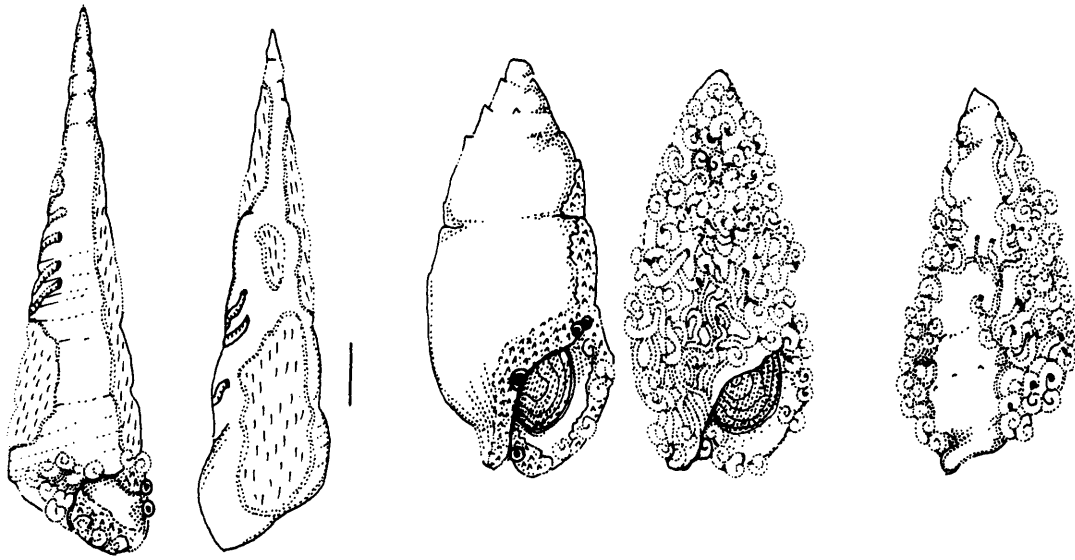


FIGURE 4—Pagurized *Polinices reclusianus*, Pleistocene, southern California, UCLA 3195, Orange Co. 1, encrusting serpulids (*Serpula* sp.) on outer lip, shell height, 77.8 mm, LACMIP No. 11491; 2, serpulids (*Salmacina* sp.) encrusting aperture with spionid trace fossils on outer lip and algal borings (*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>Bullioopsis</i> , <i>Natica</i>	Maryland, St. Mary's Formation	Miocene	Walker, this paper

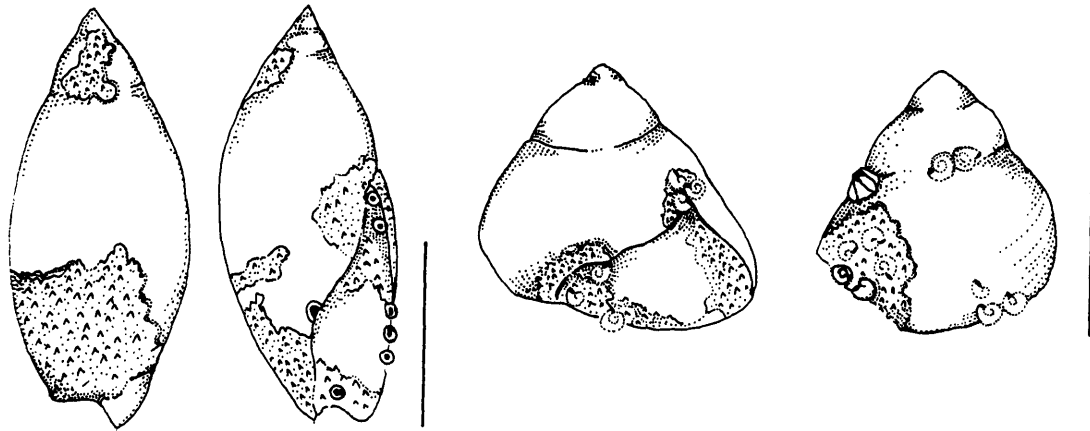
SUBTROPICAL 1



*Turritella leucostoma*

*Cerithium stercusmuscarum*

TEMPERATE 2



*Olivella biplicata*

*Tegula funebris*

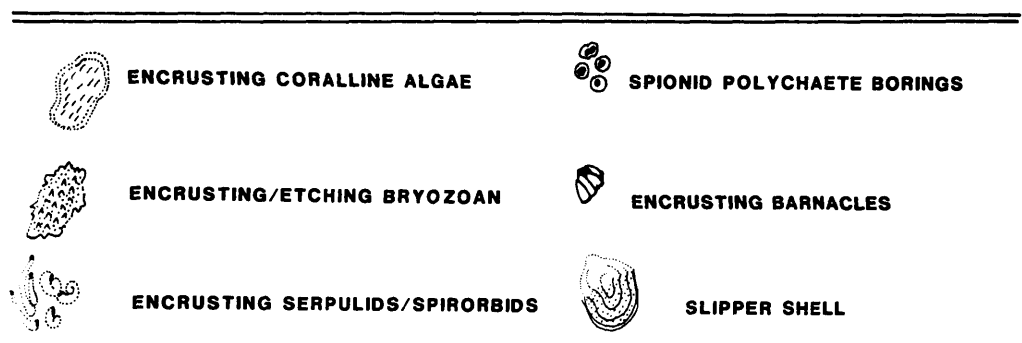


FIGURE 5—Subtle encrustation patterns on pagurized shells from the west coast of North America. 1, subtropical (Puerto Penasco, Mexico) pagurized shells of *Turritella leucostoma* and two aperture and one adaperture view of *Cerithium stercusmuscarum* encrusted with spirorbid polychaetes; 2, temperate (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,