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

S. E. WALKER[1]

Department of Paleontology, University of California, Berkeley 94720

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

HERMIT 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 importantly, 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-

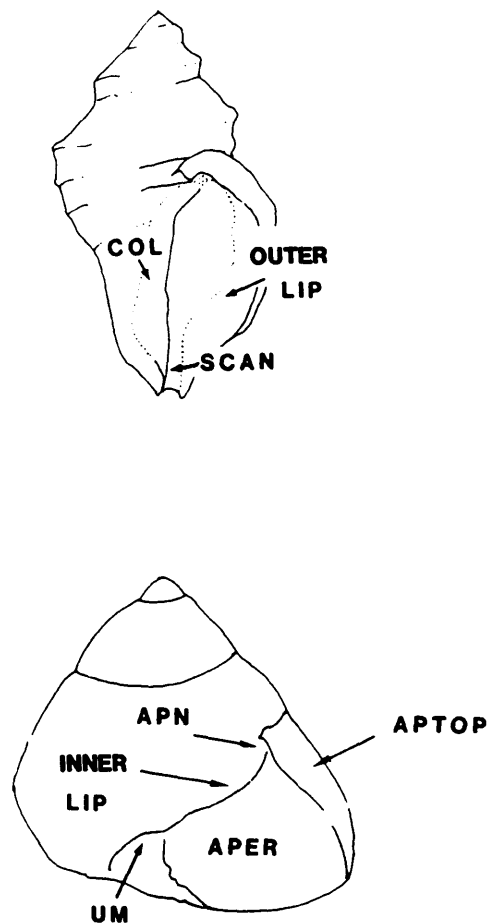[1] Current address: Geosciences Department, University of Arizona, Tucson 85721.

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

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

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

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. (=*Atractosoecia,* see Buge and Fischer, 1970) showing colony growth around a gastropod, presumably *Ataphrus* sp. (after Palmer and Hancock, 1973), specimen 2.0 cm; *7, Atractosoecia 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 parapelliculata* 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.
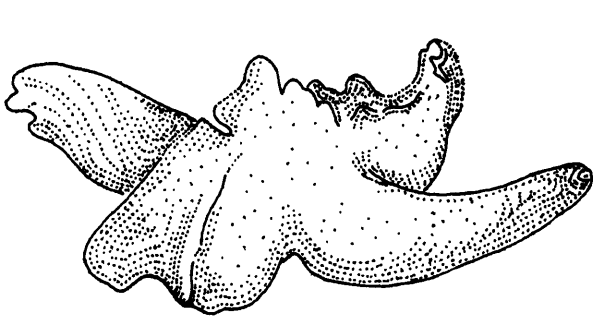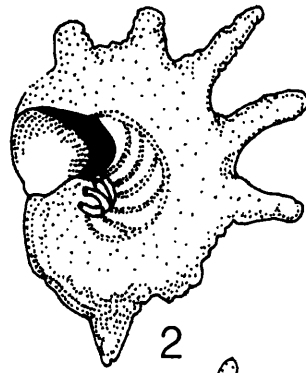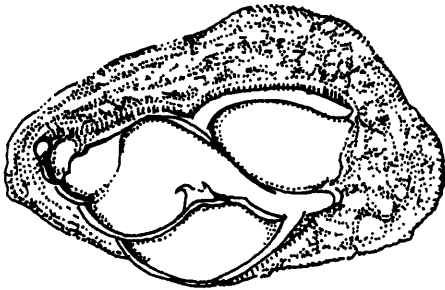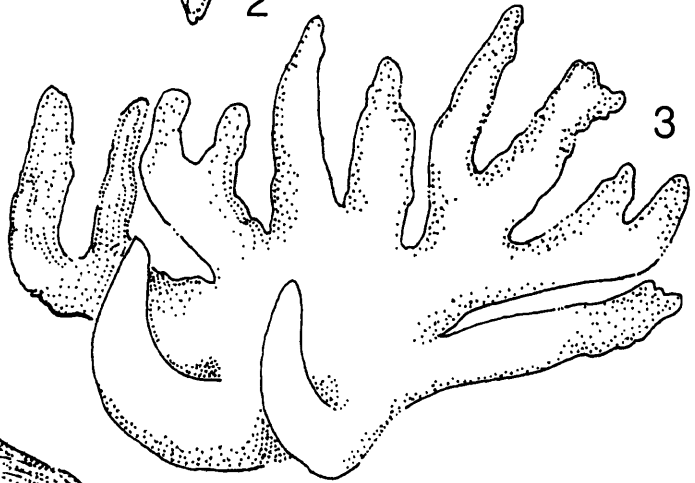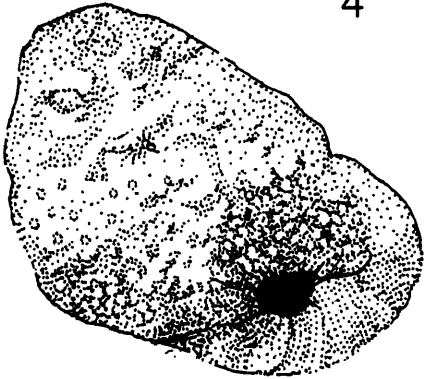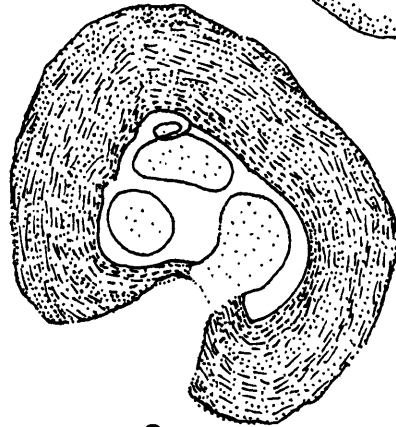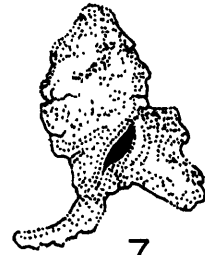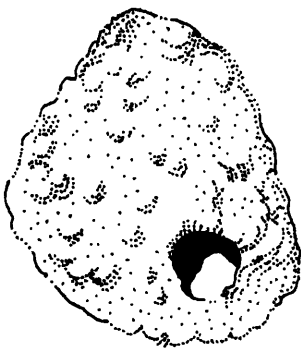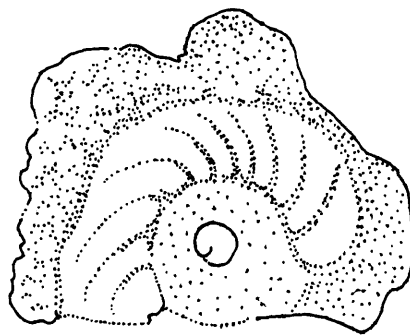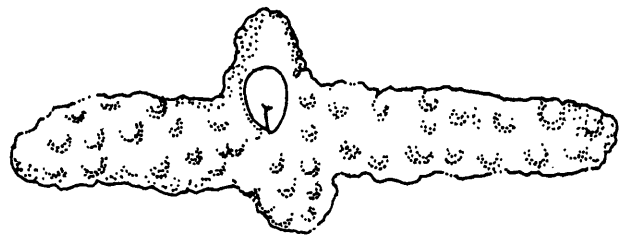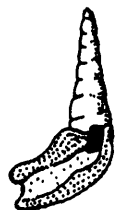
calcareous exoskeleton which obscured the *Buccinum* shell it encrusted (Figure 2.4).

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 symbiopollicarus*, 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 Penasco, 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 adapertural 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 bioccipitalis*; 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* (*Bulliopsis*) 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 naticid 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	*Pagurus cuanensis Anapagurus chrioacanthus*	external shell	Bergen, Norway	Samuelson, 1970
Hydroides norvegica	Not specified	*Pagurus bernhardus*	external, close to opening	Bergen, Norway	Samuelson, 1970
Hydroides norvegica	*Buccinum undatum *Littorina littorea *Neptunea antiqua	*Pagurus bernhardus*	external, close to shell opening	Frederikshavn, Denmark; Kristineberg, Norway	Jensen and Bender, 1973
Hydroides pseudouncinata	*Murex, Aporrhais	*Pagurus oculatus, Pagurus cuanensis*	external	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
Pomatoceras triqueter	*Murex, Aporrhais*	*Pagurus oculatus, Pagurus cuanensis*	top of shell close to opening	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
Pomatoceras triqueter	Not specified	*Pagurus bernhardus*	external shell close to opening	Bergen, Norway	Samuelson, 1970
Eupomatus dianthus (Serpulid)	*Polinices	*Clibanarius vittatus*	—	Galveston, Texas	Fotheringham, 1976
Circeis paguri	*Buccinum undatum*	*Pagurus bernhardus*	roof of last whorl, roof penulti-mate whorl	Swan Sea	Al-Ogily and Knight-Jones, 1981
Spirorbis cuneatus (Spirorbid)	*Murex, Aporrhais*	*Pagurus oculatus, Pagurus cuanensis*	bottom, aperture	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
Spirorbis spirillum	Not specified	*Pagurus bernhardus Pagurus cuanensis*	inside aperture	Bergen, Norway	Samuelson, 1970
Spirorbis spirillum	*Buccinum undatum *Littorina littorea *Neptunea antiqua	*Pagurus bernhardus*	internal shell	Oresund & Frederikshavn, Denmark; Kristineberg, Norway	Jensen and Bender, 1973
Janua pagenstecheri	*Murex, Aporrhais*	*Pagurus oculatus, Pagurus cuanensis*	bottom, aperture: outer lip	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
Filograna sp.	*Murex, Aporrhais*	*Pagurus oculatus*	aperture: inner lip	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
Sabellaria sp. (Sabellidae)	*Busycon carica*	*Pagurus pollicaris*	sandy tubes in ap-erture	Delaware Bay	Karlson and Shenk, 1983
Nereis succinea (Nerid)	*Polinices* 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					
Dodecaceria concharum (Cirratulid)	*Murex, Aporrhais*	*Pagurus oculatus*	throughout shell	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
Potamilla reniformis (Sabellid)	*Murex*	*Pagurus oculatus*	spires, columella	Gulf of Trieste, North Adriatic Sea	Stachowitsch, 1980
Boccardia tricuspa (Spionid)	*Tegula brunnea*	*Pagurus granosimanus*	—	Cayucos, California, Galapagos	Woodwick, 1963
Boccardia tricuspa	*Ceratostoma nuttalli* *Olivella biplicata* *Thais emarginata*	*Pagurus samuelis*	—	Santa Barbara, Morro Bay and Cayucos, California	Woodwick, 1963
Polydora ciliata	same as *Boccardia*	*Pagurus samuelis*		Santa Barbara, California; France	Woodwick, 1963
Polydora commensalis	—	—	columella	Maine, Massachusetts, Connecticut, North Carolina	Blake, 1971
Polydora commensalis	—	*Pagurus hirsutiusculus*	columella	Maine	Blake, 1969 Blake and Woodwick, 1972
Polydora commensalis	—	—	columella	Curacao	Foster, 1971
Polydora commensalis	*Lunatia heros* *Polinices duplicatus* *Busycon canaliculatum* *Buccinum undatum*	*Pagurus pollicaris*	columella	Noak, Connecticut; Beaufort, North Carolina	Hatfield, 1965 Andrews, 1891
Polydora commensalis	*Littorina littorea*	*Pagurus longicarpus*	columella	Noak, Connecticut; Beaufort, North Carolina	Hatfield, 1965 Andrews, 1891
Polydora commensalis	*Nassarius obsoletus*	*Pagurus longicarpus*	columella	East Coast, Canada	Berkeley and Berkeley, 1956
Polydora commensalis	*Thais lamellosa*	*Pagurus granosimanus*	columella	West Coast, North America (British Columbia)	Berkeley and Berkeley, 1936
Polydora commensalis	*Natica* spp.	*Pagurus* spp.	columella	Mazatlan, Mexico; Southern California	Hartman, 1941
Polydora commensalis	*Polinices duplicatus*	*P. pollicaris*	umblicus	Galveston, Texas	Fotheringham, 1976
Polydora websteri	various spp.	*Clibanarius vittatus* *Pagurus pollicaris*	—	Galveston, Texas	Fotheringham, 1976
Polydora unid.	*Buccinum,* unspecified	—	internal upper whorls	Bergen, Norway	Samuelson, 1970
Polydora limicola	same as *Boccardia*	*Pagurus samuelis*	—	Santa Barbara, California	Woodwick, 1963