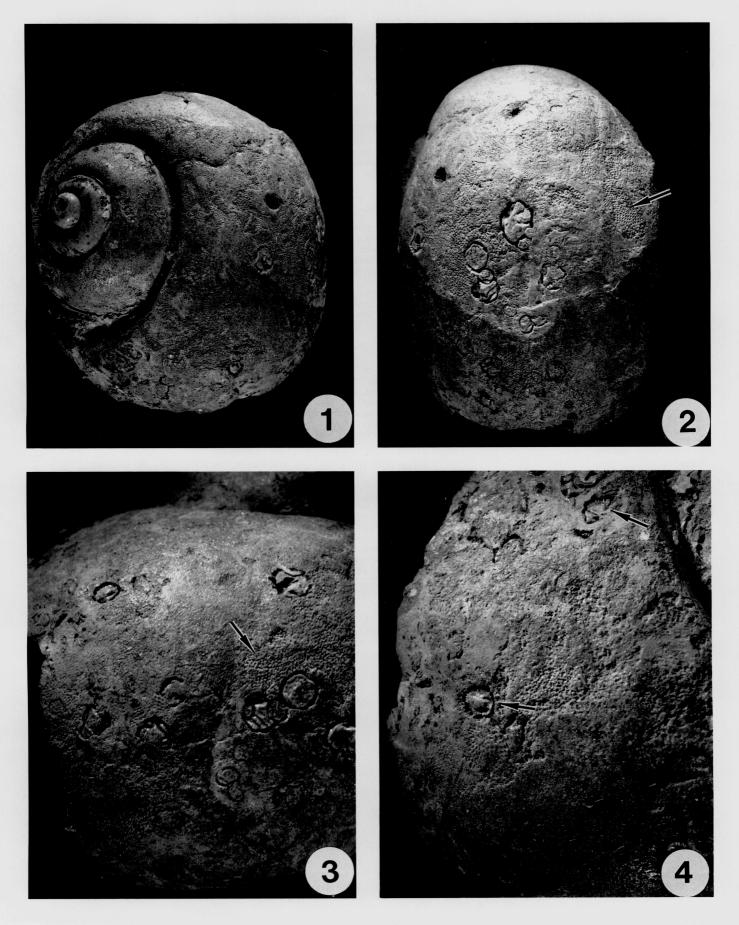
JOURNAL OF PALEONTOLOGY, V. 66, NO. 4, 1992



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 shelllimited 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 filterfeeding 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 (*Calyptraphorus ?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.

٠

.

Encrusting bryozoans	Gastropod shells	Hermit crab	Location on shell	Locality	Reference
Bryozoans			······································		
?Callopora lineata Celleporella hvalinina	-	Pagurus bernhardus	inside aperture	Bergen, Norway	Samuelson, 1970
Cellepora sp.	Murex; Aporrhais	Paguristes oculatus; Pagurus cuanensis	external	Gulf of Trieste	Stachowitsch, 1980
Cellepora parasitica	—	0			
Conopeum commensale		Petrochirus granulimanus (=Pagurus)	body whorl		Kirkpatrick and Metze- laar, 1922
Hippopodinella lata	Murex, Aporrhais	Paguristes oculatus	body whorl; near inner lip; bottom of shell	Gulf of Trieste	Stachowitsch, 1980
Hippoporidra edax	_	-	"longhorns" body whorl; aper-	Eastern United States;	Taylor and Cook, 1981
Hippoporidra spp.	_	_	ture top	Gulf of Mexico	
Hippoporidra lusitania Hippoporidra senegambiensis		– Eupagurus alcocki Diogenes ovatus	"longhorns"	British Wales Africa	Cook, 1964
Membraniopora tenuis	Busvcon carica	Pagurus pollicaris		Delaware Bay	Karlson and Shenk, 1983
Schizoporella errata	Busycon carica	Pagurus pollicaris		Delaware Bay	Karlson and Shenk, 1983
Bryozoan tube formers					
Borgiola otagoensis	_	Pylopagurus stewarti Pylopagurus n. sp. Lophopagurus 'thompsoni'	all make tubes	Otago Peninsula, South- eastern New Zealand	Taylor et al., 1989 (their table 4)
Disporella gordoni		Australeremus cooki			
Heteropora parapelliculata	_	Pylopagurus stewarti			
Arachnopusia unicornis Schizomauella trachorna	<u> </u>	Pylopagurus n. sp.			
Schizosmittina maplestonei	_				
Osthimosia monilifera	_	Pagurus n. sp. B	all make tubes	Otago Peninsula South-	Taylor et al., 1989
Osthiomosia socialis	_	Australeremus cooki		eastern New Zealand	
Crepidacantha zelanica	_	Pylopagurus stewarti			
Tubulipora cf. anderssoni	_	Pylopagurus n. sp.			
Akatopora circumsaepta	-	Paguristes barbatus Pagurus n. sp. B Pylopagurus stewarti Pylopagurus n. sp.			
Soft bodied bryozoans					
Alcyonidium polyoum	Ilynassa obsoleta	Pagurus longicarpus Pagurus pollicaris	external shell	Delaware Bay	Karlson and Cariolou, 1982
Alcyonidium polyoum	Busycon carica	Pagurus pollicaris	ventral/dorsal (also on living snail)	Delaware Bay	Karlson and Shenk, 1983
Flustrella hispida	Not specified	Paguris bernhardus	inside shell	Bergen, Norway	Samuelson, 1970
Etching bryozoans					
Electra sp.	Buccinum undatum	_	columella; inner lip; inside last whorl	Northern Netherlands	Boekschoten, 1966
Hippothoa hyalina	Olivella biplicata	Pagurus granosimanus	entire shell; columella; inner lip	Bodega Bay, Northern California	Walker, 1988b
Boring bryozoans					
Immergentia californica	Olivella biplicata	Pagurus granosimanus	callus; apex; lives on living snails only (dead on her-	Bodega Bay, Northern California	Walker, 1988b
Terebripora sp.	Buccinum undatum	Pagurid	mits) all over shell, especially colu- mella	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
Encrusting bryozoan					
Atractosoecia incrustans (=Berenicea)	Ataphrus labadyei Dicroloma tridigitatum Dicroloma cirrus	yes	France	Upper Bathonian, Jurassic	Buge and Fisher, 1970
Berenicea sp. Hippoporidra edax (=Cellepora edax)	Ataphrus sp. —	yes yes	France France; Eastern United States	Upper Bathonian, Jurassic Miocene	Palmer and Hancock, 1973 Taylor and Cook, 1981
			England, France, Italy, Belgium, Holland, Eastern United States	Pliocene	
Membranipora fusca Conopeum commensale (?Conopium)	Natica sp. —	yes —	Rio de Oro, Spanish Sahara Santa Margarita Fm, California	Quaternary Late Miocene to Recent	Buge and Lecointre, 1962 Adegoke, 1967
Membranipora sp.	Searlesia? carlsoni	no	Astoria Formation, Oregon	Miocene	Moore, 1963
Etching bryozoans					
Hippothoa-like etchings	Tegula funebralis Olivella biplicata	yes	Southern California localities	Pleistocene	Walker, 1988a, 1988b
Hippothoa-like etchings	(See Table 2, this paper)	yes	Mississippi (Red Bluff Formation) and Jackson, Mississippi	Eocene, Oligocene	Walker, this paper
Electra sp.	Buccinum sp.	no	Holland, Belgium	Pliocene, Pleistocene	Boekschoten, 1966, 1967
Boring bryozoans					
Spathipora; Terebripora Penetrantia	Ancilla glandiformis Natica redempta Ranella marginata Sveltia intermis Euthria intermedia Triton affine Triton nodiferum Fusus hoessi Ocenebra erinacea	yes	Korynica Clays, Poland	Mid-Miocene	Baluk and Radwanski, 1979
Immergentia-like	Olivella biplicata	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 USNM 136505	Co., Mississippi
Ampullinopsis missis- sippiensis	columella near apertural notch
Mitra conquisita Pleurotoma longiforma	internal aperture; columellar plications outer lip; external siphonal canal and into columella
Triton conradianus	external aperture
Eocene, Jackson, Mississippi USNM 480359	
Calyptraphorus ?stamineus	claw area outlined by bryozoan imprint on columella; siphonal canal; exter- nal shell and outer lip margins
Caricella subanulata	inner lip
Clavella humerosa	siphonal canal/columella
Cypraea finguis	base of shell
Fusinus sp.	outer lip
Lappharia pactilis	inner lip/siphonal canal; external shell
Mitra millington	internal aperture
?Papillina dumosa	inner and outer lip
Pseudoliva vetusta	inner lip/apertural notch area; interior aperture/siphonal canal
Turritella alveata	aperture
Volutalithes petrosus	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 softsediment 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.

.

.

ł

.

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