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## CRITERIA FOR RECOGNIZING MARINE HERMIT CRABS IN THE FOSSIL RECORD USING GASTROPOD SHELLS

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**ABSTRACT**—Hermit crabs have left a rich fossil legacy of epi- and endobionts that bored or encrusted hermit crab-inhabited shells in specific ways. Much of this rich taphonomic record, dating from the middle Jurassic, has been overlooked. Biological criteria to recognize hermitted shells in the fossil record fall within two major categories: 1) massive encrustations, such as encrusting bryozoans; and 2) subtle, thin encrustations, borings, or etchings that surround or penetrate the aperture of the shell. Massive encrustations are localized in occurrence, whereas subtle trace fossils and body fossils are common, cosmopolitan, and stratigraphically long-ranging. Important trace fossils and body fossils associated with hermit crabs are summarized here, with additional new fossil examples from the eastern Gulf Coast. *Helicotaphrichnus*, a unique hermit crab-associated trace fossil, is reported from the Eocene of Mississippi, extending its stratigraphic range from the Pleistocene of North America and the Miocene of Europe.

### INTRODUCTION

**H**ERMIT CRABS first appeared in the early Jurassic (Glaessner, 1969) but their body fossils are rare (Hyden and Forest, 1980; Bishop, 1983). One in situ hermit crab has been reported from the Miocene of New Zealand (Hyden and Forest, 1980). Consequently, the hermit crab fossil history, from their relative abundance to their historical use of shells, remains largely unknown. Yet, a vast record of their use of gastropod shells does exist: the trace- and body-fossil record of encrusting, etching, and boring organisms that have associated with hermit crab-inhabited shells since the mid-Jurassic.

These epi- and endobionts (bionts) are geographically widespread and abundant. For example, shells inhabited by Recent hermit crabs provide a substratum for a rich and diverse array of bionts. Jensen and Bender (1973) reported over 50 species of bionts associated with *Pagurus bernhardus* from marine waters off Sweden. On the Texas coast of North America, Fotheringham (1976) described over 20 species of bionts associated with hermitted shells. In the Adriatic Sea, Stachowitsch (1977, 1979, 1980) reported 120 species associated with hermitted shells. Shells with these bionts are termed "pagurized" and this term will be used to denote gastropod shells with trace fossils or body fossils associated with hermit crabs (after Seilacher, 1969; Carlton, 1971). Hermit crab-inhabited shells will be called "hermitted," whether or not they contain bionts (modified after Vermeij, 1978).

The earliest organisms associated with hermitted shells are thickly encrusting bryozoans from the middle Jurassic (Upper Bathonian, France; Buge and Fischer, 1970; Palmer, 1972; Palmer and Hancock, 1973). However, boring, etching and encrusting bionts that are likely to be overlooked or interpreted as occurring with the living gastropod are much more common in the fossil record.

Recognizing the patterns of epi- and endobionts that are exclusive to hermitted shells is a critical first step before evolutionary and paleoecological studies can be made concerning fossil gastropod shells. Hermit crabs have the potential to create numerous paleontological biases such as size-frequency differences (Shimoyama, 1979, 1985; Shimoyama et al., 1979), mixed shell assemblages (Frey, 1987), abundance anomalies, and bathymetric and temporal anomalies in gastropod fossil assemblages (Walker, 1986, 1988a, 1988b, 1989, 1990). Most im-

portantly, hermit crabs have the potential to affect our interpretations of gastropod paleoecology and evolution.

Reliable criteria for recognizing pagurized shells is a prerequisite for quantitative testing of evolutionary questions. For example, biont diversification may have been triggered by the advent of hermit crabs. Bionts also may indicate the type and behavior of fossil hermit crabs (Walker, 1988b). The first pursuit of any paleontologist studying gastropod systematics and paleoecology (in post-Triassic assemblages) is to recognize the biont patterns and taphonomic anomalies produced by hermit crabs.

### BIONT DIFFERENCES BETWEEN LIVING SNAILS, EMPTY SHELLS, AND HERMIT CRAB-INHABITED SHELLS

Before the systematic description of pagurized shells is discussed, it is necessary to distinguish among the taphonomic information provided by hermit crabs, living snails, and empty, abandoned shells.

Bionts usually do not grow on living infaunal snails or abandoned empty shells in soft-sedimentary habitats (Boekschoten, 1967; Stachowitsch, 1980). Empty shells are rapidly buried, which prevents biont growth (Conover, 1975; Stachowitsch, 1980). Hermitted shells will often provide the only firm substratum for biont growth in these environments (Conover, 1975, 1976, 1978, 1979; Stachowitsch, 1980; Karlson and Cariolou, 1982; Walker, 1985). In addition, empty snail shells may be attacked by durophagous predators and destroyed (Walker, 1988a, 1988b; Walker and Yamada, 1990). Therefore, in soft-sedimentary habitats, most bionts on gastropod shells, especially in and surrounding the aperture, are indicative of hermit crabs.

Walker (1986, 1988b) experimentally showed that empty shells, living snails, and hermitted shells in a soft-sedimentary habitat could be distinguished from one another on the basis of biont type and biont settlement patterns on the shell. Empty tethered shells were not colonized by preservable bionts. The tethered shells were occasionally buried, but were chiefly scoured by sand and covered by anoxic layers of algae that prevented biont settlement. Walker (1988a, 1988b) also found that bionts that etched, bored, or encrusted apertures of the infaunal gastropod, *Olivella biplicata*, were the best indicators of hermitted shells in the Pleistocene of California.

Shells of epifaunal gastropods living on hard substrates may have bionts unless the living snails have shell-cleaning behaviors or possess a periostracum that inhibits biont settlement (Bottjer, 1981; Jones, 1984). Bionts settle on experimentally tethered, empty shells (but plugged, to prevent hermit crab occupancy) in rocky intertidal habitats (Walker, 1988a). However, the di-

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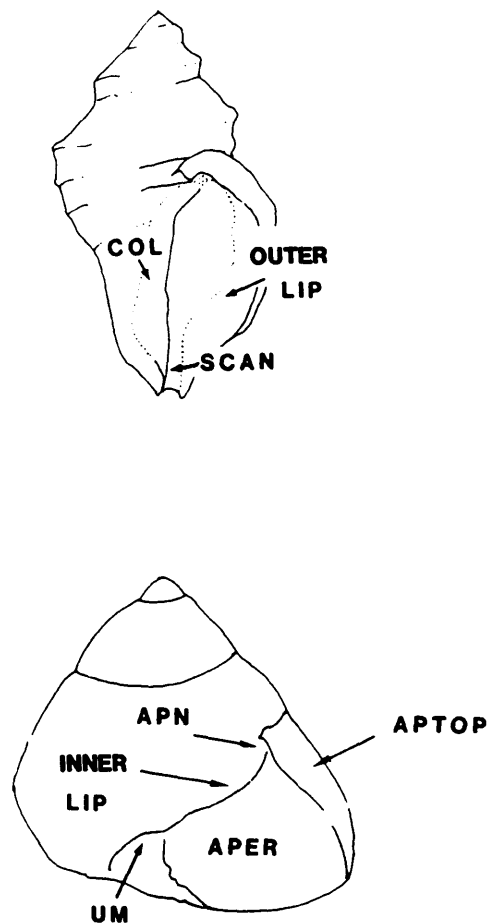


FIGURE 1—Typical biont settlement areas on pagurized gastropod shells. Abbreviations: COL, columella; SCAN, siphonal canal; APN, apertural notch; APTOP, aperture top; APER, aperture; UM, umbilicus.

versity, amount, and location of encrustation is different between empty and hermitted shells in these habitats.

Most importantly, in living gastropods the aperture, callus, collumella, and siphonal canal are not colonized by boring and encrusting bionts because of the presence of the fleshy mantle (Figure 1). Any biont that occurs in this region is postmortem and, depending on biont type and location, is attributable to hermit crabs or other secondary inhabitants of the shell (Walker, 1990).

Many shells worn by hermit crabs exhibit a "pagurid facet," usually delimited by abraded bionts or shell wear, where the hermit crab has dragged the shell (Ehrenberg, 1931; Häntzschel, 1975); however, living snails may also possess similar wear spots

caused by the shell resting on the operculum. Unless additional information is used, such as bionts that colonize the aperture of the shell, misinterpretations may result.

#### IMPORTANT TRACE AND BODY FOSSILS OF BIONTS ASSOCIATED WITH HERMIT CRAB-OCCUPIED SHELLS

**Hydractinians.**—Hydractinians have long been recognized as hermit crab shell associates because they form very noticeable and curious-looking calcareous crusts on shells. These large crusts may enhance their preservation. Many of these hydractinians are not obligate to hermitted shells (additional examples in Merrill, 1967a, 1967b), but they are very common in fossil deposits when they do occur.

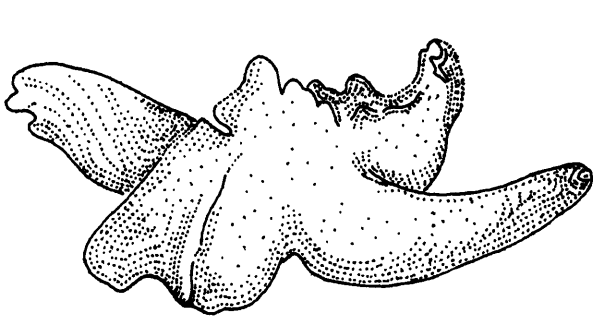
Calcified hydractinians are represented by three Recent species, *Janaria mirabilis*, *Hydrocorella africana*, and *Polyhedra carnea* (Cairns and Barnard, 1984). These three species all associate with hermit crabs. There are many examples of calcareous hydractinians in the fossil record, but their systematics are poorly known (Hill and Wells, 1956). The best known of these is the strange Eocene fossil from Egypt, *Kerunia cornuta* (Figure 2.1). *Kerunia* is the first text-book example of a symbiosis between a fossil hydractinian and a hermit crab (Abel, 1912). *Kerunia* was originally described as a cephalopod (Mayer-Eymar, 1900) because of its coiled and spine-like appearance, but was later reinterpreted as a hydractinian (Fraas, 1911). Some workers have also argued that *Kerunia* was a bryozoan (Ehrenberg, 1931; Zapfe, 1947); however, it is very similar to *Hydractinia calcarea* from Fiji (Figure 2.2), which has been synonymized with the calcareous hydractinian, *Janaria mirabilis* (see Fraas, 1911; Cairns and Barnard, 1984).

Living *Janaria mirabilis* overgrow hermitted shells in the eastern Pacific (Gulf of California to Panama and Fiji) in deep water below 20 m (Cairns and Barnard, 1984). *Janaria* forms thick crusts in the shape of "staghorns" (Smith, 1966) (Figure 2.3). This staghorn morphology is very similar to that of the fossil *Kerunia*.

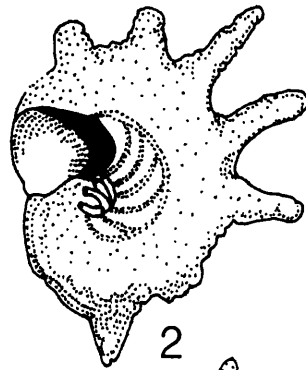
Hydractinians may have appeared in the fossil record during the Triassic but are reliably known from the Eocene to present (Hill and Wells, 1956; Cairns and Barnard, 1984). Many of these fossil species are apparently calcareous in composition, but are in need of careful systematic and taphonomic analysis. For example, *Hydractinia cretacea* Fischer (Cretaceous, France), *Hydractinia michelini* Fischer (Miocene of France), and *Hydractinia pliocena* Allman (Pliocene of England), according to Allman (1872), have had their original chitin replaced with "carbonate of lime." This observation of Allman's has not been fully examined. These species were indistinguishable from each other and could only be recognized by stratigraphic position. Carter (1877) carefully examined one of Allman's fossils (*H. pliocena* = *H. pliocoena*) and determined that *H. pliocena* possessed a

FIGURE 2—Thick encrusters on hermitted gastropod shells. 1–4, calcified hydractinians and 5–12, calcified bryozoans. 1, *Kerunia cornuta* Mayer-Eymar, Eocene, Egypt (after Fraas, 1911, fig. 1), specimen 6.5 cm; 2, *Hydractinia calcarea* Carter, Recent, Fiji, cross section to show pagurid home and serpulid tubes in the interior of the shell (after Fraas, 1911, fig. 5), specimen 3.0 cm; 3, *Janaria mirabilis* Stechow, "staghorn," Recent, Gulf of California (after Smith, 1966), specimen 6.5 cm; 4, *Hydractinia pliocena* Allman encrusting *Buccinum* fossil, Pliocene, Coralline Crag, England (after Carter, 1882, fig. 7), gastropod length 4.5 cm; 5, *Berenicea* sp., Upper Bathonian (middle Jurassic), Calvados, France (after Palmer and Hancock, 1973, fig. 1), specimen 2.8 cm; 6, cross section of *Berenicea* sp. (= *Atractosocia*, see Buge and Fischer, 1970) showing colony growth around a gastropod, presumably *Ataphrus* sp. (after Palmer and Hancock, 1973), specimen 2.0 cm; 7, *Atractosocia incrustans* encrusting the gastropod, *Dicroloma cirrus*, Upper Bathonian, Calvados, France (after Buge and Fischer, 1970, fig. 8), specimen 2.5 cm; 8, *Hippoporidra edax* (Busk), Pliocene, Coralline Crag, Suffolk, England, encrusting a gastropod shell (after Taylor and Cook, 1981, fig. 1), specimen 2.0 cm; 9, *Hippoporidra* sp., a cross section of the "longhorn" depicted in 10, Recent, Gulf of Mexico (after Smith, 1966, p. 31), specimen 4.0 cm; this bryozoan produces a "shell" for the hermit crab, as indicated by the curved lines in the cross section; 10, *Hippoporidra* sp., Recent, Gulf of Mexico (after Smith, 1966, p. 31), specimen 8.0 cm; 11, tube-building bryozoan, *Heteropora parapelluculata* Taylor, Schembri, and Cook 1989, Recent, Otago Shelf, New Zealand, occupied by the hermit crab, *Pylopagurus* (after Taylor et al., 1989, fig. 3a), specimen 5.0 cm; 12, *Cellepora* encrusting *Turritella* sp., Miocene and/or Pliocene, Faluns de Touraine, France (after Lecointre, 1929, and reinterpreted from Andre and Lamy, 1936), specimen 3.0 cm.

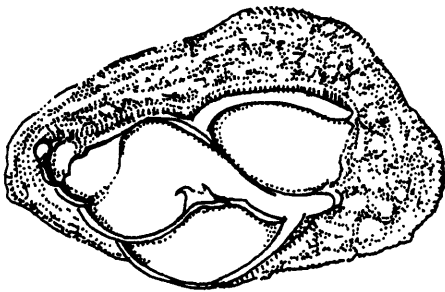




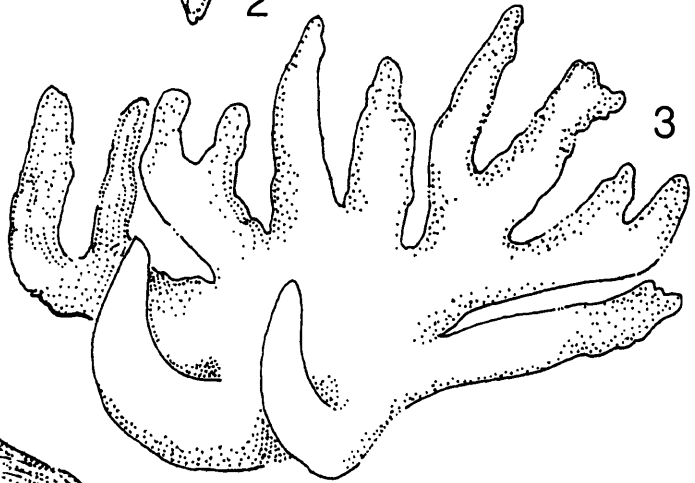
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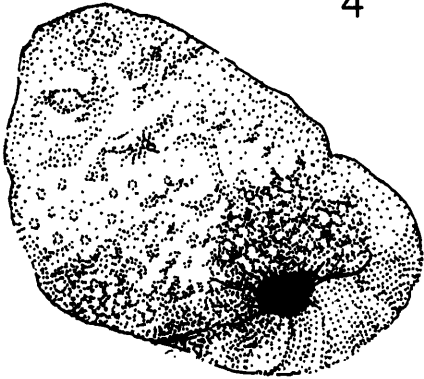
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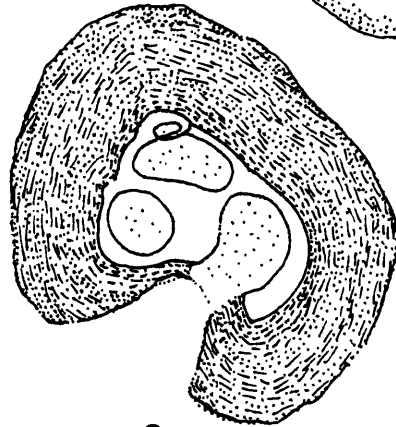
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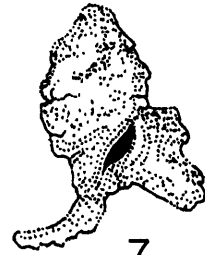
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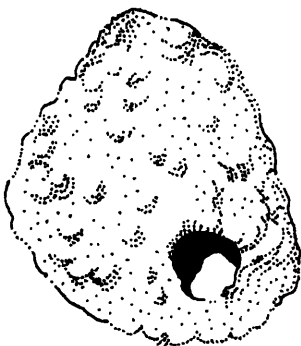
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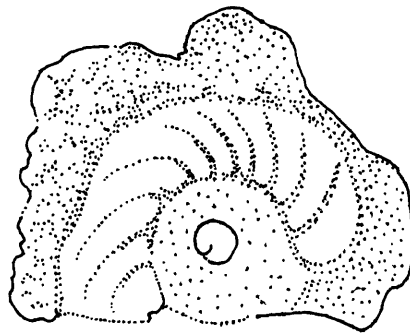
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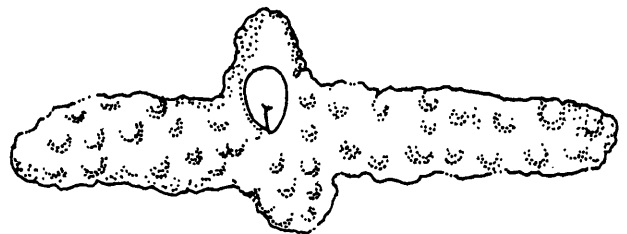
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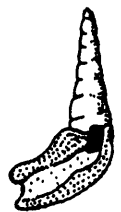
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calcareous exoskeleton which obscured the *Buccinum* shell it encrusted (Figure 2.4).

Ehrenberg (1931) was one of the first to describe bionts, specifically hydractinians, associated with marine hermit crabs and suggested they might have biostratigraphic importance. He meticulously described the location of the hydractinians on recent shells (overgrowing the aperture) and provided fossil examples from the Miocene of Vienna, Austria. He also suggested that hydractinians, as well as bryozoans and serpulid polychaetes, could be used for recognizing hermitted shells in fossil deposits.

Hydractinians with chitinous exoskeletons do not appear to have a fossil record. Often in recent studies, the skeletal composition of the hydractinian is not specified; therefore, it is difficult to extrapolate the preservation potential for many hydractinian species. For example, Schafer (1972) described the perisarc (exoskeleton) of *Hydractinia echinata* as calcareous (made of aragonite needles), but others have described the exoskeleton as chitinous (Buss and Yund, 1989). This differing composition may be due to a species complex within *H. echinata*.

*Hydractinia echinata* forms many sibling species which may be evolutionarily tied to the hermit crab (Yund and Parker, 1989). Recently, two species have been named from within *Hydractinia "echinata"* (Buss and Yund, 1989). *Hydractinia symbiolongicarpus* occurs predominately on shells inhabited by *Pagurus longicarpus*. The name *symbiolongicarpus* refers to the symbiotic relationship between the two. The second species, *Hydractinia symbiopollicaris*, occurs on *Pagurus pollicaris*. These species are chitinous in composition and are morphologically indistinguishable from each other (Yund and Parker, 1989). The studies on hydractinians strongly suggest that hermit crabs are an evolutionary force behind hydractinian evolution.

Studies on settlement of *Hydractinia echinata* (sibling species not denoted) show that the planula larvae settle commonly on the apertural notch (where the aperture meets the last whorl) (Yund and Parker, 1989). The siphonal canal and sutures of the external whorls are also areas where *H. echinata* will initially settle (Mills, 1976; Yund et al., 1987). Colonies of newly recruited *H. echinata* were more likely to survive in the apertural area of the shell possibly because of the enhanced food supplies provided by the feeding activities of the crab (Yund et al., 1987).

*Hydractinia echinata* recruit consistently to the apertural areas of hermitted shells; however, recruitment patterns of hydractinians may not be deducible from the fossil record. Twenty-two fossil gastropods from the Plum Point Marl Member, Calvert Formation of Maryland, had hydractinian crusts (inferred as chitinous) covering more than 50 percent of the shells (Buss and Yund, 1988). Initial recruitment patterns were thus obscured. Although not identified, the species examined by Buss and Yund (1988) may have been the calcareous *Hydractinia multispinosa*, which is very common in the Plum Point Marl (Ulrich, 1904).

A fruitful line of taphonomic research would be to determine the extent of calcareous versus chitinous forms of hydractinians and how each may preserve in the fossil record. Recent *H. echinata* that completely encrust hermitted shells may peel off, leaving clean, unpitted, and unencrusted shell surfaces (Figure 3). It is not known what conditions will enhance fossilization of these chitinous skeletons.

In summary, hydractinians are more likely to be preserved in the fossil record as complete, massive encrustations on gastropod shells, rather than small "spot" encrustations. Preserved hydractinians are mostly calcareous. The association between hydractinians and hermit crabs is not obligate. It is a very common association in recent environments and has had a long fossil history.

**Corals.**—Fossil corals have only recently been reported to

occur with hermit crabs (Petuch, 1986; Darrell and Taylor, 1989). Pliocene Pinecrest beds in Florida contain abundant corals (*Septastrea marylandica*) that encrust gastropod shells. This species, although in need of systematic revision, is distributed along the east coast of North America to Colombia, dating from the late Miocene to Pliocene (Weisbord, 1974).

*Septastrea* overgrows the hermitted shell, at times creating two extra whorls (Darrell and Taylor, 1989). *Septastrea* has a growth form similar to deep-water bryozoans, sponges, and other cnidarians that associate with hermitted shells—they consistently overgrow the shell in a helical pattern. Vermeij (1987) has suggested that this helical overgrowth is a coevolutionary adaptation between the colonial organisms and the hermit crab. The hermit crab is presumably shell limited in deep-water habitats; however, Darrell and Taylor (1989) believe this association is a shallow-water phenomenon.

Coral growth, like *Septastrea*, has not been reported for hermit crabs in recent environments. Corals have been reported to grow on gastropod shells inhabited by sipunculids (Rice, 1976). Sipunculids make small apertural openings in coral skeletons that are unlike the larger "D-shaped" apertures of hermitted shells (Darrell and Taylor, 1989).

**Polychaetes-encrusting species.**—Many species of encrusting polychaetes, such as serpulids and spirorbids that secrete calcareous tubes, occur with hermitted shells. These polychaetes are often located within or surrounding the aperture of hermitted shells (Table 1).

Serpulid polychaete tubes (e.g., *Pomatoceras triqueter*, *Serpula concharum*) that overgrow gastropod apertures are diagnostic of hermitted shells. Serpulids rapidly settle on shells occupied by hermit crabs (Stachowitsch, 1980). Serpulids were not able to grow on experimental tagged shells because the shells were rapidly buried in the soft sediments (Stachowitsch, 1980). Stachowitsch (1980) further suggested that serpulids strengthen the hermitted shell. This buttressing of the shell may enhance the shell's preservation, but has not been experimentally tested.

Serpulid tubes are present on gastropod shells from the Pleistocene of California. For example, fossil *Polinices reclusianus* shells with serpulid tubes within the apertures of the shells are excellent indicators of hermitted shells (Figure 4.1, 4.2).

Another characteristic of serpulids that enhances their preservation in the fossil record is their ability to etch their substratum upon which they encrust (Radwanski, 1977). Radwanski (1977) stated that serpulids etch limestone rock and not shells. However, serpulids can "etch" and change the composition of the shell matrix beneath them. This characteristic of some serpulids is fortuitous, especially if museum specimens had been thoroughly cleaned of encrusting bionts. The etched surface cannot be scraped away by overzealous preparators.

Spirorbid polychaetes are also common inhabitants of hermitted shells (Table 1). Spirorbids make small, circular calcareous tubes on the external and internal areas of hermitted shells. The key characteristic settling areas are the apertural notch, inner and outer lip, siphonal canal, and umbilicus. For example, recent hermitted shells from a subtropical locality (Puerto Peñasco, Mexico, northern Gulf of California) and the temperate zone of northern California have typical spirorbid settling patterns (Figure 5). Spirorbids thickly encrust subtropical shells, often obscuring the shape of the gastropod shell (*Cerithium* shells, Figure 5.1).

The living snail may also be covered with spirorbids, but it rests the shell on the apertural side, creating a bare space with no spirorbid settlement. Hermit crabs rest the shell on the apertural side, creating a bare space on the "top" of the shell (see Figure 5.1 for *Cerithium*). The pagurid facet is thus on the top of the shell and not on the ventral side.

A few species of spirorbids are specific to hermit crab shells,

such as *Circeis paguri* (Al-Ogily and Knight-Jones, 1981). *Circeis paguri* are commonly found on the interior roof of the penultimate and last whorl of large (>7 cm) *Buccinum* shells in waters off of Great Britain (Al-Ogily and Knight-Jones, 1981). These spirorbids also settle on the telson of the hermit crab and are transferred to other hermit crabs during shell swapping.

*Polychaetes that bore into the shell.*—Polychaete worms that bore (e.g., spionids) are commonly present surrounding the aperture, especially in the columella, apertural notch, and outer lip, of hermitted shells (Table 1).

The most important indicator of a hermitted shell, with a wide biogeographic and stratigraphic distribution, is the borehole produced by the spionid, *Polydora commensalis*, in the columella of hermitted shells (Blake and Evans, 1973; Kern et al., 1974). This borehole may also be produced by other species of spionids (e.g., *Polydora biocipitalis*; Kern, 1979). The borehole trace fossil, *Helicotaphrichnus commensalis*, was named after the living spionid polychaete, *P. commensalis* (Kern et al., 1974).

Recent *P. commensalis* bores a deep hole into the columella of hermitted shells and roofs this furrow over with a thin calcareous layer (Andrews, 1891; Blake and Evans, 1973). This tube frequently extends from the lower columella to the apex of the shell. In some specimens, the shell must be cracked open to see the tube, but usually the bore hole can be seen upon careful inspection of the columella. The borehole occurs with many species of hermit crabs and in many gastropod shell types. The worm can only exist with hermitted shells and dies when the hermit crab abandons the shell (Blake and Evans, 1973).

Boreholes are infrequently encountered in Recent specimens. Walker (1988b) reported 12 percent of 1,414 hermitted *Olivella biplicata* shells with this borehole; in fossil specimens the incidence varies with geographic location. For example, *Helicotaphrichnus* occurs more commonly in *O. biplicata* fossils in southern California Pleistocene localities than in northern localities (Walker, 1988b). However, this trace fossil has not been reported from many localities presumably because it has been overlooked (Table 2).

*Helicotaphrichnus* is ubiquitous in the eastern Gulf Coast fossil fauna dating from the Eocene to Pleistocene, a considerable biogeographic and stratigraphic extension for this trace fossil (Table 3). This trace fossil occurs on the gastropods *Mitra* (Eocene, Mississippi) and *Cassis brevidenta* (Oligocene, Mississippi) (Figure 6). The occurrence of *Helicotaphrichnus* on these specimens represents a range extension for this trace fossil, which was previously known from the Plio-Pleistocene of North America and the Miocene of Europe (Kern, 1979).

*Helicotaphrichnus* and *Helicotaphrichnus*-like trace fossils occur with many other genera in the eastern Gulf Coast fauna. The genera *Cancellaria*, *Murex*, and *Mitra*, when present in an assemblage, consistently have this trace fossil from the Eocene to Pleistocene (Table 3). Other hermit crab-associated bionts also occur with these shells.

The Maryland Miocene also contains many hermitted shells. For example, over 50 percent of *Bullia (Bullioopsis)* surveyed had *Helicotaphrichnus* present in the columella (Table 4). Darrell and Taylor (1989) also reported a high percentage of shells with *Helicotaphrichnus* from the Pliocene Pinecrest beds in Sarasota, Florida (82 percent of their coral-encrusted gastropod shells contained this trace fossil).

*Helicotaphrichnus* has a wide biogeographic distribution. Not only is it reported from the warm-water late Miocene of Poland (Kern, 1979; Baluk and Radwanski, 1984), but it occurs in the Pleistocene of the Galapagos Islands (Walker, in press) and the northern Gulf of California. It appears that this trace fossil has a warm temperate to tropical water distribution from the Eocene to Pleistocene of North America and other localities.



FIGURE 3—*Hydractinia echinata* encrusting a hermit crab-occupied nautilus shell, Recent, Friday Harbor, Washington, shell height, 30.0 mm, UCMP Type No. 39690. The hydractinian species is chitinous and is easily peeled off, leaving a clean shell. UCMP = University of California Museum of Paleontology.

Many other boring spionid polychaetes may inhabit a hermitted shell. For example, *Nucella emarginata* shells inhabited by the hermit crab, *Pagurus samuelis*, may house four species of boring spionids (*Polydora commensalis*, *P. cilita*, *P. liminicola*, and *Boccardia columbiana*; Woodwick, 1963). Fossil gastropods also exhibit multiple infestations of spionid trace fossils. Multiple boreholes commonly surround the aperture, especially the apertural notch and outer lip, of hermitted shells (Figure 7.1, 7.4). Such infestation contributes to the taphonomic breakdown of the shell, creating large holes in the last whorl near the apertural notch (Figure 7.1, 7.2).

Other species of polychaetes bore into hermitted shells and are quite destructive. The sabellid polychaete, *Potamilla reniformis*, and the cirratulid polychaete, *Dodecaceria concharum*, bore into hermitted shells in the Gulf of Trieste, north Adriatic Sea (Stachowitsch, 1980). *Potamilla* was present on 51 percent of 45 hermitted shells (mostly *Aporrhais pes-pelecani*). *Potamilla* bores along the spire and into the columella of those shells, thus weakening the shells along the main internal structure of the shell. *Dodecaceria*, on the other hand, bores into shells previously weakened by other boring organisms. *Dodecaceria* occurred on 27 percent of 45 hermitted shells in Stachowitsch's study. The presence of these polychaetes would greatly affect the preservation of these shells. Gastropod specimens with *Do-*

TABLE 1—Boring or encrusting calcareous polychaetes associated with hermitted shells, their biogeographical distribution and location on shells. \* Denotes species that were not explicitly stated associated with biont; "not specified" indicates any of these species: *Natica alderi*, *Littorina littorea*, *Littorina obutusa*, *Gibbula cineraria*, *Bittium reticulatum*, *Buccinum undatum*, and others (from fig. 16, Samuelson, 1970); — = not known.

Polychaete species	Gastropod shell	Hermit crab	Location on shell	Locality	Reference
Encrusting polychaetes					
Serpulids Unid.	Not specified	<i>Pagurus cuanensis</i> <i>Anapagurus chrioacanthus</i>	external shell	Bergen, Norway	Samuelson, 1970
<i>Hydroides norvegica</i>	Not specified	<i>Pagurus bernhardus</i>	external, close to opening	Bergen, Norway	Samuelson, 1970
<i>Hydroides norvegica</i>	* <i>Buccinum undatum</i> * <i>Littorina littorea</i> * <i>Neptunea antiqua</i> * <i>Murex</i> , <i>Aporrhais</i>	<i>Pagurus bernhardus</i>	external, close to shell opening	Frederikshavn, Denmark; Kristineberg, Norway	Jensen and Bender, 1973
<i>Hydroides pseudouncinata</i>	* <i>Murex</i> , <i>Aporrhais</i>	<i>Pagurus oculatus</i> , <i>Pagurus cuanensis</i>	external	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
<i>Pomatoceras triqueter</i>	<i>Murex</i> , <i>Aporrhais</i>	<i>Pagurus oculatus</i> , <i>Pagurus cuanensis</i>	top of shell close to opening	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
<i>Pomatoceras triqueter</i>	Not specified	<i>Pagurus bernhardus</i>	external shell close to opening	Bergen, Norway	Samuelson, 1970
<i>Eupomatus dianthus</i> (Serpulid)	* <i>Polinices</i>	<i>Clibanarius vittatus</i>	—	Galveston, Texas	Fotheringham, 1976
<i>Circeis paguri</i>	<i>Buccinum undatum</i>	<i>Pagurus bernhardus</i>	roof of last whorl, roof penultimate whorl	Swan Sea	Al-Ogily and Knight-Jones, 1981
<i>Spirorbis cuneatus</i> (Spirorbid)	<i>Murex</i> , <i>Aporrhais</i>	<i>Pagurus oculatus</i> , <i>Pagurus cuanensis</i>	bottom, aperture	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
<i>Spirorbis spirillum</i>	Not specified	<i>Pagurus bernhardus</i> , <i>Pagurus cuanensis</i>	inside aperture	Bergen, Norway	Samuelson, 1970
<i>Spirorbis spirillum</i>	* <i>Buccinum undatum</i> * <i>Littorina littorea</i> * <i>Neptunea antiqua</i>	<i>Pagurus bernhardus</i>	internal shell	Oresund & Frederikshavn, Denmark; Kristineberg, Norway	Jensen and Bender, 1973
<i>Janua pagenstecheri</i>	<i>Murex</i> , <i>Aporrhais</i>	<i>Pagurus oculatus</i> , <i>Pagurus cuanensis</i>	bottom, aperture: outer lip	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
<i>Filograna</i> sp.	<i>Murex</i> , <i>Aporrhais</i>	<i>Pagurus oculatus</i>	aperture: inner lip	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
<i>Sabellaria</i> sp. (Sabellidae)	<i>Busycon carica</i>	<i>Pagurus pollicaris</i>	sandy tubes in aperture	Delaware Bay	Karlson and Shenk, 1983
<i>Nereis succinea</i> (Nerid)	<i>Polinices</i> sp.	—	"etches" burrows into shell	Galveston Bay, Texas	Fotheringham, 1976

TABLE 1—Continued.

Polychaete species	Gastropod shell	Hermit crab	Location on shell	Locality	Reference
Boring species of polychaetes					
<i>Dodecaceria concharum</i> (Cirratulid)	<i>Murex, Aporrhais</i>	<i>Pagurus oculatus</i>	throughout shell	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
<i>Potamilla reniformis</i> (Sabellid)	<i>Murex</i>	<i>Pagurus oculatus</i>	spires, columella	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
<i>Boccardia tricuspa</i> (Spionid)	<i>Tegula brunnea</i>	<i>Pagurus granosimanus</i>	—	Cayucos, California, Galapagos	Woodwick, 1963
<i>Boccardia tricuspa</i>	<i>Ceratostoma nuttalli</i> <i>Olivella biplicata</i> <i>Thais emarginata</i>	<i>Pagurus samuelis</i>	—	Santa Barbara, Morro Bay and Cayucos, California	Woodwick, 1963
<i>Polydora ciliata</i>	same as <i>Boccardia</i>	<i>Pagurus samuelis</i>	—	Santa Barbara, California; France	Woodwick, 1963
<i>Polydora commensalis</i>	—	—	columella	Maine, Massachusetts, Connecticut, North Carolina	Blake, 1971
<i>Polydora commensalis</i>	—	<i>Pagurus hirsutiusculus</i>	columella	Maine	Blake, 1969
<i>Polydora commensalis</i>	—	—	columella	Curacao	Blake and Woodwick, 1972
<i>Polydora commensalis</i>	<i>Lunatia heros</i> <i>Polinices duplicatus</i> <i>Busycon canaliculatum</i> <i>Buccinum undatum</i>	<i>Pagurus pollicaris</i>	columella	Noak, Connecticut; Beaufort, North Carolina	Foster, 1971
<i>Polydora commensalis</i>	<i>Littorina littorea</i>	<i>Pagurus longicarpus</i>	columella	Noak, Connecticut; Beaufort, North Carolina	Hatfield, 1965
<i>Polydora commensalis</i>	<i>Nassarius obsoletus</i>	<i>Pagurus longicarpus</i>	columella	East Coast, Canada	Andrews, 1891
<i>Polydora commensalis</i>	<i>Thais lamellosa</i>	<i>Pagurus granosimanus</i>	columella	West Coast, North America (British Columbia)	Berkeley and Berkeley, 1956
<i>Polydora commensalis</i>	<i>Natica</i> spp.	<i>Pagurus</i> spp.	columella	Mazatlan, Mexico; Southern California	Berkeley and Berkeley, 1936
<i>Polydora commensalis</i>	<i>Polinices duplicatus</i>	<i>P. pollicaris</i>	umbilicus	Galveston, Texas	Hartman, 1941
<i>Polydora websteri</i>	various spp.	<i>Clibanarius vittatus</i> <i>Pagurus pollicaris</i>	—	Galveston, Texas	Fotheringham, 1976
<i>Polydora</i> unid.	<i>Buccinum</i> , unspecified	—	internal upper whorls	Bergen, Norway	Fotheringham, 1976
<i>Polydora limicola</i>	same as <i>Boccardia</i>	<i>Pagurus samuelis</i>	—	Santa Barbara, California	Samuelson, 1970
					Woodwick, 1963



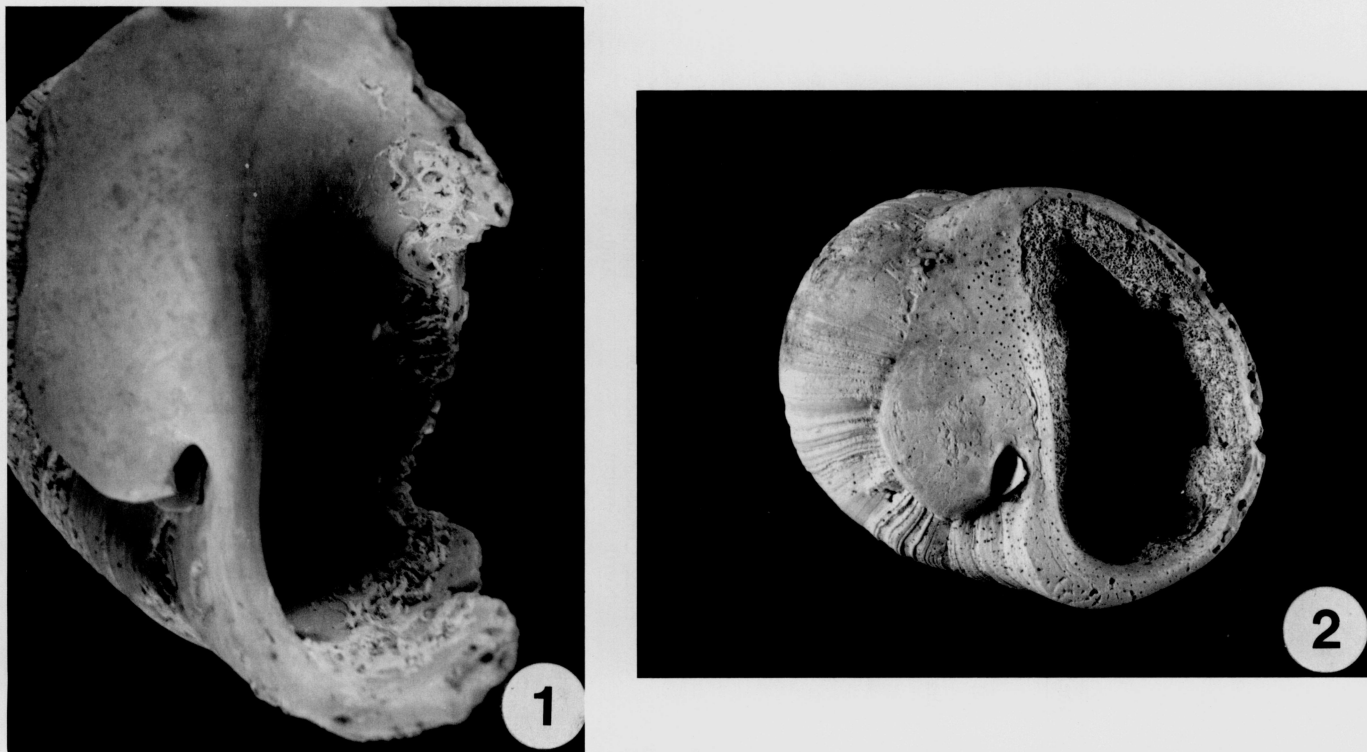


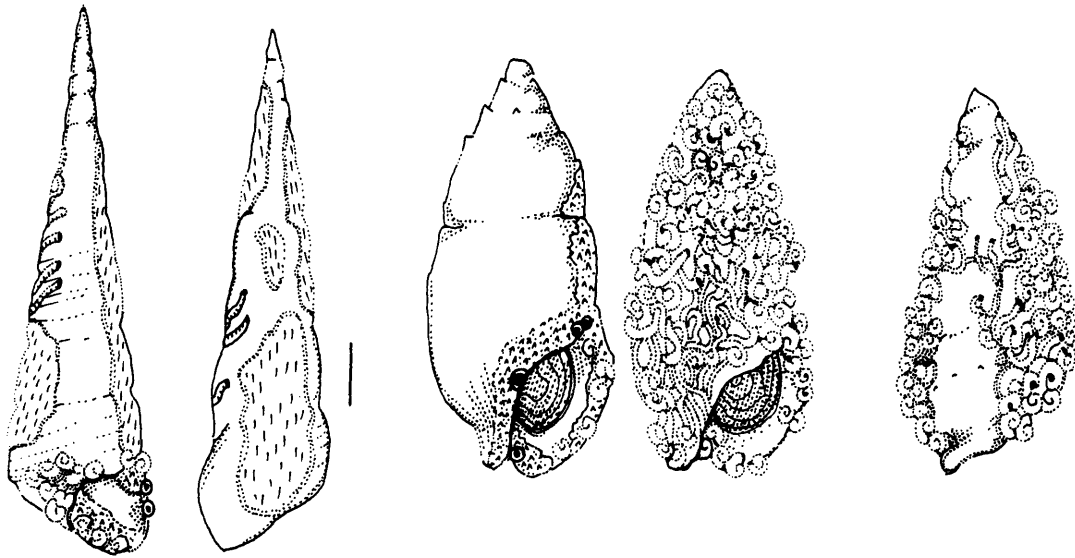
FIGURE 4—Pagurized *Polinices reclusianus*, Pleistocene, southern California, UCLA 3195, Orange Co. 1, encrusting serpulids (*Serpula* sp.) on outer lip, shell height, 77.8 mm, LACMIP No. 11491; 2, serpulids (*Salmacina* sp.) encrusting aperture with spionid trace fossils on outer lip and algal borings (*Gomotia*) on callus, shell height, 60.6 mm, LACMIP No. 11492. UCLA = University of California, Los Angeles specimens housed at Los Angeles County Museum of Natural History—Invertebrate Paleontology (LACMIP).

TABLE 2—Trace fossil *Helicotaphrichnus commensalis* in columellae of fossil gastropods attributed to *Polydora commensalis*. *Polydora biocipitalis* and other species also make this characteristic borehole only in hermitted shells.

Gastropod species	Fossil locality	Age	Reference
<i>Acanthina spirata</i>	various localities from Baja California and 11 southern to central California areas	Pleistocene	Kern et al., 1974
<i>Macron lividus</i>			
<i>Megasurcula stearnsiana</i>			
<i>Mitrella carinata</i>			
<i>Mitra idae</i>			
<i>Nassarius mendicus</i>			
<i>Nassarius</i> spp.			
<i>Ocenebra foveolata</i>			
<i>Ocenebra interfossa</i>			
<i>Ocenebra poulsoni</i>			
<i>Olivella biplicata</i>			
<i>Olivella pedroana</i>			
<i>Ophiodermella incissa</i>			
<i>Olivella biplicata</i>	34 Pleistocene localities from southern to northern California	Pleistocene	Walker, 1988a, 1988b
<i>Cancellaria</i> cf. <i>gemmulata</i>	Galapagos Islands	Pleistocene	Walker, in press
<i>Sveltia inermis</i>	Korytnica Clays, Holy Cross Mountains, Central Poland	Mid-Miocene	Kern, 1979 (p. 241, table 1)
<i>Triton affine</i>			
<i>Murex friedbergi</i>			
<i>Murex austriacus</i>			
<i>Ocenebra erinacea</i>			
<i>Ranella marginata</i>			
<i>Triton nodiferum</i>			
<i>Triton affine</i>			
<i>Triton tarbellianum</i>			
<i>Fusus hoessi</i>			
<i>Euthria puschi</i>			
<i>Trigonostoma puschi</i>			
<i>Ancilla glandiformis</i>			
<i>Clavatula laevigata</i>			
<i>Clavatula camillae</i>			
Many species	East Gulf Coast Fossil localities	Eocene–Pleistocene	Walker, this paper
<i>Bullioptis</i> , <i>Natica</i>	Maryland, St. Mary's Formation	Miocene	Walker, this paper



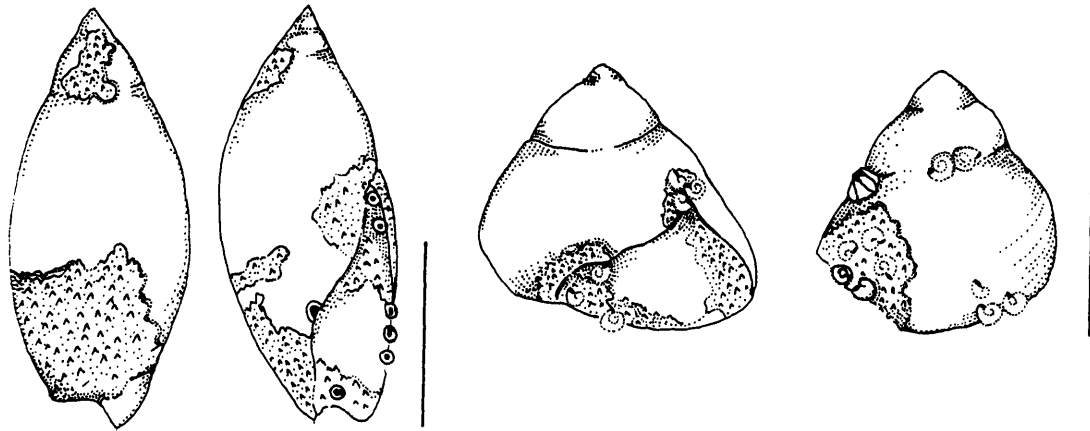
SUBTROPICAL 1



*Turritella leucostoma*

*Cerithium stercusmuscarum*

TEMPERATE 2



*Olivella biplicata*

*Tegula funebris*

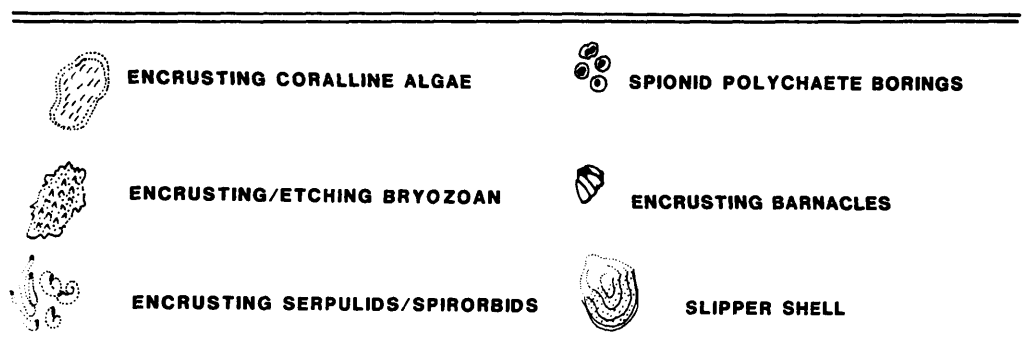


FIGURE 5—Subtle encrustation patterns on pagurized shells from the west coast of North America. 1, subtropical (Puerto Penasco, Mexico) pagurized shells of *Turritella leucostoma* and two aperture and one adaperture view of *Cerithium stercusmuscarum* encrusted with spirorbid polychaetes; 2, temperate (Bodega Bay, California) pagurized shells of *Olivella biplicata* and *Tegula funebris*. Scale bars indicate one centimeter.

TABLE 3—Stratigraphic distribution of East Gulf Coast gastropod species with *Helicotaphrichnus* trace fossils. All specimens listed here are housed at the United States National Museum, USNM; Tu = Hoerle collection; USGS = United States Geological Survey; — = no other bionts present.

Gastropod species	Other bionts present
Pleistocene, South Bay, Florida Tu 978, USGS 26545	
<i>Busycon contrarium</i>	—
<i>Cancellaria ?reticulata</i>	encrusting bryozoan apertural notch; serpulids outer lip
<i>Fusinus</i> sp.	spionids apertural notch and siphonal canal; serpulids outer lip
<i>Oliva</i> sp.	encrusting bryozoans inner and outer lip
<i>Xancus ?regina</i>	—
Pliocene, Pinecrest beds, Florida Tu 1177 = USGS 26439	
<i>?Anachis</i> sp.	—
<i>Architectonica</i> sp.	—
<i>Astraea</i> sp.	spirorbids interior aperture
<i>Cancellana ?amoena</i>	bryozoans present in outer lip; spionids siphonal canal
<i>Conus ?spurius</i>	—
<i>Fasciolaria</i> sp.	—
<i>Fusinus</i> sp.	spirorbids and encrusting bryozoans in aperture
<i>Melongena</i> sp.	—
<i>Mitra ?heilprini</i>	—
<i>Oliva</i> sp.	encrusting bryozoan siphonal canal; <i>Crepidula</i> in aperture
<i>Polinices</i> sp.	—
<i>Solenosteira</i> sp.	—
<i>Terebra</i> sp.	—
<i>Trigonostoma</i> sp.	gastrochaenids apertural notch
<i>Turritella</i> sp.	—
<i>?Urosalpinx</i> sp.	—
<i>Vasum</i> sp.	—
Miocene, Chipola Formation, Florida Tu 951 = USGS 26578	
<i>Busycon ?sicyoides</i>	external gastrochaenids
<i>Cancellaria</i> sp.	with serpulids in aperture
<i>Chicoreus gardnerae</i>	—
<i>Chicoreus nicholsi</i>	—
<i>Clavatula ?eleutheria</i>	—
<i>Conus ?dodona</i>	with clionids; serpulids outer lip
<i>Engoniphos chipolanus</i>	—
<i>Fasciolaria kindlei</i>	—
<i>Ficus</i> sp.	serpulid outer lip
<i>Hexaplex reatchi</i>	—
<i>Marginella</i> sp.	—
<i>Melongena ?sculpturata</i>	serpulids outer lip
<i>Mitra</i> sp.	encrusting bryozoan; internal outer lip; serpulid remnants outer lip; clionids with <i>Crepidula</i> in aperture
<i>Mitra (Tiara) mitrodita</i>	encrusting bryozoan aperture area
<i>Orthaulax gabbi</i>	—
<i>Panamurex fusinoides</i>	—
<i>Panamurex laccopola</i>	—
<i>Panamurex lychnia</i>	serpulids outer lip
<i>Terebra</i> sp.	—
<i>Vasum haitense</i>	—
<i>Vasum</i> sp.	gastrochaenids, encrusting bryozoan, serpulid tubes in aperture
<i>Xancus chipolanus</i>	etching bryozoan; clionid borings in aperture
Oligocene, Red Bluff, Mississippi USNM 136505	
<i>Caricella reticulata</i>	—
<i>Cassia brevidentata</i>	—
<i>Clavella huminosa</i>	encrusting bryozoan, clionids in aperture
<i>Latirus protractus</i>	—
<i>Lyria costata</i>	?serpulids outer lip
<i>Mitra conquisita</i>	—
<i>Murex mississippiensis</i>	—
<i>Pleurofusis oblivia</i>	—
<i>Triton conradianus</i>	bryozoan imprint in aperture

TABLE 3—Continued.

Gastropod species	Other bionts present
Eocene, Jackson, Mississippi USNM 480359	
<i>Lappharia pacitilis</i>	serpulid tubes; bryozoan imprint in aperture
<i>Mitra</i> sp.	—
<i>Murex angulatus</i>	encrusting bryozoan external
<i>Papillina dumosa</i>	bryozoan imprint in aperture
<i>Volutilia petrosus</i>	bryozoan imprint, serpulids apertural notch; <i>Anomia</i> scar aperture

*decacera*, for example, may be destroyed before they become fossils.

*Encrusting barnacles*.—Encrusting barnacles leave whole skeletons, basal plates, etch scars, or leave impressions on fossil molluscs (Darwin, 1854; Miller, III and Brown, 1979; Radwanski, 1977). Encrusting barnacles are present on hermitted shells in modern habitats but are rarely found in fossil assemblages (Table 5). When barnacles are present, they occur on external shell surfaces in rugosities or sutures. These areas protect the barnacle from taphonomic loss.

Barnacles are also present near the apertural notch in both living snails and hermitted shells. Occasionally barnacles will grow in the apertural notch of living snails. The snails will often overgrow the living barnacles, creating a flared ridge near the notch.

Living epifaunal snails and epifaunal hermitted shells have encrusting barnacles on the external shell surfaces. In contrast, infaunal snail shells usually do not have encrusting barnacles. There are exceptions to this rule. For example, infaunal naticids, such as *Polinices*, have encrusting barnacles on the apex of the shell and not elsewhere, an indication that the apex is exposed above the sediment. If barnacles completely cover infaunal shells, the shell was most likely occupied by a hermit crab.

Steinkerns may reveal important taphonomic histories of the postmortem shell. On large gastropod shells, such as naticids, encrusting and boring organisms may be preserved as impressions within the steinkern (Figure 8). Impressions of encrusting barnacles and associated bryozoans on steinkerns may indicate hermit crab-inhabitation.

*Boring barnacles*.—Boring barnacles (Acrothoracica: family Trypetesidae) are excellent indicators of fossil pagurized shells (Boekschoten, 1966; Seilacher, 1969). Their fossil record dates back to the Devonian (Tomlinson, 1987). They have only been reported from hermitted shells from the Miocene (Seilacher, 1969; Tomlinson, 1969a, 1969b). A few species of boring barnacles are exclusively associated with hermitted shells (Table 5).

These barnacles are commonly overlooked because of their habitat: the interior whorls and columellae of pagurized gastropod shells. Unless the shell is broken, it is difficult to detect their presence. A convenient way of determining the presence of boring barnacles is to "candle" the shell—backlight the shell and look for the presence of borings that are highlighted by the light (Tomlinson, 1969b). Occasionally the hermit crab's abdomen is outlined on the columella by the boreholes of the barnacle (Seilacher, 1969).

Boring barnacles cannot survive on shells filled with sediment and are dependent on a hermit crab to keep the shell above the sediment-water interface (Tomlinson, 1969b). The hermit crab's feeding currents provide the necessary aeration and access to food for the boring barnacles.

Large hermitted shells, such as *Buccinum*, are affected with numerous slit-like borings of adult female barnacles (White,

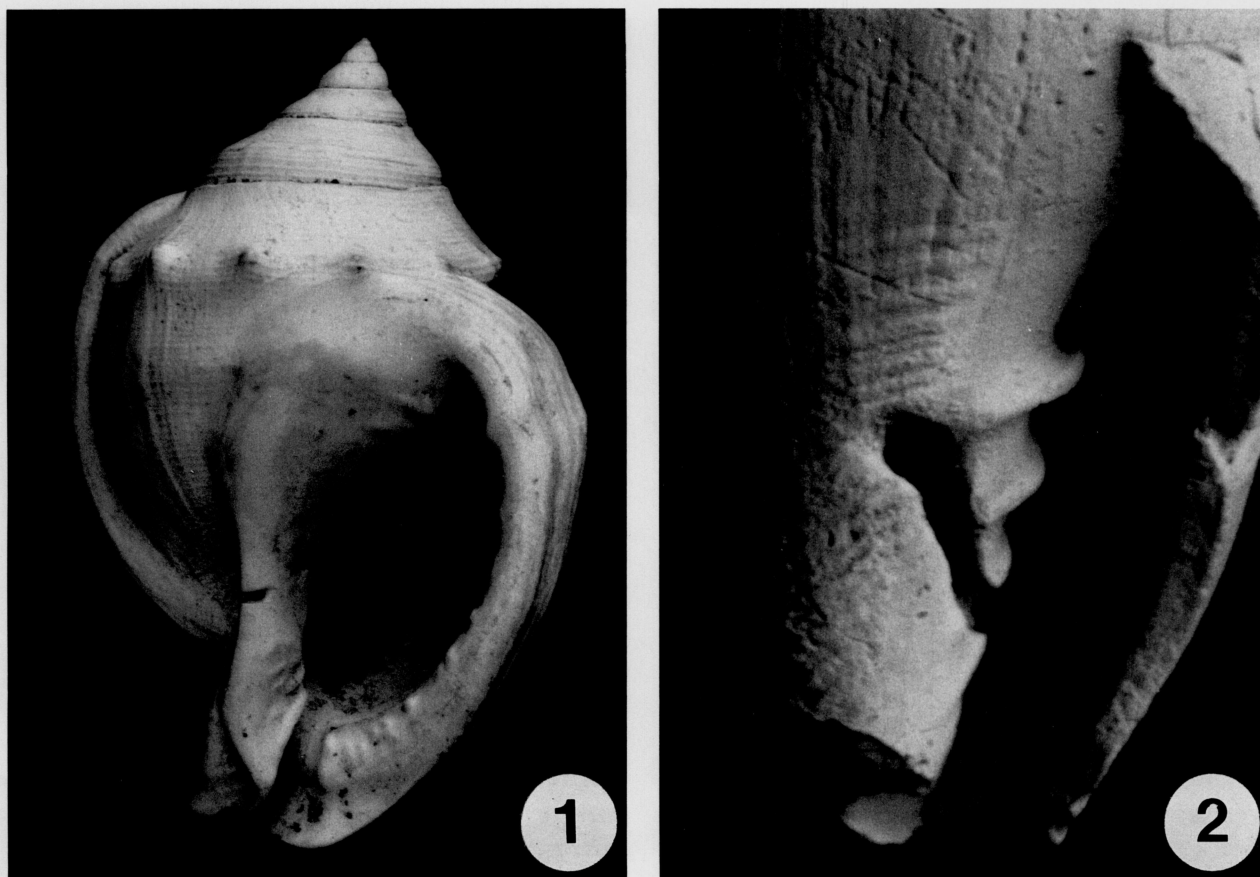


FIGURE 6—Eocene and Oligocene pagurization. *Helicotaphrichnus* bore holes in outer lip of 1, *Cassis brevidentata*, Oligocene, USGS 14721, Jackson, Mississippi, shell height, 39.0 mm and 2, *Mitra* sp., Eocene, USNM 480359, Hinds Co., Jackson, Mississippi, shell height 35.5 mm (siphonal canal damaged). Specimens are housed at the United States National Museum (USNM).

1969). The dwarf males, which never bore, enter the burrow of the female as a cyprid larva and attach to her. Young are brooded in the female's burrow and released. Small boreholes (assumed to be offspring) are often present around the original individual (Boekschoten, 1966).

The families of boring barnacles can be separated by burrow shape. In Trypetesidae, the aperture which opens toward the interior of the shell, is a tapered slit a few millimeters long and less than a millimeter wide (Tomlinson, 1969b). Some species of trypetesidae may be restricted to thick-shelled gastropods. On thin-shelled gastropods they have two openings: one pinpoint sized hole exiting the exterior of the shell and one slit-like hole exiting the interior of the shell.

*Trypetesa lampas* (Hancock) was the first boring barnacle to be described (Hancock, 1849). This species is widely distributed in cooler Atlantic and European waters (5–46 m) and inhabits a wide variety of pagurized shells (Table 5). It commonly inhabits pagurized *Buccinum undatum* and is not present on intertidal hermitted shells (White, 1969). This species may indicate deep-water hermitted shells if present in fossil assemblages. *Trypetesa habeii*, a boring barnacle associated with hermitted shells in Japan, is also present in deep-water habitats (Tomlinson, 1969b; Utinomi, 1962).

A west coast boring barnacle, *Trypetesa lateralis*, is present only in high intertidal open coast habitats of central California (Tomlinson, 1969b). Because of their restricted geographic distribution and specific depth zonation, boring barnacles may provide important depth and water temperature indicators when present in fossil assemblages.

*Encrusting bryozoans (thick encrusters)*.—Bryozoans are the best known Recent and fossil associates with hermit crabs (Tables 6, 7). Fossil pagurid–bryozoan associations are characterized by the bryozoan's multilayered appearance, characteristic monticulae (bumps), overgrowth of the shell aperture, and growth outward from the surface of the shell (Taylor, 1981). Multilayered bryozoans may be abraded on the bottom of the shell, producing a "pagurid facet" where the hermit crab presumably

TABLE 4—*Helicotaphrichnus* borehole in columellae of *Bullia* (*Bulliosis*) from the Maryland Miocene. Percentages are calculated from shells with and without boreholes, not from total sample. Localities noted within parentheses. (Data provided by W. and R. Allmon.)

Species	Total sample	With borehole	Without borehole	Indeterminate (damaged shell)
<i>B. (B.) marylandica</i> (Little Cove Point)	260	88 (59%)	61	111
<i>B. (B.) integra</i> (Windmill Point)	18 12	5 (55%) 7 (77%)	4 2	9 3
<i>B. (B.) quadrata</i> (Deep Point) (Windmill Point)	12 63	1 (50%) 23 (53%)	2 20	9 20
<i>B. (B.) q. bowlerensis</i> (no locality given)	59	19 (47%)	21	19
Totals	424	143 (56.5%)	110	171

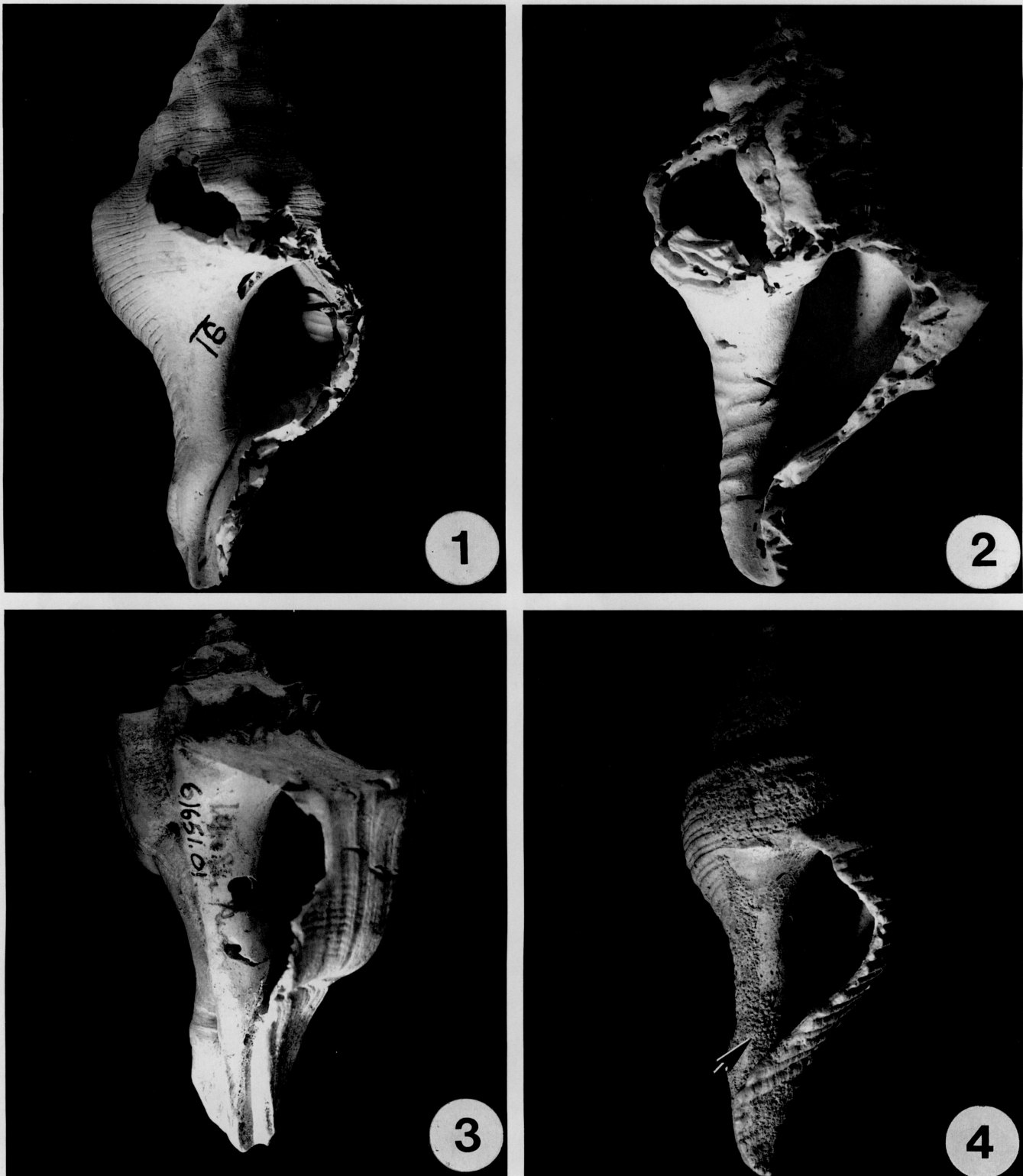


FIGURE 7—Spionid polychaete trace fossils in apertural notch and columella of subtidal Pleistocene gastropods (pagurized) from southern California. 1, *Kelletia kelletii* (Forbes) with pencil-thin spionid trace fossil on columella and anastomosing spionid tunnels on apertural notch and outer lip, Palos Verdes Sand, Los Angeles Co., California, CAS Loc. 91.01, shell height, 68.0 mm; 2, *Bursa californica* (Hinds) with bifurcating spionid trace fossils in columella and a tunnel on columella near siphonal canal, with other spionid trace fossils on apertural notch, Orange Co., California, UCLA Loc. 3195, LACMIP No. 11493, shell height, 68.5 mm; 3, *Forreria belcheri* (Hinds) with multiple boreholes in columella, Palos Verdes Sand, Newport Beach, Orange Co., California, CAS Loc. 61651.01, shell height, 63.2 mm; 4, *Fusinus barborensis* (Trask) with enlarged borehole in columella, encrusting bryozoans also present on columella (arrow), Dead Man Island, Los Angeles, California, CAS Loc. 61652.01, shell height, 41.5 mm.

TABLE 5—Boring and encrusting barnacles associated with hermit crabs.

Barnacles	Hermit crab	Gastropod shell	Locality	Reference
<b>Encrusting barnacles</b>				
<i>Balanus</i> sp.	<i>Clibanarius vittatus</i>	unidentified	Galveston, Texas	Fotheringham, 1976
<i>Balanus eburneus</i>			St. Joseph's Bay, Florida	McLean, 1983
<i>Chthamalus</i> sp.				
<i>Balanus crenatus</i>	<i>Pagurus granosimanus</i>	<i>Olivella biplicata</i>	Bodega Bay, California	Walker, 1988b
<b>Boring barnacles</b>				
<i>Trypetesa lampas</i> ( <i>Alcippe lampas</i> )	<i>Pagurus bernhardus</i> <i>Pagurus prideauxi</i> <i>Pagurus cuanensis</i>	<i>Buccinum undatum</i> <i>Colus gracilis</i> <i>Neptunea antiqua</i> <i>Natica alderi</i>	North Sea, Helgoland; NE Britain; English channel; Sweden; Isle of Man; Denmark; Mediterranean; Woods Hole, Massachusetts; Beaufort, North Caro- lina; North Wales	White, 1969
<i>Trypetesa lampas</i>	—	<i>Buccinum undatum</i> <i>Littorina littorea</i> <i>Natica catena</i> <i>Natica poliana</i> <i>Turritella communis</i> <i>Trochids</i>		Turquier, 1967
<i>Trypetesa lampas</i>	—	<i>Fusus antiquus</i> <i>Buccinum undatum</i> <i>Buccinum undatum</i>	Durham (Britain)	Hancock, 1849
<i>Trypetesa lampas</i>	—	<i>Buccinum undatum</i>	North Sea; E. Coast of United States	Boekschoten, 1966
<i>Trypetesa lateralis</i>	<i>Pagurus samuelis</i>	<i>Tegula</i>	Central California	Tomlinson, 1955
<i>Trypetesa lateralis</i>	—	<i>Strombus</i>	Puerto Rico Japan	Seilacher, 1969
<i>Trypetesa nassaroides</i>	<i>Anapagurus hyndmanni</i> <i>Pagurus bernhardus</i> <i>Pagurus cuanensis</i>	<i>Nassarius</i> sp. <i>Trophon</i> sp. <i>Mangelia</i> sp. <i>Tectus conus</i> <i>Chlorostoma nigerrium</i> <i>Monilea</i> sp. <i>Tegula rustica</i>	Roscoff, France	Tomlinson, 1969b after Turquier, 1967
<i>Trypetesa habeii</i>			Japan	Tomlinson, 1969b
<b>Encrusting fossil barnacles</b>				
Balanids	—	<i>Thais lapillus</i>	Pleistocene, Red Crag, Suffolk	Boekschoten, 1967
<i>Balanus</i> sp.	—	<i>Olivella biplicata</i>	Pleistocene, Moonstone Beach	Walker, 1988b
<b>Boring fossil barnacles</b>				
<i>Trypetesa</i> -like borings (unnamed)	—	<i>Pyrula</i>	Hungary	Seilacher, 1969
Unidentified burrows	—	<i>Pyrula cornuta</i> <i>Fasciolaria tarbelliana</i> <i>Triton nodiferum</i>	Varpolata and Grund	Tomlinson, 1969b after Zapfe, 1936

dragged the shell (Palmer and Hancock, 1973). These abraded areas represent discontinuities in bryozoan growth.

Multilaminar associations are reported from the middle Jurassic of France (Buge and Fischer, 1970; Palmer and Hancock, 1973). The amount of encrustation varies on these shells from large, multilaminar crusts that completely engulf the snail shell (Figure 2.5, 2.6) to thinner crusts with the snail shape still visible (Figure 2.7). It was once thought that these bryozoans dissolved the shell underneath, but this is not the case (Taylor and Cook, 1981). The shell may be difficult to find under 30–50 layers of zooecia (see Cook, 1964), but is invariably present.

Amazingly, multilaminar bryozoans appear to mimic the gastropod spiral. For example, the encrusting bryozoan *Hippoporida edax* grows helically and apparently uses the hermit crab as a template for making a coiled shell (Taylor and Cook, 1981). This globular growth form can be seen in fossils from the Pliocene of England (Coralline Crag, Suffolk; Taylor and Cook, 1981) (Figure 2.8, 2.9). *Hippoporida edax* are found on gastropod fossils dating from the Miocene and are extant in offshore habitats of the southeastern United States (Table 6). *Hippoporida*

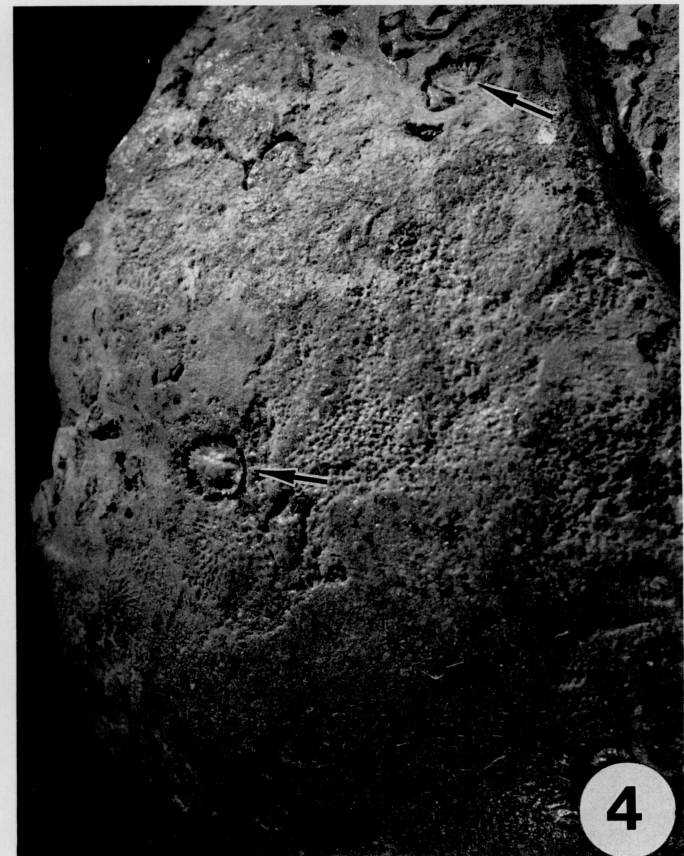
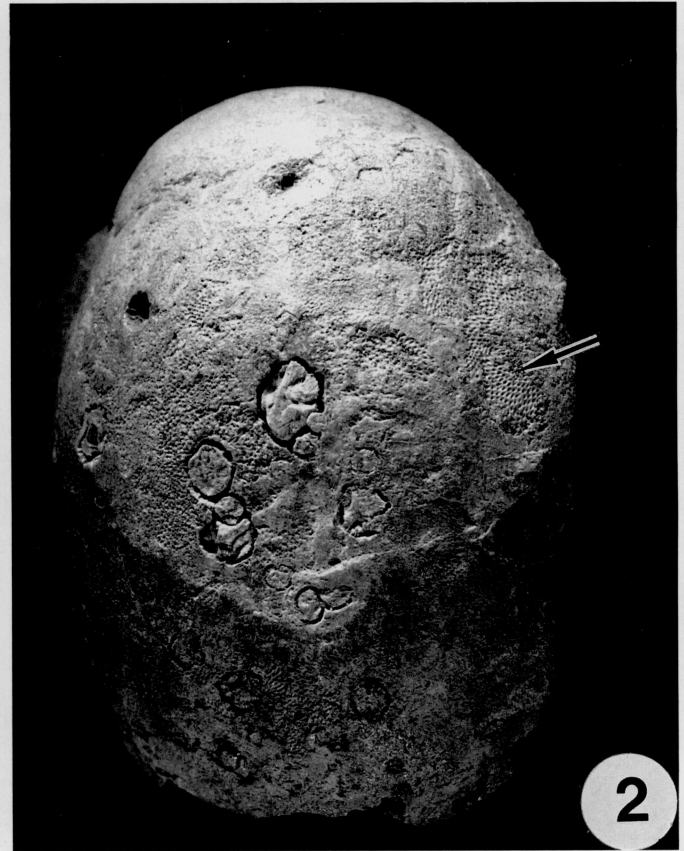
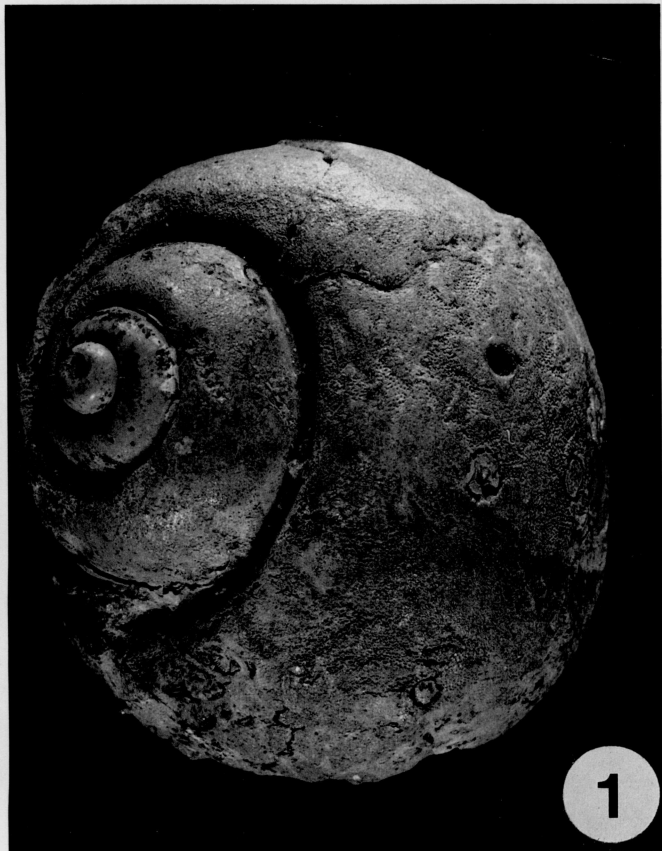
may also have two color and growth forms, which appear to mimic cnidarians (McKinney and Jackson, 1989).

*Conopeum commensale* is another encrusting bryozoan that produces a ball-shaped form (Kirkpatrick and Metzelaar, 1922). Ball-forming bryozoans on gastropod shells are reported from fossil deposits from the west coast of the United States (Miocene, Santa Margarita Formation, San Luis Obispo County, Adegoke, 1967; Astoria Formation, Moore, 1963; and Pliocene, Imperial Formation, Gyllenhaal and Kidwell, 1989) (Table 7).

Encrusting bryozoans may also have elongated projections radiating out from a multilaminar colony. *Hippoporida*, a round encrusting form, is also noted for its unusual growth, called "Texas longhorns," when associated with hermit crabs (Deichmann, 1954; Smith, 1966) (Figure 2.10). The zooecia grow out from the shell in the form of long "arms" that resemble horns (Smith, 1966; Glaessner, 1969). This growth form is not restricted to *Hippoporida* in the Gulf of Mexico, but is also present in *Hippoporida* species off the coast of Africa (Cook, 1964).

Longhorn bryozoans are associated with deep-water pagurids. Interestingly, these longhorns are very similar to staghorns of







the hydractinian, *Janaria*, that are also found in deep water (Cairns and Barnard, 1984). Longhorn bryozoans and staghorn hydractinians have had a long geological history in association with hermit crabs (presumably Eocene for *Janaria* and Miocene for *Hippoporidra*). Consequently, they are excellent indicators of pagurized shells. *Hippoporidra* and *Janaria* are excellent candidates for studying the evolution of deep-water pagurid "symbionts." Modularity may allow for variable morphology such that extra "shells" can be made for these presumably shell-limited deep-water hermit crabs.

Encrusting bryozoans not only form extra helical shell material for deep-water hermit crabs, they may also form tubes extending from the aperture of the shell. Schembri (1982) noted that many deep-water pagurids from Otago Peninsula, southeastern New Zealand, possess bryozoan tubes. A detailed study of these associations revealed a startling diversity of bryozoans: 13 species were tube formers and three of these species were obligate with hermit crabs (Taylor et al., 1989) (Table 6). In addition, 47 non-tube building bryozoans also associated with the hermit crabs.

The Otago tube-builders have two main forms of growth: a round ball-shaped form and a form with the tube extending out from the shell (Taylor et al., 1989) (Figure 2.11). The growth of the bryozoan is thought to co-occur with the hermit crab occupant as it grows. Eleven species of fossil tube-builders (inferred to be hermit crab associates) were also discovered in the early Miocene of New Zealand (Taylor et al., 1989). Tube-like bryozoans have also been reported from the Miocene and Pliocene of France (Andre and Lamy, 1936, after Lecointre, 1929) (Figure 2.12). This fossil form shares a long geological history with the longhorn bryozoans. The Miocene appears to be an important turning point for the diversification of morphological patterns in the bryozoans (see Taylor, 1981). Perhaps it also reflects a similar diversification in the pagurids.

Several species of bryozoans are obligate with pagurids but few pagurid species are specific with a particular bryozoan. For example, *Hippoporidra senegambiensis* (Carter) is a specific associate with hermit crabs (Cook, 1964, 1968; see Carter, 1882). Cook (1968) performed a simple settling experiment with *Turritella* shells and bryozoan larvae from *H. senegambiensis*. Her results indicated that most larvae settle near the mouth of *Turritella* shells inhabited by pagurids. She suggested that this settlement location was the most advantageous for these filter-feeding bryozoans. Although Gordon (1972) did not perform experiments with larvae, he reported that the bryozoan *Hippopodinella adpressa* exclusively associated with *Pagurus novaezelandiae* from northern New Zealand. Taylor et al. (1989) reported that three species of tube-building bryozoans are obligate with hermit crabs, but were not tied to a particular hermit crab species, with one possible exception. Unlike hydractinians that may be specific to certain species of hermit crabs, bryozoan evolution may be tied to a guild of hermit crabs (and their diversity) rather than to certain species.

Not all bryozoans make such thick and noticeable crusts. Subtle encrusting patterns of bryozoans can occur with marine hermit crabs. On fossils, remnants of encrusting bryozoans are usually retained in the apertural notch, siphonal canal, and outer lip area of the shell. These patterns may be caused by abrasion

on the outer parts of the shell. The apertural notch and other interior surfaces function as "taphonomic refugia" for the bryozoans.

On living hermitted shells the patterns of encrusting bryozoans may be limited to the apertural side for a variety of reasons (e.g., preferred settlement locality; less susceptible to desiccation; competition between encrusting species). For example, *Hippopodinella adpressa* surrounds the apertures of hermitted shells of *Cerithium stercusmuscarum* in the northern gulf of California (Figure 5.1). Similarly, *Hippothoa hyalina* surrounds and invades the apertures of shells in shallow intertidal areas in California and Baja (Figure 5.2) (Walker, 1988a). These subtle encrusting patterns are often overlooked and may be more common than the multilaminar forms.

*Etching bryozoans.*—Some species of bryozoans chemically etch the calcareous substrate they encrust (Tables 5, 7). Cyclostome bryozoans and many cheilostomes can etch pits in shells (Boekschoten, 1966, 1967; Pinter Morris, 1974). Etching bryozoans have been used to infer hermitted shells in the fossil record (Boekschoten, 1967; Walker, 1988a, 1988b, 1989).

The cheilostome *Hippothoa hyalina* is an excellent indicator of fossil pagurized shells (Walker, 1988a, 1988b, 1989). This species may represent a species complex, members of which all have the ability to etch oval-shaped pits in molluscan shells (Pinter Morris, 1974). *Hippothoa hyalina* has a recent distribution from Alaska to southern California and has been reported from cold-water upwelling areas in Mexico (Pinter Morris, 1974). The trace fossils of this species occur in many localities and were used to infer pagurized shells in the California Pleistocene (Walker, 1988a, 1988b) (Table 7). The etched pits were frequently encountered in the siphonal canal, apertural notch, columella, and above the aperture of fossil gastropod shells (Walker, 1988b). Occasionally, the pits outline the cheliped resting places on the columella of the shell (Walker, 1988b). The potential for using this species as an indicator of paleo-pagurids is great. The genus *Hippothoa* has a fossil record dating from the Cretaceous (Bassler, 1953).

*Hippothoa*-like trace fossils on gastropod shells are reported here for the first time from the Eocene and Oligocene of Mississippi (Table 8). The etch marks are frequently encountered on the columella and inner and outer lip, indicating a pagurized shell. In fact, on one fossil specimen (*Calyptrophorus ?stamineus*) the bryozoan etched around the cheliped-resting areas on the columella. This pattern was also seen with *Hippothoa* trace fossils on *Olivella biplicata* from the Pleistocene of California (Walker, 1988a, 1988b).

*Electra* and *Conopeum* are other species of encrusting bryozoans that etch gastropod shells. *Electra* etchings were used to infer pagurized shells in the Pliocene of Belgium (Boekschoten, 1966).

*Boring ectoprocts.*—Many boring bryozoans associate with living gastropods (Silen, 1947; Pohowsky, 1978) and not necessarily with hermitted shells. Occasionally, boring bryozoans have been interpreted to indicate a pagurized fossil shell. The bryozoans penetrate areas thought to be "uncolonizable" on living snails, such as the callus and parts of the columella. For example, boring bryozoans (*Spathipora*, *Terebripora*, and *Penetrantia*) that occur on the callus (near the aperture) of fossil

←  
FIGURE 8—*Polinices steinkern* with impressions of encrusting barnacles and bryozoans on the interior aperture, Pliocene, UCMP A-3293, San Benito Co., Priest Valley Quad., Pancho Rico Formation, shell height, 53.8 mm, UCMP Type No. 39687. 1, full view of steinkern; 2, aperture view of *Polinices* in 1, barnacle impressions are outlined as concentric circles and impressions of encrusting bryozoans (arrow) are shallow pits in steinkern; 3, 4, Close-up of bryozoan and barnacle pits on *Polinices* steinkern, arrows mark encrusting bryozoans (3) and barnacle impressions (4).

TABLE 6—Recent encrusting and boring bryozoans associated with hermitted shells; — = no information.

Encrusting bryozoans	Gastropod shells	Hermit crab	Location on shell	Locality	Reference
<b>Bryozoans</b>					
? <i>Callopora lineata</i>	—	<i>Pagurus bernhardus</i>	inside aperture	Bergen, Norway	Samuelson, 1970
<i>Celleporella hyalinina</i>	<i>Murex, Aporrhais</i>	<i>Paguristes oculatus</i> ; <i>Pagurus cuanensis</i>	external	Gulf of Trieste	Stachowitsch, 1980
<i>Cellepora</i> sp.					
<i>Cellepora parasitica</i>	—	<i>Petrochirus granulimanus</i> (= <i>Pagurus</i> )	body whorl	Gulf of Trieste	Kirkpatrick and Metzelaar, 1922 Stachowitsch, 1980
<i>Conopeum commensale</i>	—				
<i>Hippopodinella lata</i>	<i>Murex, Aporrhais</i>	<i>Paguristes oculatus</i>	body whorl; near inner lip; bottom of shell	Eastern United States; Gulf of Mexico	Taylor and Cook, 1981
<i>Hippoporidra edax</i>	—	—	“longhorns” body whorl; aperture top	British Wales	Cook, 1964
<i>Hippoporidra</i> spp.	—	—			
<i>Hippoporidra lusitania</i>	—	—	“longhorns”	Africa	Cook, 1964
<i>Hippoporidra senegambiensis</i>	<i>Turritella annulata</i>	<i>Eupagurus alcocki</i> <i>Diogenes ovatus</i>			
<i>Membraniopora tenuis</i>	<i>Busycon carica</i>	<i>Pagurus pollicaris</i>	Delaware Bay	Delaware Bay	Karlson and Shenk, 1983 Karlson and Shenk, 1983
<i>Schizoporella errata</i>	<i>Busycon carica</i>	<i>Pagurus pollicaris</i>			
<b>Bryozoan tube formers</b>					
<i>Borgiola otagoensis</i>	—	<i>Pylopagurus stewarti</i> <i>Pylopagurus</i> n. sp. <i>Lophopagurus 'thompsoni'</i> <i>Australeremus cooki</i>	all make tubes	Otago Peninsula, South-eastern New Zealand	Taylor et al., 1989 (their table 4)
<i>Disporella gordonii</i>	—	<i>Pagurus</i> n. sp. B <i>Australeremus cooki</i> <i>Pylopagurus stewarti</i> <i>Pylopagurus</i> n. sp. <i>Paguristes barbatus</i> <i>Pagurus</i> n. sp. B <i>Pylopagurus stewarti</i> <i>Pylopagurus</i> n. sp.	all make tubes	Otago Peninsula South-eastern New Zealand	Taylor et al., 1989
<i>Heteropora parapelluculata</i>	—				
<i>Arachnopusia unicornis</i>	—				
<i>Schizomauella trachorna</i>	—				
<i>Schizosmittina maplestoni</i>	—				
<i>Osthimosia monilifera</i>	—				
<i>Osthimosia socialis</i>	—				
<i>Crepidacantha zelanica</i>	—				
<i>Tubulipora</i> cf. <i>anderssoni</i>	—				
<i>Akatopora circumsaepia</i>	—				
<b>Soft bodied bryozoans</b>					
<i>Alcyonidium polyoum</i>	<i>Ilynassa obsoleta</i>	<i>Pagurus longicarpus</i> <i>Pagurus pollicaris</i>	external shell	Delaware Bay	Karlson and Cariolou, 1982
<i>Alcyonidium polyoum</i>	<i>Busycon carica</i>	<i>Pagurus pollicaris</i>	ventral/dorsal (also on living snail)	Delaware Bay	Karlson and Shenk, 1983
<i>Flustrella hispida</i>	Not specified	<i>Pagurus bernhardus</i>	inside shell	Bergen, Norway	Samuelson, 1970
<b>Etching bryozoans</b>					
<i>Electra</i> sp.	<i>Buccinum undatum</i>	—	columella; inner lip; inside last whorl	Northern Netherlands	Boekschoten, 1966
<i>Hippothoa hyalina</i>	<i>Olivella biplicata</i>	<i>Pagurus granosimanus</i>	entire shell; columella; inner lip	Bodega Bay, Northern California	Walker, 1988b
<b>Boring bryozoans</b>					
<i>Immergentia californica</i>	<i>Olivella biplicata</i>	<i>Pagurus granosimanus</i>	callus; apex; lives on living snails only (dead on hermits)	Bodega Bay, Northern California	Walker, 1988b
<i>Terebripora</i> sp.	<i>Buccinum undatum</i>	<i>Pagurid</i>	all over shell, especially columella	North Sea Coast	Boekschoten, 1966

TABLE 7—Fossil occurrence of encrusting, etching, and boring bryozoans associated with hermit crabs.

Bryozoan	Gastropod species	Inferred pagurid	Locality	Age	Reference
<b>Encrusting bryozoan</b>					
<i>Atractosoecia incrustans</i> (= <i>Berenicea</i> )	<i>Ataphrus labadyei</i> <i>Dicroloma tridigitatum</i> <i>Dicroloma cirrus</i>	yes	France	Upper Bathonian, Jurassic	Buge and Fisher, 1970
<i>Berenicea</i> sp.	<i>Ataphrus</i> sp.	yes	France	Upper Bathonian, Jurassic	Palmer and Hancock, 1973
<i>Hippoporidra edax</i> (= <i>Cellepora edax</i> )	—	yes	France; Eastern United States	Miocene	Taylor and Cook, 1981
<i>Membranipora fusca</i>	<i>Natica</i> sp.	yes	England, France, Italy, Belgium, Holland, Eastern United States	Pliocene	
<i>Conopeum commensale</i> (? <i>Conopium</i> )	—	—	Rio de Oro, Spanish Sahara Santa Margarita Fm, California	Quaternary Late Miocene to Recent	Buge and Lecointre, 1962 Adegoke, 1967
<i>Membranipora</i> sp.	<i>Searlesia? carlsoni</i>	no	Astoria Formation, Oregon	Miocene	Moore, 1963
<b>Etching bryozoans</b>					
<i>Hippothoa</i> -like etchings	<i>Tegula funebris</i> <i>Olivella biplicata</i>	yes	Southern California localities	Pleistocene	Walker, 1988a, 1988b
<i>Hippothoa</i> -like etchings	(See Table 2, this paper)	yes	Mississippi (Red Bluff Formation) and Jackson, Mississippi	Eocene, Oligocene	Walker, this paper
<i>Electra</i> sp.	<i>Buccinum</i> sp.	no	Holland, Belgium	Pliocene, Pleistocene	Boekschoten, 1966, 1967
<b>Boring bryozoans</b>					
<i>Spathipora; Terebripora</i> <i>Penetrantia</i>	<i>Ancilla glandiformis</i> <i>Natica redempta</i> <i>Ranella marginata</i> <i>Sveltia inermis</i> <i>Euthria intermedia</i> <i>Triton affine</i> <i>Triton nodiferum</i> <i>Fusus hoessi</i> <i>Ocenebra erinacea</i> <i>Olivella biplicata</i>	yes	Korynica Clays, Poland	Mid-Miocene	Baluk and Radwanski, 1979
<i>Immergentia</i> -like		yes: but not diagnostic of pagurids	localities in California	Pleistocene	Walker, 1988b

TABLE 8—Location of bryozoan trace fossil on fossil gastropods from the Eocene and Oligocene of the East Gulf Coast.

Gastropod species	Location of etching bryozoan on shell
Oligocene, Red Bluff, Wayne Co., Mississippi USNM 136505	
<i>Ampullinopsis mississippiensis</i>	columella near apertural notch
<i>Mitra conquisita</i>	internal aperture; columellar plications
<i>Pleurotoma longiforma</i>	outer lip; external siphonal canal and into columella
<i>Triton conradianus</i>	external aperture
Eocene, Jackson, Mississippi USNM 480359	
<i>Calyptrophorus ?stamineus</i>	claw area outlined by bryozoan imprint on columella; siphonal canal; external shell and outer lip margins
<i>Caricella subanulata</i>	inner lip
<i>Clavella humerosa</i>	siphonal canal/columella
<i>Cypraea finguis</i>	base of shell
<i>Fusinus</i> sp.	outer lip
<i>Lappharia pactilis</i>	inner lip/siphonal canal; external shell
<i>Mitra millington</i>	internal aperture
<i>?Papillina dumosa</i>	inner and outer lip
<i>Pseudoliva vetusta</i>	inner lip/apertural notch area; interior aperture/siphonal canal
<i>Turritella alveata</i>	aperture
<i>Volotalithes petrosus</i>	outer lip/aperture notch columella

gastropods were interpreted to have been occupied by hermit crabs (Baluk and Radwanski, 1979) (Table 7).

However, boring bryozoans that occur on the apertural side may not be indicators of hermit crabs. Living colonies of the boring bryozoan, *Immergentia*, occurred on living *Olivella biplicata* but the colonies were dead on shells occupied by hermit crabs (Walker, 1988b). In fossil specimens that have been abraded, the occurrence of *Immergentia*-like borings on the columella can be misleading. The living snail overgrows the boreholes (many borings can be seen through a glossy inductura on living *Olivella* shells). If this inductura is abraded, then the fossils will give the appearance that the boreholes were actually on the columella of the shell. Using boring bryozoans as a diagnostic feature for hermitted shells is not recommended, unless the bryozoan invades deeply into the shell's aperture.

Boring bryozoans are difficult to distinguish from each other. Their bore holes are very similar to young colonies of boring sponges or boring green algae. Silen (1947) warned of the danger of identifying them by their traces on shells. Several different types of bryozoans have invaded the shell niche (*Stolonifera*, *Carnosa*, *Penetrantidae*, *Immergentidae*) and unless the soft body is present, it is difficult to associate a species to a bore hole.

**Gastropods.**—Slipper shells of the genus *Crepidula* inhabit both the interior and exterior of hermitted shells (Conover, 1976; Scully, 1979; Karlson and Cariolou, 1982). *Crepidula* that inhabit the exterior of shells are not necessarily diagnostic of paleo-pagurids. Most of these *Crepidula* inhabit the external shells of living snails, and it appears that the hermit crab inherits the *Crepidula* once the snail dies (Table 9) (Figure 9.1). In most cases, these *Crepidula* are disassociated from the shell upon burial. The attachment scar of *Crepidula* can be seen on recent shells (e.g., *Calliostoma ligatum*, Figure 9.2), but has rarely been observed in fossil specimens. *Crepidula*-like trace fossils can be seen on fossil gastropods from the eastern Gulf Coast, but they are rare (Figure 10.1).

*Crepidula convexa*, an East Coast species, takes on a high, narrow shape on hermitted shells (Hendler and Franz, 1971). Shell growth in this species is restricted by the length and curvature of the host shell. Large *C. convexa* overgrow the hermitted shell, producing a "skirt" of shell material that flanks

the gastropod shell. According to Hendler and Franz (1971), these hermit *Crepidula* also possess different reproductive modes. No attempt has been made to determine the extent of these high, narrow-shaped *Crepidula* in the fossil record of the East Coast.

Unlike the external shell-inhabiting species, *Crepidula* that inhabit gastropod apertures are excellent indicators of hermit crab occupancy. Slipper shells that occupy hermitted shells are usually thin and curved to fit the interior shell aperture. These slipper limpets are cosmopolitan in distribution (Hoagland, 1977) except for the northwestern Pacific, where they are lacking (Vermeij et al., 1987). Aperture-inhabiting *Crepidula* have a Cenozoic fossil record, dating from the Oligocene in the Americas and Eocene in Europe (Hoagland, 1977; Baluk and Radwanski, 1985).

Paleontological reports usually interpret the crepidulid aperture-inhabiting mode of life as associated with empty gastropod shells. Steinkerns with *Crepidula* trace fossils are known from Neogene deposits in Europe (Baluk and Radwanski, 1985). The *Crepidula* were interpreted to settle on empty shells in soft-sediment habitats; however, the apertural *Crepidula* is characteristic of co-habitation with hermit crabs.

*Crepidula plana*, on the east coast of North America, is the best studied of the slipper limpets, but does not appear to be common in modern habitats. Scully (1979) reported 6 percent (84/1,404 shells) of a Narragansett Bay population of hermit crabs had *Crepidula plana* in the internal aperture of *Littorina littorea*. Fotheringham (1976) reported 3–8 percent of hermitted gastropod shells had *C. plana*. However, it is rare to find aperture-inhabiting *Crepidula* in fossil gastropods. This rarity, in part, is caused by its friable skeletal composition and the removal of *Crepidula* from shell apertures during fossil preparation.

On the California coast, *Crepidula nummaria* and *Crepidula perforans* are present within the aperture of hermitted shells and appear to be more common than their East Coast relatives (Carlton and Roth, 1975; Walker, 1989). These species have also been reported from the California Pleistocene (Hoagland, 1977; Woodring et al., 1946), but in most cases have not been correlated with the presence of hermit crabs. Walker (1988b) found *Crepidula* spp. in the apertures of recent hermitted (13/30) and Pleistocene *Olivella biplicata* shells (2/30) from the same locality (Coal Oil Point, Goleta, California). *Crepidula* are also common (up to 40 percent: 91/197 hermitted shells) in Puerto Penasco, Mexico (Table 10).

**Other molluscs.**—A few other molluscs are also reported to occur on hermitted shells. Some species encrust the interior of the shell (e.g., *Anomia* spp. and oyster spat), others bore into the shell, either into spines or the siphonal canal (e.g., *Gastrochaena dubia*), or bore elsewhere on the shell (e.g., *Hiatella artica*) (Table 9). Little attention has been given to these species, some of which could be quite destructive to the shell.

*Gastrochaena* weakens a hermitted shell and will cause the eventual destruction of the shell (Stachowitsch, 1980). It is unclear how gastrochaenids contribute to shell destruction compared to other boring organisms present on the shell (especially, *Cliona* and boring spionid polychaetes). Gastrochaenids may settle first on the living snail and will continue their boring activities during hermit crab tenancy of the shell. The end result of gastrochaenid borings is a riddled and nonusable shell, which is discarded by the hermit crab population.

#### THE HERMITTED SHELL, AN OVERVIEW

Hermit crabs are shell-limited in many Recent habitats. Their populations are usually limited by the number of available gastropod shells (Vance, 1972; Spight, 1977; Shimoyama et al.,

TABLE 9—Molluscs associated with hermitted shells. Unless specified, all of these molluscs settle/live within the aperture of the shell.

Mollusc—Crepidula species	Gastropod shell	Hermit crab	Locality	Reference
<b>External shell attachment</b>				
<i>Crepidula adunca</i>	<i>Tegula funebris</i> <i>Tegula brunnea</i> <i>Calliostoma ligatum</i>	<i>Pagurus samuelis</i> <i>Pagurus granosimanus</i>	San Diego to Vancouver Island	Morris et al., 1980; Hoagland, 1977; Vermeij et al., 1987
<i>Crepidula convexa</i>	<i>Ilyanassa obsoleta</i>	<i>Pagurus longicarpus</i> <i>Pagurus pollicaris</i>	Delaware	Karlsou and Cariolou, 1982
<i>Crepidula convexa</i>	—	—	East Florida, Nova Scotia; West Indies-Puerto Rico; Introduced to San Francisco Bay	Hoagland, 1977
<i>Crepidula fornicata</i>	—	—	Narragansett Bay, Rhode Island	Scully, 1979
<i>Crepidula fornicata</i> <i>Crepidula fornicata</i>	<i>Busycon carica</i> —	<i>Pagurus pollicaris</i> —	Delaware Bay St. Joseph's Bay	Karlsou and Shenk, 1983 McLean, 1983
<b>Aperture inhabiting crepidula</b>				
<i>Crepidula nummaria</i>	<i>Tegula funebris</i>	<i>Pagurus samuelis</i>	Pt. Cabrillo, California	Walker, 1988a
<i>Crepidula fornicata</i> <i>Crepidula nummaria</i> (in general)	—	—	San Pedro to Puget Sound; Alaska, Mazatlan, Bering Strait	Hoagland, 1977
<i>Crepidula perforans</i> (in general)	—	—	Matzatlan; Monterey, California; Vancouver, Canada	Hoagland, 1977
<i>Crepidula plana</i> (in general)	—	—	Trinidad to Prince Edward Island; Buenos Aires to Uruguay; Venezuela; Texas	Hoagland, 1977
<i>Crepidula plana</i> <i>Crepidula plana</i>	—	<i>Clibanarius vittatus</i> —	Galveston Bay, Texas Narragansett Bay, Rhode Island	Fotheringham, 1976 Scully, 1979
<i>Crepidula unquiformis</i> (in general)	—	—	Mediterranean and Adriatic Seas; Coast of Portugal; ?West Africa	Hoagland, 1977
<i>Crepidula unquiformis</i>	<i>Murex</i> ; <i>Aporrhais</i>	<i>Paguristes oculatus</i> ; <i>Pagurus cuanensis</i>	Gulf of Trieste, Adriatic Sea	Stachowitsch, 1980
<i>Crepidula glandis</i>	<i>Euspira</i> , <i>Buccinum</i> , <i>Neptunea</i>	—	Japan	Vermeij et al., 1987
<b>Crepidulids associated within apertures of fossil gastropods</b>				
<i>Crepidula crepidula</i>	<i>Natica</i> sp. <i>Astraea</i> sp. <i>Bursa</i> <i>Ancilla</i> <i>Tudicla</i> <i>Murex</i> <i>Conus</i>	None inferred	Korynica Clays, Holy Cross Mountains, Poland	Baluk and Radwanski, 1985
<i>Crepidula crepidula</i>	—	None inferred	Vienna Basin, Miocene	Baluk and Radwanski, 1985
<i>Crepidula</i>	Steinkerns of <i>Natica oostoma</i>	None inferred	Kressenberg, Bavarian Alps, Eocene	Baluk and Radwanski, 1985
<i>Crepidula plana</i>	—	None inferred	Gatun Formation (Panama), middle Miocene; Water Cay, Panama, late Miocene; Dominican Republic, Miocene; Maryland to Florida, early to late Miocene; North Carolina to Florida, Pliocene; Massachusetts to Florida, Pleistocene	Woodring, 1956 (see also Hoagland, 1977)
" <i>Capulus planus</i> " (like <i>Crepidula plana</i> )	<i>Clavilites vicksburgensis</i>	Inferred	Red Bluff Formation, Mississippi, lower Oligocene	MacNeil and Dockery, III, 1984
<i>Crepidula unquiformis</i>	—	—	Vienna Basin, France, Switzerland, Italy, Holland, Miocene; Italy, Algeria, Belgium, France, Pliocene; Italy, Pleistocene	Hoagland, 1977
<i>Crepidula nummaria</i>	—	—	San Diego to Monterey, California, Pliocene	Hoagland, 1977
<i>Crepidula perforans</i>	—	—	San Pedro to Monterey, California, Pleistocene Monterey, California, Pleistocene	Hoagland, 1977 Hoagland, 1977
<b>Non-crepidula molluscs that inhabit apertures</b>				
<i>Anomia ephippium</i>	<i>Murex</i> ; <i>Aporrhais</i>	<i>Paguristes oculatus</i> ; <i>Pagurus cuanensis</i>	Gulf of Trieste, Adriatic Sea	Stachowitsch, 1980
<i>Gastrochaena dubia</i>	<i>Murex</i>	<i>Paguristes oculatus</i>	Gulf of Trieste, Adriatic Sea	Stachowitsch, 1980
Oyster spat	—	<i>Clibanarius vittatus</i>	Galveston Bay, Texas	Fotheringham, 1976
<i>Hiatella arctica</i>	—	<i>Pagurus bernhardus</i>	Bergen, Norway	Samuelson, 1970

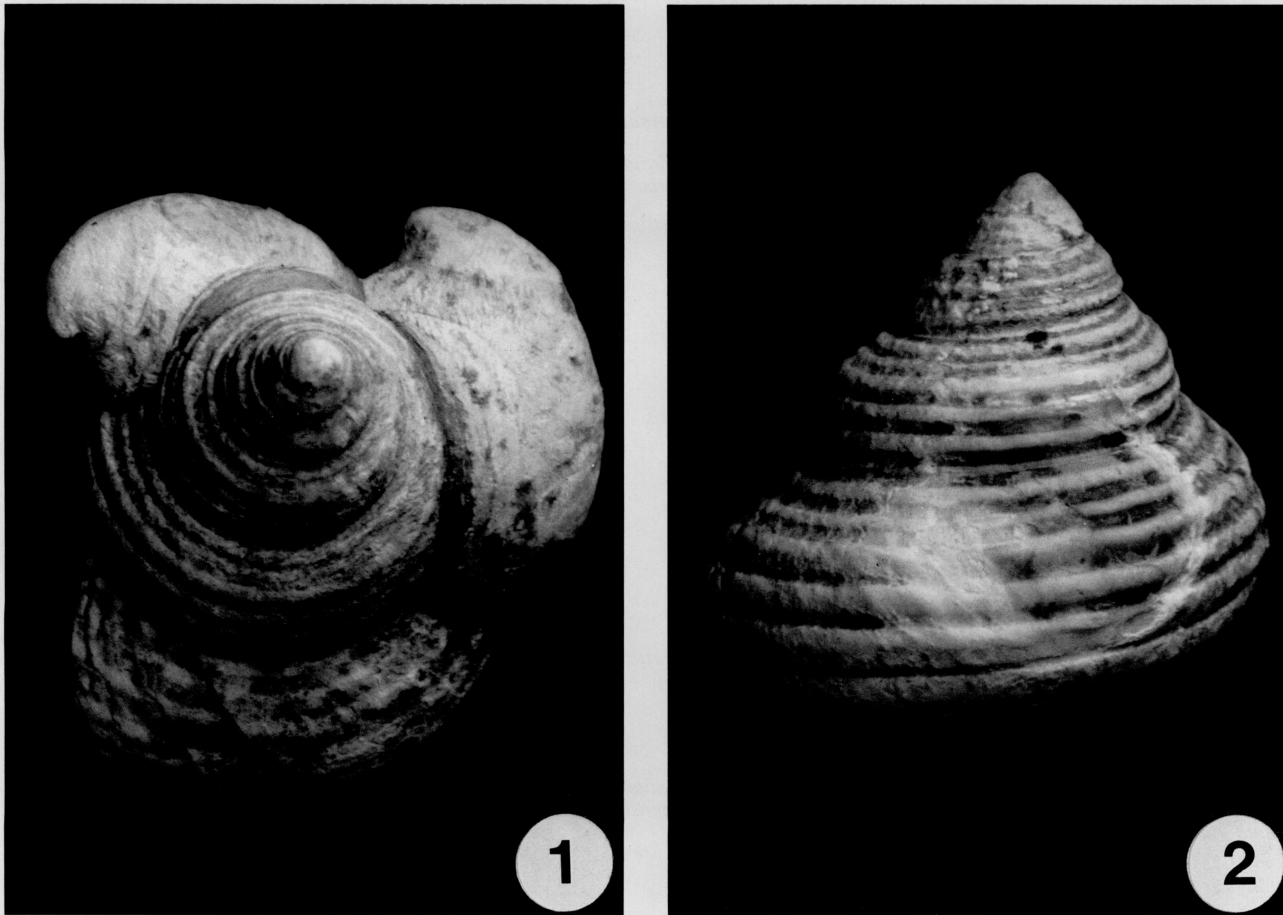


FIGURE 9—*Crepidula adunca* encrusting living *Calliostoma ligatum*, Friday Harbor, Washington, shell height of *C. ligatum*, 21.0 mm, UCMP Type No. 39688. 1, two *C. adunca* conforming to upper whorls of *C. ligatum*; 2, *C. adunca* permanent scar on last whorl of hermitted *C. ligatum*, shell height, 22.0 mm, UCMP Type No. 39689.

1979). Other species also compete for, or inhabit, gastropod shells (McLean, 1983; Vermeij, 1987; Walker, 1990). Because empty shells may be rare, post-Triassic gastropod fossil assemblages have most likely been taphonomically affected by secondary occupants of shells. Because hermit crab modification of gastropod assemblages is great, Shimoyama et al. (1979) suggested that the bivalve fossil record provided a more accurate paleoecological record than gastropod assemblages. However, gastropod fossil assemblages provide valuable paleoecological information for the history of the hermit crab.

Hermit crab body fossils are rare. Therefore, it is important to study their other fossil record: that of the epi- and endobionts associated with hermit shells. As a rule, hermit crabs are not preserved within the gastropod shell (Schafer, 1972). Only one fossil hermit crab has been reported from a gastropod shell

(Hyden and Forest, 1980). However, the shell-encrusting and boring organisms that occur with hermit crabs have a long fossil record, dating from the middle Jurassic. Determining the extent of hermit shells in fossil assemblages should be the first line of inquiry before paleoecological or evolutionary assessments are made.

Pagurized shells can be recognized by the settlement of bionts in specific locations on fossil shells (Palmer and Hancock, 1973; Walker, 1988b, 1989, this paper). Recent and fossil biont patterns appear to be conservative from the Oligocene to the present. That is, taphonomically preserved biont patterns (e.g., east Gulf Coast examples) are similar to Recent pagurized shells. The common patterns of subtle encrusters are as follows: hermit crabs do not occlude the apertural area like the living snail. Accordingly, bionts settle on the following areas on hermit shells: the apertural periphery, the junction between the last whorl and the aperture (the apertural notch), callus, columella, and the interior whorls of the shell. Bionts that settle in these areas are filter feeders, taking advantage of the feeding and respiratory currents generated by the hermit crab (see Carlton, 1971; Tomlinson, 1969b). Bionts also settle on the shell exterior, especially if an infaunal snail shell has been used by an epifaunal hermit crab (Walker, 1988b).

Fossil pagurized shells are present in middle Jurassic strata to the present. The first recognized fossil bionts associated with hermit crabs are thickly encrusting bryozoans. Bryozoans, hydractinians, and corals have received the most notoriety as they

TABLE 10—Frequency of occurrence of *Crepidula* sp. in apertures of *Cerithium stercusmuscarum* from Cholla Bay, Puerto Penasco, Mexico (May 1990 data).

Size class (mm)	Total hermit crabs	<i>Crepidula</i>
1.0–9.9	22	1 (0.45)
10.0–19.9	97	50 (0.51)
20.0–29.9	78	37 (0.47)
Totals	197	91 (0.46)



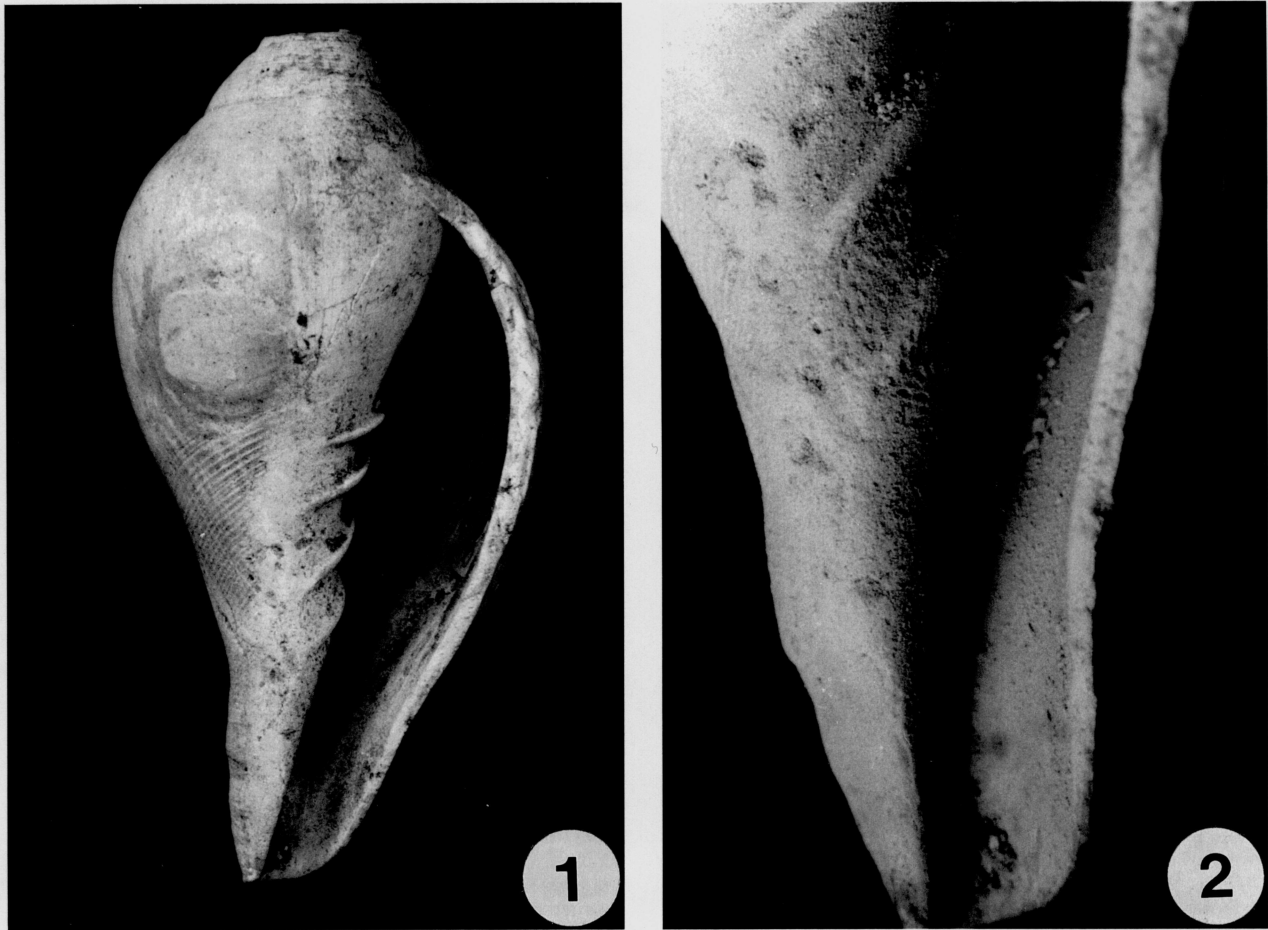


FIGURE 10—1, *Crepidula*-like scar on *Caricella subangulata*, Eocene, USGS 3735, Mississippi, shell height, 37.0 mm. 2, *Hippothoa*-like etching imprint on *C. subangulata*, same specimen as in 1. Specimen housed at United States National Museum (with United States Geological Survey, USGS, Numbers).

form unusual shapes when associated with fossil hermitted shells (e.g., Palmer and Hancock, 1973). These organisms also overgrow and extend the helical shape of the fossil shell. The similarity in growth patterns among hydractinians, corals, and bryozoans on fossil and Recent gastropod shells associated with hermit crabs is remarkable. Evolutionary studies on the developmental biology of these modular species are warranted.

Thick encrusting organisms associated with fossil hermitted shells are rare occurrences. However, when these bionts do occur, they are very abundant (Palmer and Hancock, 1973; Taylor and Cook, 1981). In contrast, subtle boring and encrusting species are more common in the fossil record but are often overlooked (Walker, 1988b). These bionts are: encrusting and boring polychaetes such as, spirorbids, serpulids and boring sponids; boring barnacles, encrusting and etching bryozoans, and aperture-inhabiting slipper limpets (*Crepidula*). These bionts are important for identifying the fossil occurrence of hermit crabs when crab body fossils are lacking. They also indicate the type of shell the crab used, thus providing information on shell "preference" by hermit crabs through time. In effect, bionts provide the missing information on the poor fossil history of hermit crabs.

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