps the predator on the snail (represented by the torn aperture lip in Figure 5).

If the shells are not immediately buried, a number of processes can occur. The shells can be inhabited by a wide variety of organisms (e.g., hermit crabs, sipunculids, octopuses) (McLean, 1983; Vermeij, 1987; Walker, in press). These organisms also have the potential to affect the taphonomic history of gastropod shells. For *O. biplicata*, only hermit crabs secondarily inhabit the shell. It is at this pre-burial stage that many of the hermit crab-associated anomalies occur.

Within-habitat complexity is generated if the habitat has more than one type of hermit crab. For example, two species of hermit crabs, an epifaunal species (*Pagurus granosimanus*) and an infaunal species (*Isocheles pilosus*) can occupy *Olivella* shells. The shell of the epifaunal hermit crab will have numerous bionts whereas the infaunal hermit crab will have no bionts, or will have bionts in restricted areas of the shell (e.g., bionts in the aperture notch) or none at all. The shell, then, has two different taphonomic histories depending on the behavior of the hermit crab: an epifaunal history and/or an infaunal history. Each of these histories provides a taphonomic overprint that can be recognized in the fossil record.

Another complication to unraveling complex gastropod taphonomic histories is "mistaken predation" on empty shells or predation on hermit shells. Empty tethered *Olivella* shells can be crushed by durophagous crabs, a case of mistaken predation (Walker, 1988). In addition, durophagous crabs eat hermit crabs and usually crush the shells to get to their prey. In habitats with many shell destroying predators, whole gastropod shells may not survive to be represented in the fossil record.

If the pagurized shell survives, that is, if it is not destroyed by bioerosion or other factors, it may be buried. Short-term burial may erase some taphonomic information. For example,

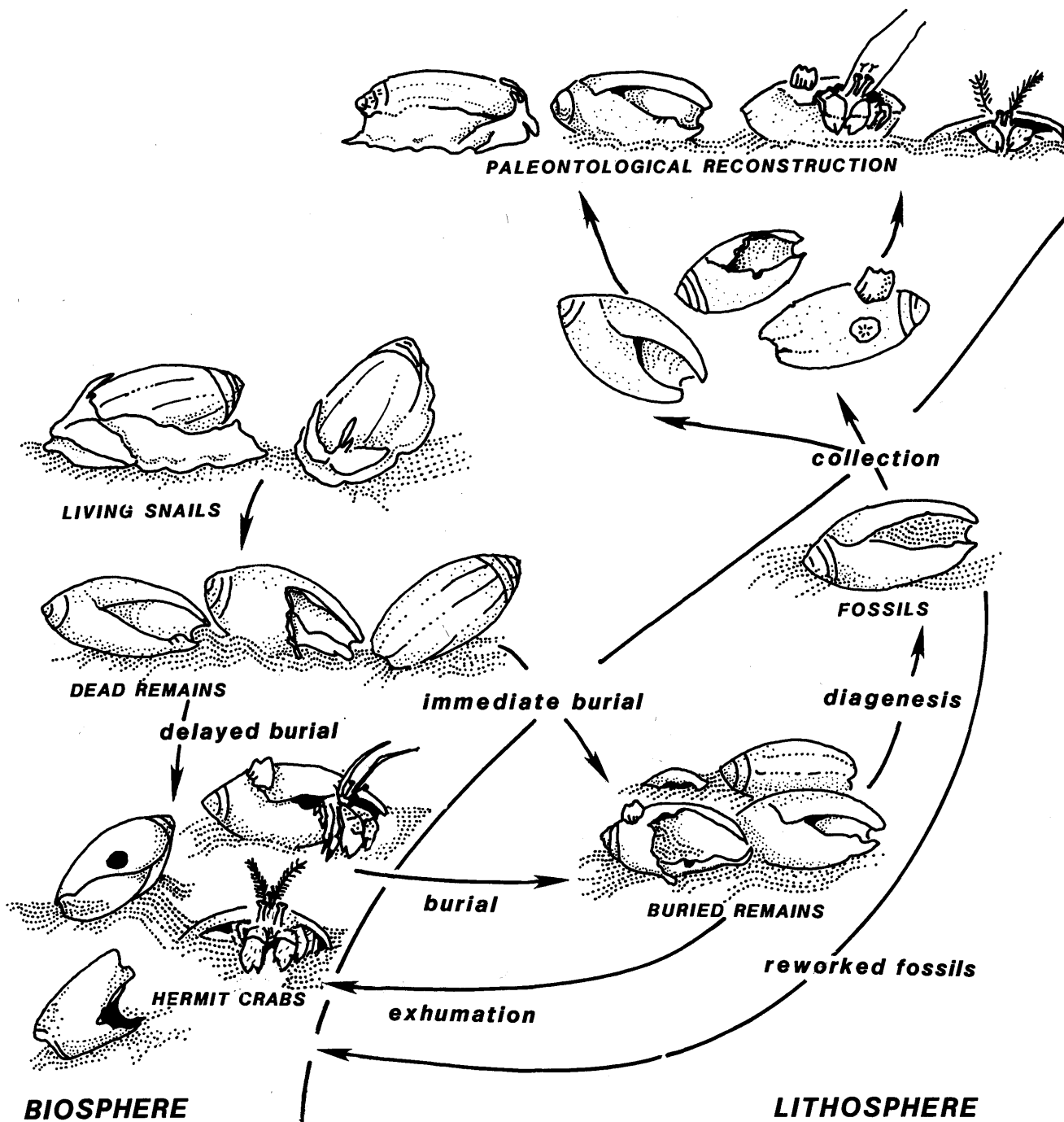


FIGURE 5—A taphonomic scenario illustrating the points at which hermit crabs can affect the preservation of gastropod shells.

shell-encrusting barnacles are least likely to be preserved and encrusting bryozoans are more likely to be represented in the resultant fossil record based on modern burial experiments (Walker, 1988). Some of these buried shells will resurface and

again be inhabited by hermit crabs. Usually, these exhumed shells have black iron oxide discoloration. Hermit crabs also seek out and exhume buried shells, presumably cueing in on calcium carbonate from specific shells (Mesce, 1982). In this

way, recent shells are "reworked" by hermit crabs, further complicating the shell's taphonomic history.

Once the shell has undergone diagenesis, these fossils can be exhumed by hermit crabs as in the classic case described by Hass (1950) and Gould (1982) for the Bermuda land crab *Coenobita diogenes* and its use of fossil *Cittarium*. Temporally anomalous gastropods in fossil deposits have rarely been attributed to hermit crabs (for exception, see Valentine, 1980). However, these temporal "interchanges" mediated by hermit crabs may be more common than have previously been reported.

An additional taphonomic bias exists at the museum level. Many museum shell collections house pristine examples of shells. Damaged shells are usually discarded or relegated to bulk collections. Usually, shells thickly encrusted with bionts, such as bryozoans, are relegated to the phylogenetic drawer under bryozoans and are rarely categorized with gastropods. In fact, recognizing hermit crab bionts in the fossil record has been done mostly by bryozoan workers (Palmer, 1972; Palmer and Hancock, 1973; Taylor, 1981; Taylor and Cook, 1981).

At the paleontological reconstruction level, the paleoecologist may overlook the bionts on the shell or interpret them as associated with the living snail. However, these taphonomic overprints are instrumental in determining if the shell was once inhabited by a hermit crab or another secondary occupant. As Lawrence (1968) observed, paleoecologists must be detectives to unravel the complex preservational histories of organisms and their associated taphonomic overprints. In this manner, much work on Recent communities, from a historical and taphonomic perspective, is needed to identify and refine these clues to organisms (and other factors) that affect gastropod shell preservation.

### CONCLUSIONS

Hermit crabs may have had a greater taphonomic impact on individual gastropod shells, fossil gastropod communities, and gastropod representation in the fossil record than previously acknowledged. This paper has classified seven major taphonomic anomalies potentially created or produced by hermit crabs and discusses their consequences for interpreting gastropod paleoecology and taphonomy. Although hermit crabs are the focus of this paper, there are many other secondary inhabitants of gastropod shells (McLean, 1983; Vermeij, 1987; Walker, in press). These secondary occupants all have the potential to affect the preservation of the shell. However, their contributions to gastropod taphonomic histories has yet to be explored.

Success in paleoecology depends largely on the worker's ability to strip away the taphonomic overprint (Lawrence, 1971). Hermit crabs provide a unique habitat (the postmortem shell) that can be colonized by suspension-feeding bionts; the bionts in turn provide a unique taphonomic overprint that can be recognized in the fossil record.

Understanding the complex interaction between the living community of hermit crabs, their dead shell resource, and the associated shell biota will bracket the range of taphonomic possibilities for what we can expect in gastropod assemblages. Understanding these patterns will not only elucidate little-known biological taphonomic processes, but will also provide

insights into the evolution of hermit crabs and their shell-inhabiting biota through time.

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