

# 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).

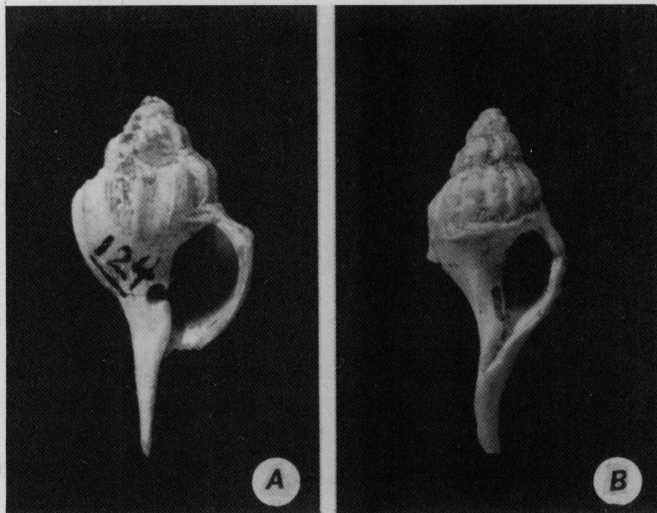
Many organisms can act as taphonomic agents and thereby affect the preservation of molluscan shells. Fungi, blue-green bacteria, and eukaryotic algae bore into mollusc shells (e.g., Perkins and Tsentas, 1976; Kobluk and Kahle, 1978; Tudhope and Risk, 1985) and consequently may accelerate the destruction 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 (Behrensmeier 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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**FIGURE 1**—Deep-water Pleistocene gastropods from California found in shallow-water deposits. **A**) *Trophonopsis dalli* (Kobelt, 1878), Moonstone Beach, Humboldt Co., CAS loc. 124, shell height 14.8 mm. **B**) *Trophonopsis fleenerensis* Martin, 1914, Crannell Junction, Humboldt Co., CAS loc. 58202, shell height 14.2 mm. (CAS=California Academy of Sciences, San Francisco, CA; LACMIP=Los Angeles County Museum of Natural History Invertebrate Paleontology, Los Angeles, CA.)

(Boucot, 1981, p. 332). This consideration is in part because hermit crabs have a poor fossil record (Bishop, 1983) and therefore have not figured in paleoecological research. Even in modern communities, their ecological dynamics are not well known; research on hermit crabs in modern environments has focused chiefly on shell selection (Schembri, 1988; see Hazlett, 1981, for review).

I have reinterpreted the fossil and recent literature, with additions from my research, to provide a new synthesis of and perspective on how hermit crabs may potentially bias fossil accumulations. Seven preservational biases, under the rubric “anomalies” are codified here to call attention to the variety of biological taphonomic processes to which hermit crabs may contribute.

In environments where hermit crabs are common, they may be a significant taphonomic force, a source of bias generally not recognized in studies of the evolution and structure of fossil gastropod communities.

#### POTENTIAL TAPHONOMIC ANOMALIES CREATED BY HERMIT

Crabs Between Habitat Anomalies

##### Bathymetric

A perplexing problem in paleoecology is the occurrence of deep-water fossil gastropods found in shallow-water deposits. These anomalous bathymetric distributions may be explained by biological agents either transporting the shells into shallow water or maintaining the shells that have “washed” into shallow-water areas. Distinctions between shell “transport”

and “shell maintenance” are not clear and will be discussed in more detail later.

Most bathymetric anomalies are identified from Pleistocene deposits because the fossil gastropod shells have living analogues from which their fossil depth distributions are inferred. The California Pleistocene provides many examples of anomalous species (Table 1). Physical processes (such as storms), different thermal tolerances between modern and Pleistocene species, and reworked older shell deposits have been used to explain these anomalous distributions (e.g., Woodring et al., 1946; Emerson and Addicott, 1953; Emerson, 1956; Valentine and Mallory, 1965; Addicott, 1966, 1969; Zimmeister, 1974).

Biological factors, such as kelp and diving marine birds, may contribute to anomalous bathymetries. Kelp, washed up on beaches after storms, can carry deep-water shells (Valentine, 1961; Dell and Fleming, 1973). Neogene marine birds may have contributed to mixed molluscan fossil assemblages by bringing fish (that had eaten deep-water molluscs) to their nearshore rookeries (e.g., Teichert and Serventy, 1947; Smith, 1952; Lindberg and Carlton, 1969; Lindberg and Kellogg, 1982). Molluscivorous fish are size-selective in the type of prey they prefer and may transport shells inshore, thereby biasing shell accumulations (see Boucot, 1981, p. 220, 226-230, 235-236). Hermit crabs have also been implicated in shell transport (Kohl, 1974; Arntz et al., 1976). Kohl (1974) reported two anomalous deep-water gastropods, *Trophonopsis fleenerensis* and *Trophonopsis dalli*, from his Crannell Junction (Humboldt County, California) shallow-water Pleistocene locality. He suggested that hermit crabs and/or currents brought the deep-water shells into shallower water. Hermit crab body fossils were not present at his locality. In fact, only five localities in California are known to have pagurid body fossils (Rathbun, 1926). Is it possible to dismiss Kohl's hermit crab hypothesis on the lack of body fossils at his locality?

No. The bathymetric distribution of Pacific Northwest hermit crabs are well within the range of deep-water snail species (Table 2). Seven species of hermit crabs range from shallow subtidal waters to deep water (>90m) off the coast of California (Table 2) and one could argue that most of these species may have lived in the Pleistocene. In addition, a unique trace fossil, *Helicotaphrichnus commensalis*, which occurs in the columella of only hermit crab-inhabited shells, is present in many Pleistocene localities and can be used to document the hermit crabs' occurrence in those localities (Kern et al., 1974). I obtained specimens of *T. fleenerensis* (collected by Kohl from Crannell Junction) and *T. dalli* (collected from Moonstone Beach, a nearly fossil locality) and examined them for the occurrence of this trace fossil. Both specimens had *Helicotaphrichnus* bore holes in their columellae (Figs. 1A and 1B), indicating that these deep-water shells were previously occupied by a hermit crab.

It is clear that hermit crabs occupied these shells and maintained them in shallow water, but it is not known whether they physically transported the shells into the shallow habitat. Marine hermit crabs have the ability to transport tagged shells long distances (S. Gilchrist, pers. comm., 1988) but no studies have been done to address this question from a historical (taphonomic) perspective.

In addition to *Helicotaphrichnus* bore holes, there are many

**TABLE 1**—Reported anomalous deep-water gastropods from California Neogene deposits (Recent examples are noted). Present depth distributions from these sources: (1) Kohl, 1974, (2) McLean, 1978, (3) Lindberg and Kellogg, 1982; S = southern California, N = northern California.

GASTROPOD SPECIES	PRESENT DEPTH DISTRIBUTION	REFERENCE
<i>Buccinum</i> cf. <i>B. strigillatum</i> Dall 1891	S:150-732m (1)	Kohl, 1974
<i>Cancellaria cooperi</i> (Gabb 1865)	S:rare, offshore (2)	Recent, Lindberg and Kellogg, 1982
<i>Fusinus</i> aff. <i>F. barbarentis arnoldi</i> (Cossman 1903)	S:80-400m (3)	Emerson and Addicott, 1953
<i>Fusitriton oregonensis</i> (Redfield 1848)	S:>140m (3)	Emerson and Addicott, 1953
<i>Megasurcula carpenteriana</i> (Gabb 1865)	S:50-365m (2)	Addicott, 1969
<i>Polinices reclusianus</i> (Deshayes 1839)	N:183m, 549m (1)	Kohl, 1974
<i>Trophonopsis dalli</i> (Kobelt 1878)	intertidal mostly (2)	Recent, Lindberg and Kellogg, 1982
<i>Trophonopsis fleenerensis</i> (Martin 1914)	N:293m, 365m, 569m (1)	Kohl, 1974
	N:183m, 329m, 366m (1)	Kohl, 1974

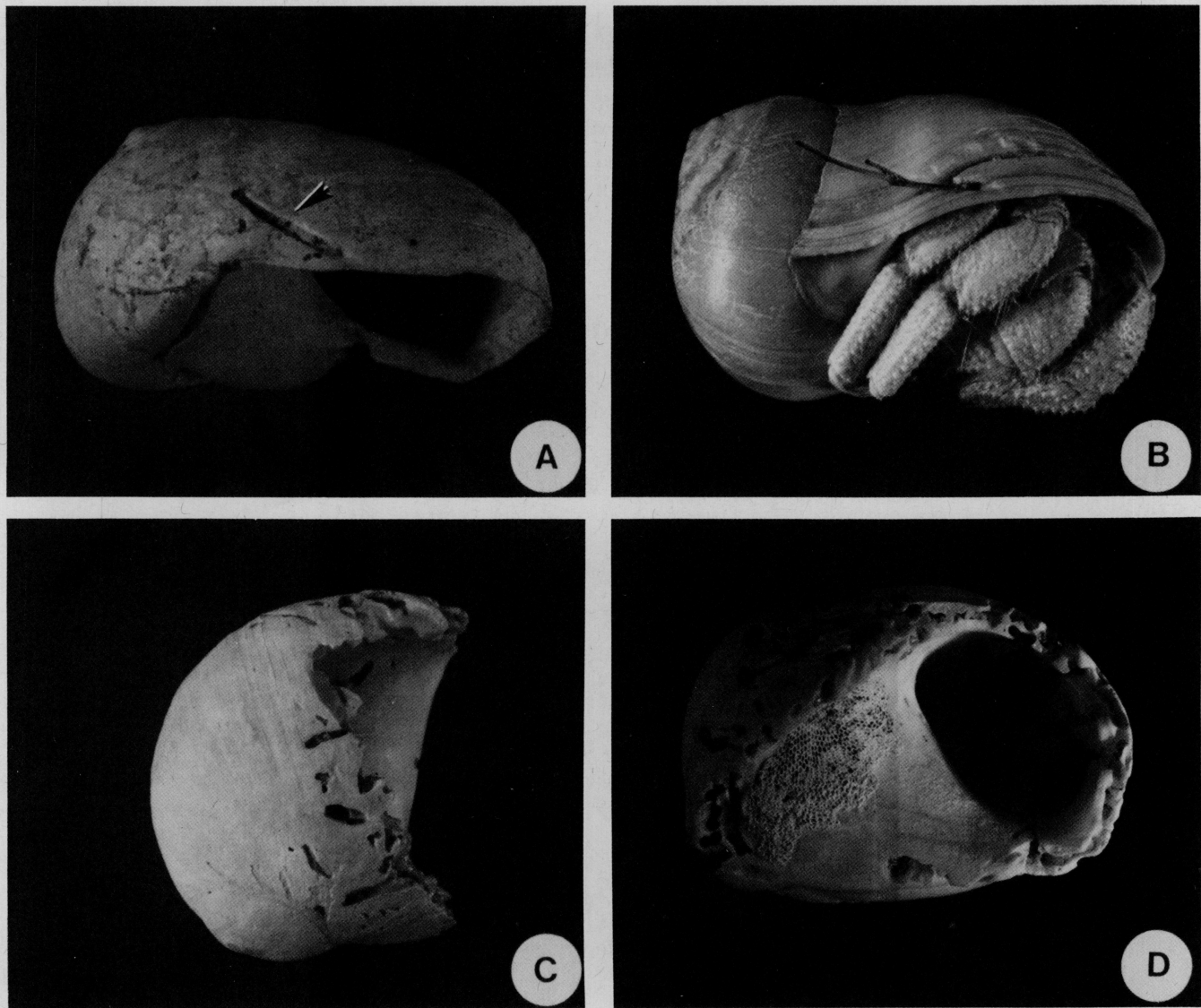
**TABLE 2**—Bathymetric ranges of hermit crabs from the Bering Sea to Baja California, Mexico (after McLaughlin, 1974).

FAMILY AND SPECIES	DISTRIBUTION	BATHYMETRIC RANGE
Diogenidae		
<i>Paguristes ulreyi</i>	Mexico, Baja California California; San Diego; San Nicolas Island	intertidal-56m
<i>Paguristes turgidus</i>	British Columbia, Chukchi Sea, San Diego	subtidal-420m
<i>Isocheles pilosus</i>	Bodega Bay, California to Baja California	low intertidal-100m
Paguridae		
<i>Pagurus armatus</i>	Alaska to San Diego	11-46m
<i>Pagurus quaylei</i>	British Columbia; Baja California	2-97m
<i>Pagurus capillatus</i>	Bering Sea; British Columbia; California	4-432m
<i>Pagurus setosus</i>	Kodiak, Alaska; Santa Cruz Island, California	9-476m
<i>Pagurus beringanus</i>	Bering Sea, Aleutian Islands to Monterey, California	intertidal-82m
<i>Pagurus granosimanus</i>	Alaska to Ensenada, Baja California	intertidal-32m
<i>Pagurus samuelis</i>	Vancouver Island to Baja California	intertidal (depth range unknown)
<i>Pagurus hirsutiunculus</i>	Siberia; Japan; Pribolof Islands to California	intertidal-110m

other bionts that produce fossilizable skeletons or traces that also indicate a hermit crab-occupied shell (i.e., a pagurized shell, after Seilacher, 1969). Three other gastropod species, *Polinices* (= *Neverita*) *reclusianus*, *Megasurcula carpenteriana*, and *Fusitriton oregonensis* are usually reported as anomalous deep-water species in shallow-water Pleistocene deposits (e.g., Addicott, 1969; Kohl, 1974). I have observed biont fossils and/or traces on fossil gastropods of these species collected from shallow-water deposits.

For example, pagurized *Polinices reclusianus* have a spionid

trace fossil located above the aperture notch (where aperture and last whorl meet) (Fig. 2A). These bore holes are similar to spionid bore holes on Recent *Polinices* shells inhabited by the burrowing diogenid hermit crab, *Isocheles pilosus* (Fig. 2B). This spionid trace fossil has not been reported previously; fossil shells with this bore hole above the aperture notch, then, indicate that an infaunal hermit crab occupied the shell (Walker, unpub. data). Shells that have many spionid bore holes on the outer lip (Fig. 2C, 2D) or encrusting bryozoa on the columella (Fig. 2D) indicate the occurrence of an epifaunal hermit crab.



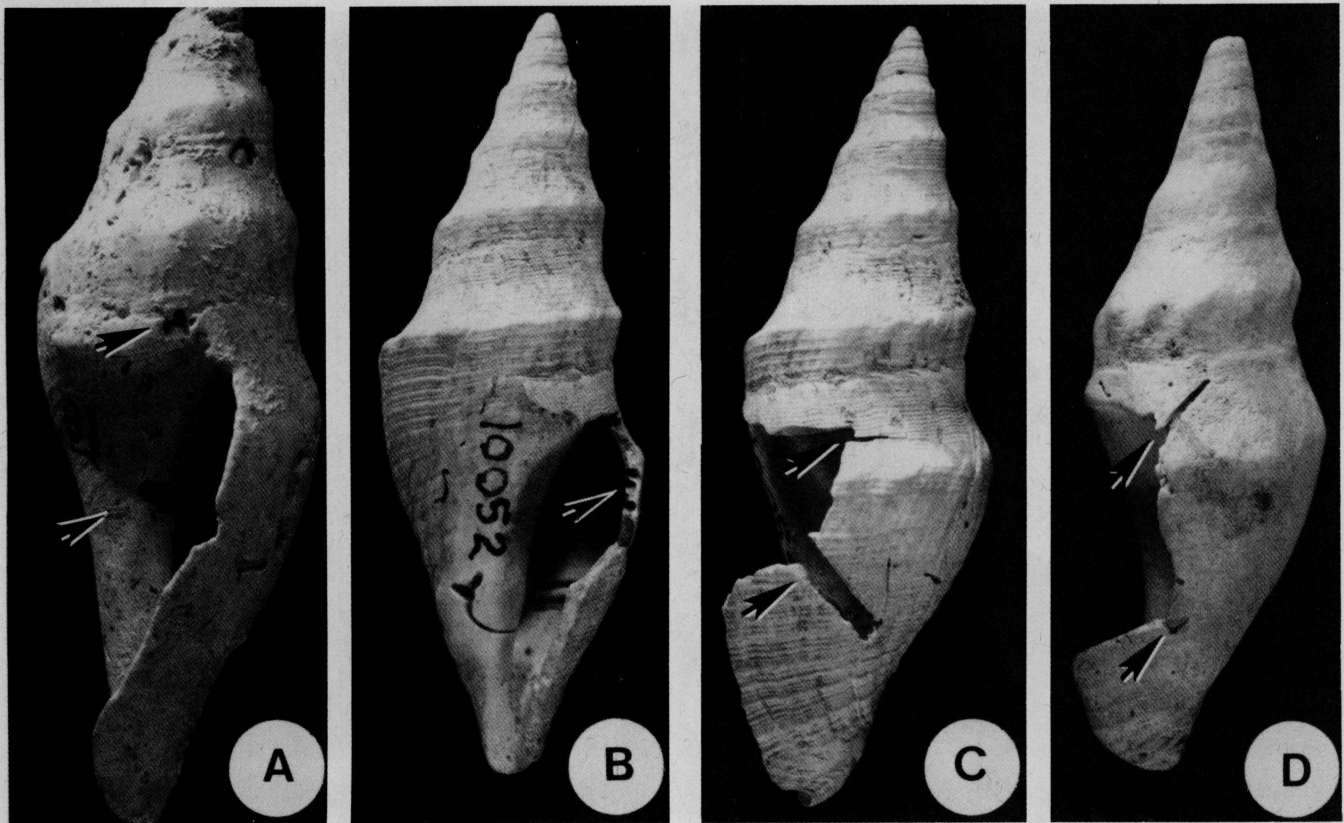
**FIGURE 2**—Pagurized *Polinices* from central and southern California. **A**) Spionid trace fossil (arrow) in aperture notch of *Polinices reclusianus* (Deshayes 1839), Pleistocene, Palos Verdes Sand, San Pedro, LACMIP 7809 (UCLA loc. 2381), 23.2 mm shell height. **B**) *Polinices* with *Isocheles pilosus* (Holmes 1900); spionid trace fossil in aperture notch, Recent, Pajaro Dunes beach drift, Watsonville, shell height 39 mm. **C**) Spionid bore holes in outer lip of *Polinices reclusianus* (Deshayes), Pleistocene, above Upper Newport Bay, Orange Co., LACMIP 7810 (UCLA loc. 3195), shell height 33.7 mm. **D**) Spionid trace fossils on outer lip and encrusting bryozoan on columella of *P. reclusianus*, Pleistocene, above Upper Newport Bay, Orange Co., LACMIP 7811 (UCLA loc. 3195), shell height 28 mm.

Similarly, epifaunal hermit crabs are indicated by *Helicotaphrichmus* bore holes in the columella and spionid bore holes on the outer lip of the deep-water *Megasurcula carpenteriana* (Figs. 3A, 3B). Whereas, *M. carpenteriana* with singular spionid trace fossils above the aperture notch indicate a burrowing hermit crab (Fig. 3C). I have collected Recent *Megasurcula carpenteriana* inhabited by *Isocheles pilosus* from the shallow intertidal of San Pedro that also have this spionid bore hole (Fig. 3D). *Isocheles pilosus* does not have a reported

fossil record although this species is abundant in California, occurring in intertidal waters to depths of over 100 m (Morris et al., 1980).

Pagurized *Fusitriton oregonensis* can be recognized by columellar spionid bore holes (Fig. 4A), encrusting bryozoans (Fig. 4B, 4C), or encrusting bryozoan trace fossils (etchings) (Fig. 4D). These traces again indicate that an epifaunal hermit crab inhabited the shells.

Bionts provide important clues to determine if a shell had



**FIGURE 3**—Pleistocene and Recent *Megasurcula* with spionid trace fossils in the columella and aperture notch. **A**) Bore hole of *Helicotaphrichnus* in columella (arrow) and an unidentified spionid trace fossil in aperture notch (arrow) of *Megasurcula tryoniana* (Gabb, 1866), Pleistocene, Palos Verdes Sand, Los Angeles Co., CAS loc. 91.02, shell height 51.0 mm. **B**) Spionid trace fossils in columella and outer lip (arrow) of *Megasurcula carpenteriana* (Gabb, 1865), Pleistocene, Potrero Canyon, Los Angeles, LACMIP 7812 (UCLA 10052 from UCLA loc. 3225), shell height 64.8 mm. **C**) Spionid trace fossils as elongate tunnels causing breakage at aperture notch and outer lip (arrows), specimen figured in 3B. **D**) Spionid trace fossil in aperture notch and outer lip (arrows) of Recent *Megasurcula carpenteriana* from San Pedro, 83.2 mm shell height.

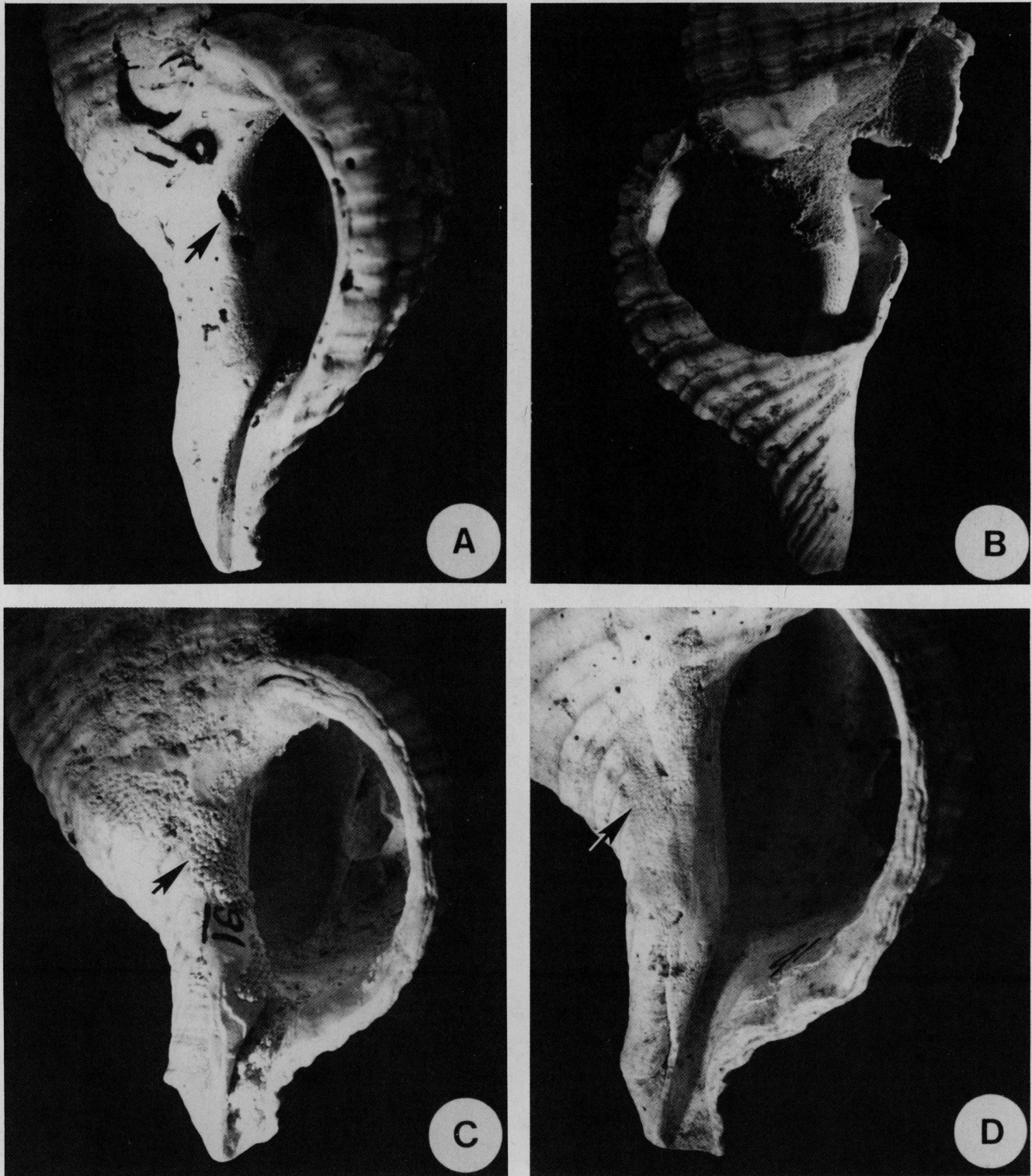
been previously occupied by a hermit crab. The behavior and infaunal life mode of living *Polinices* and *Megasurcula* prevent the settlement of bionts on the shell. Bionts do not settle within or around the aperture of these snails (including *Fusitriton*), because of the presence of the mantle. Empty shells have rarely been found in soft sediment environments exposed on the substrate (see Conover, 1975; Stachowitsch, 1980), thus preventing biont settlement. Further, the distribution and type of epi- and endobionts on or within shell apertures are characteristic of hermit crab inhabitation (Walker, 1988).

#### Transport

Hermit crab shell transport is invoked when a large number of gastropod shells (worn by hermit crabs) are present in a habitat in which the living snail is not represented. Many workers in Japan have documented that hermit crabs inhabit allochthonous shell species (i.e., shells imported from outside the habitat) of which the living snail is not represented in the

habitat (Shimoyama, 1979; Shimoyama et al., 1979; Yajima and Yamaguchi, 1983; Asakura and Kikuchi, 1984; Shimoyama, 1985). Although some transport was thought to result from water currents, these workers suggest that hermit crabs transported many of these shells into the "anomalous" habitat.

Allochthonous shells coalesced by hermit crabs may represent many different species. Asakura and Kikuchi (1984) discovered that the sand flat hermit crab, *Diogenes nitidimanus*, inhabited 26 species of gastropod shells of which only 6 were represented by the living snail in the habitat. In another study, Shimoyama (1979) reported that *D. nitidimanus* acquired 55% of its shells from snails present outside the crab's usual habitat. He later (1985) provided evidence that *D. nitidimanus* (densities up to 2000m<sup>2</sup> in the study area) inhabited 33 gastropod species and transported at least 3 species of gastropod shells (*Batillaria zonalis*, *Batillaria cumingus*, and *Umbonium moniliferum*) from an inner bay to the bay entrance, a total of approximately 750 m. However, none



**FIGURE 4**—Pagurized *Fusitriton oregonensis* (Redfield, 1848), Pleistocene, Palos Verdes Sand, San Pedro, Los Angeles Co., California, CAS loc. 91.07. **A**) *Fusitriton oregonensis* with two sponiid trace fossils in columella (arrow) and doubled hole sponiid tubes on outer lip, incomplete specimen: aperture length (to end of siphonal canal) 35 mm. **B**) Fragmented *F. oregonensis* with encrusting bryozoan in interior aperture and on columella, shell height 59.4 mm. **C**) Encrusting bryozoan in columella (arrow) and siphonal canal of *F. oregonensis*, incomplete specimen, shell height approximately 59 mm. **D**) Trace fossil of encrusting bryozoan in columella (arrow) and interior of outer lip of *F. oregonensis*, shell height 74.7 mm.

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,

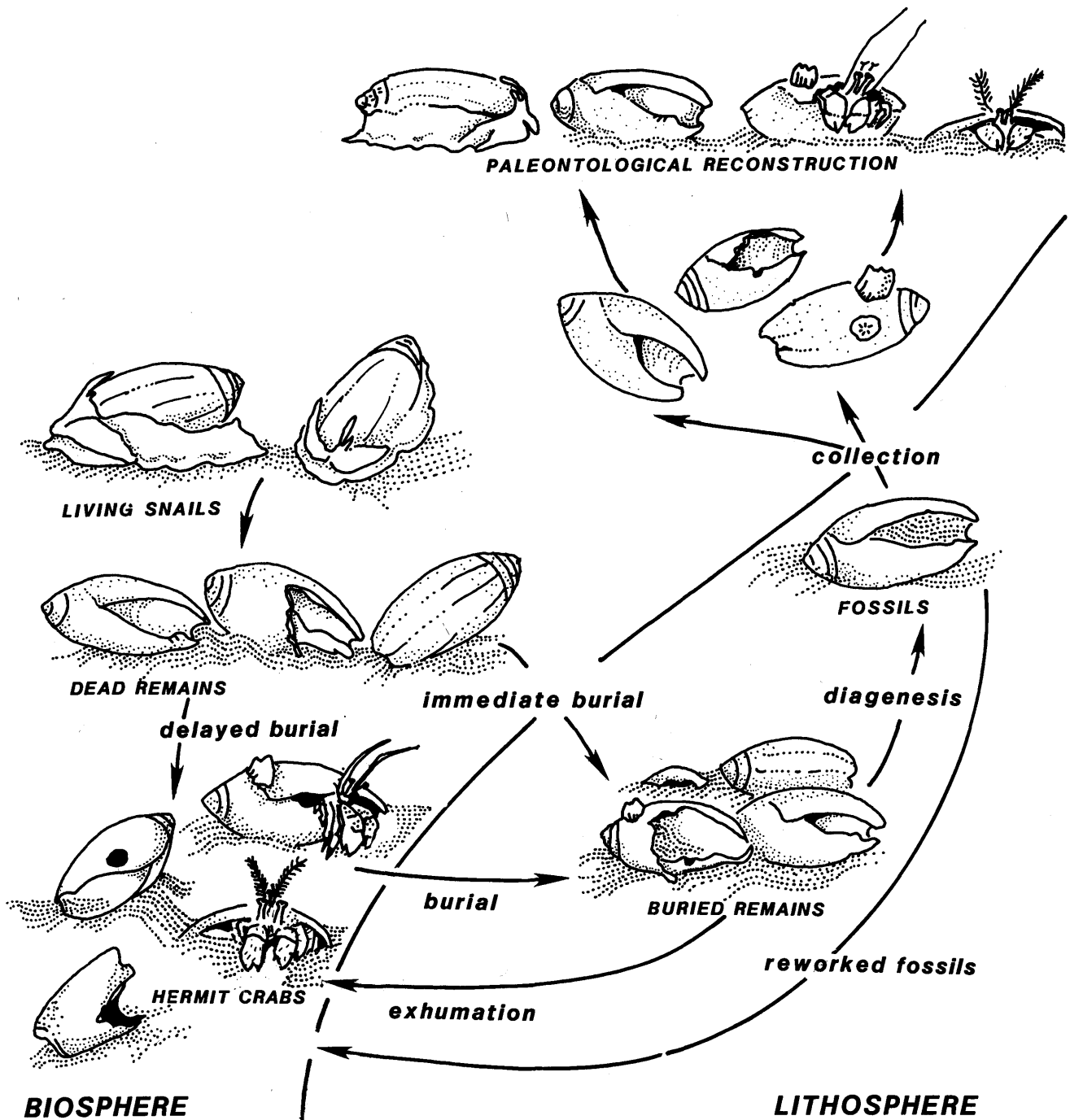


FIGURE 5—A taphonomic scenario illustrating the points at which hermit crabs can affect the preservation of gastropod shells.

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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