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Association of Benthic Foraminifera with a Gammarid Amphipod on Tidal Flats of San Francisco Bay, California

Martin Langer† and Douglas J. Long‡

†Museum of Paleontology
Berkeley, CA 94720, U.S.A.

‡Department of Integrative
Biology and
Museum of Paleontology
Berkeley, CA 94720, U.S.A.

ABSTRACT

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The gammarid amphipod *Oligochinus lighti* Barnard is an abundant and conspicuous component of the intertidal benthic fauna in San Francisco Bay, California. This crustacean lives protected in an agglutinated tube, feeding mainly on diatoms and smaller metazoans. Five foraminiferal species were observed as epizoans either attached or free-living at the outer surface of the host's tube. The epizoic association of benthic foraminifera with a filter-feeding invertebrate is considered advantageous in terms of access to increased trophic resources, provision of otherwise limited hard substrates, and possibly shelter. Host selection, benefits and constraints of foraminifera/invertebrate associations are reviewed briefly.

ADDITIONAL INDEX WORDS: *Invertebrate, epizoan, microhabitat, crustacean, mud flats.*

INTRODUCTION

Foraminifera have adopted a variety of lifestyles to acquire suitable nutrition from virtually all marine environments. Among them, numerous species have been reported to benefit as epizoans associated with various invertebrate taxa. Associations of foraminifera with invertebrates are widespread and have been reported from shallow to bathyal and tropical to polar environments (ZUMWALT and DELACA, 1980). As indicated by strong preferences for filter-feeding organisms as selected host substrates (Table 1), access to increased nutritional resources is apparently one key factor for foraminifera to adopt an epizoic lifestyle.

This paper reports on attached and free-living benthic foraminifera associated with the filter feeding amphipod *Oligochinus lighti* (BARNARD, 1969a) from tidal flats of San Francisco Bay, California. Amphipods often constitute the most abundant and diverse group of crustaceans in intertidal environments along the coast of California. Approximately 200 species have been described between the San Francisco Bay and La Jolla (*e.g.*, BARNARD, 1969a,b; BARNARD *et al.*, 1980). Among the species that live in the marshes and mud flats of San Francisco Bay, *Oligochinus lighti* lives in an agglutinated tube of sand grains, mud and organic debris that is cemented by secretions. Numerous foraminifera were observed living epizoically on the outer wall of agglutinated amphipod tubes. Epizoic associations of foraminifera with crustaceans have been reported to be rather rare and a "significant exceptions to the general rule" (MOORE, 1985). Findings of foraminifera associated with amphipods are thus of general interest and may provide new informations, particularly in terms of criteria for host selection.

MATERIAL AND METHODS

San Francisco Bay is the largest estuary system along the coast of California. Approximately three quarters of its area is shallower than 5 m (SUMNER *et al.*, 1914), forming large expanses of tidal flats, marshes and shallow shoals. For the most part, its bottom is covered by Holocene muddy clays, silts and patches of sandy sediments that harbor a rich fauna and flora of intertidal organisms (MORRIS *et al.*, 1980). Tides in the bay are predominantly semi-diurnal, ranging from 1.7 m at the mouth of the Golden Gate in the West, to up

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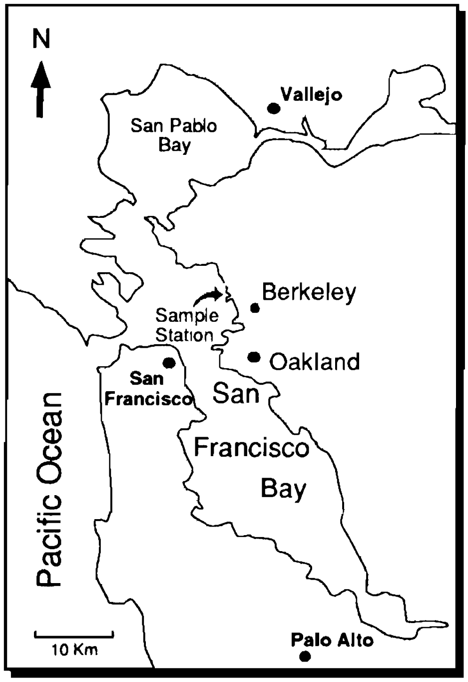

Figure 1. Map of San Francisco Bay showing location of sample station (37°52′N, 122°18′W).

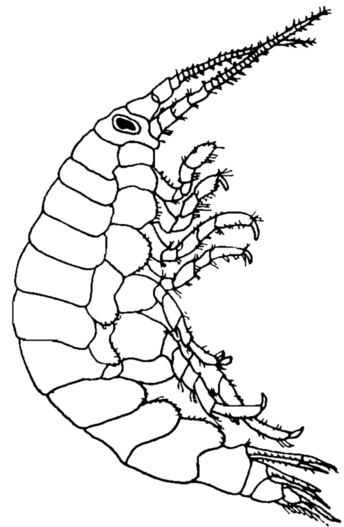

Figure 2. Lateral view of external structure of the gammaridean amphipod *Oligochinus lighti* Barnard, 1969.

to 2.7 m in southern parts of the bay (U.S. COAST AND GEODETIC SURVEY, 1973). Sampling was carried out in May and June 1993 at low tide in the Hoffman mud flats, north of the Golden Gate Fields (Figure 1).

The Hoffman mud flats extend along the eastern shoreline of the bay between Berkeley and Richmond, and are characterized by dark, fine-grained muds containing approximately 5–10% organic material. Sediments at the sampling station are vertically stratified, with a thin, oxygenated surface layer (0–0.5 cm) underlain by a black, hydrogen sulphide-rich reducing zone depleted of oxygen.

Sample material consisted of three box cores (diameter = 20 cm) and two surface sediment samples. Cores were gently pushed into the sediment to remove the top 10 cm of sediment and transported to the laboratory to inspect undisturbed sediment surfaces for live foraminifera. On core surfaces a total of 23 tubes containing live amphipods were inspected for epizoic foraminifera. To determine if foraminifera may be part of the amphipod diet, twelve of these tubes were dissected and examined for live, dead or damaged specimens of foraminifera. Sediment samples from the same location were washed over a 63 μm mesh sieve and oven dried at 40 °C. Approximately 250 specimens were picked out from both sediment samples to determine which foraminiferal species are present in the tidal flats.

RESULTS

On surfaces of undisturbed core samples, numerous living *Oligochinus lighti* specimens were observed in the laboratory by light microscopy (Figure 2). Specimens may reach 11 mm in length and are characterized by their reddish brown color, a short cleft telson, long third uropods, and the flagellum on the first antenna. Typically four specimens shared an area of approximately 25 cm^2. *Oligochinus lighti* lives in a tube composed of mineral grains, mud, clay, and plant fragments that are bound together by a secreted cement. Tubes were commonly found sticking slightly into the sediment, angled into the oxygenated surface layer and protruding approximately 1 cm into the water column. Tubes are usually elongate, 3–6 mm in diameter and may reach 2 cm in length. Amphipods were observed mainly retreated into the tube but actively creating currents by their pleopods. Occasionally specimens ventured out of the tube, possibly to feed or to defend their territory. Mechanically induced agitation of the surrounding sediments by needles, however, led to a fast retreat of the amphipod into the tube, indicating that tubes serve as protection.

Five species of both motile and attached foraminifera were found on the agglutinated amphipod tubes. Foraminifera were observed attached to the open end or the outer wall and seen crawling over the outer agglutinated tube, apparently grazing for food. All of the motile and most of the attached epizoic foraminifera were alive at the time of observation, as indicated by the extrusion of pseudopodial strands. Preferential site selection of motile foraminifera appeared to be as close as possible to the open end of the amphipod tube (Figure 3), but attachment to the outer tube wall was also common. Neither dead nor living specimens were observed inside dissected tubes. Foraminifera showed no signs of test damage, indicating that the epizoans were not harmed by the amphipod or were not part of its diet. Specimens of *Oligochinus lighti* commonly supported one to two foraminifera per tube and included the following species: *Ammonia batava* Hofker, *Trochammina pacifica* Cushman, *Elphidium williamsoni* Haynes, *Quinqueloculina angulostriata* Cushman and Valentine, and *Quinqueloculina vulgaris* d'Orbigny. A total of 35 living foraminifera was counted on the 23 amphipod tubes examined. Among them, *A. batava* was most frequent (23 specimens = 65.7%), followed by *T. pacifica* (5 = 14.2%), *Q. angulostriata* (3 = 8.5%), *Q. vulgaris* (3 = 8.5%), and *E. williamsoni* (1 = 2.8%). All species were observed as vagrant forms grazing over the amphipod tube, but *Trochammina pacifica* also commonly attached by secreted glycoproteins (LANGER, 1992).

In the sediment, *A. batava* was found to be the dominant species (69%) followed by *T. pacifica* (13%), *Q. angulostriata* (8%), *Q. vulgaris* (6%), and *E. williamsoni* (4%). Other than these, no additional species were present at the sampling site.

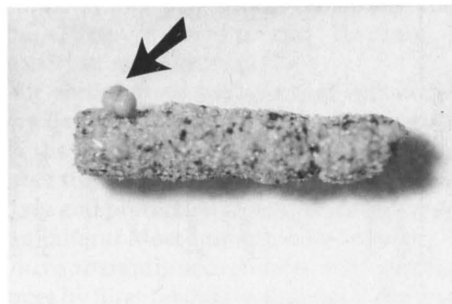

Figure 3. Epizoic foraminifera *Trochammina pacifica* attached to the outer agglutinated wall of the amphipod tube.

DISCUSSION

Visual surface examinations of cores collected in the mud flats of San Francisco Bay revealed that individual foraminifera were commonly present as epizoans on tubes of the amphipod *Oligochinus lighti*. Oxidized surface layers of the sediments are rich in bacteria, diatoms and other unicellular algae known to constitute major parts of the foraminiferal diet (LEE and ANDERSON, 1991; BERNHARD and BOWSER, 1992; LANGER *et al.*, 1989; LANGER and GEHRING, 1993). The adoption of an epizoic association with a crustacean and settlement on elevated substrates above an otherwise nutrient-rich sedimentary habitat thus raises questions of function and benefits for foraminifera.

Epizoic foraminifera/invertebrate relationships are generally regarded as commensal (ZUMWALT and DELACA, 1980). An overview of previously published records demonstrates that the vast majority of invertebrate hosts for epizoic foraminifera are filter feeders (Table 1). In most of these cases, neither the host appears to be affected nor are the epizoans harmed (DOBSON and HAYNES, 1973; ZUMWALT and DELACA, 1980), although cases of parasitism by and predation on foraminifera have been reported (TODD, 1965; LIPPS and RONAN, 1974; ALEXANDER and DELACA, 1987). Observations of preferential site selection, aggregated distribution patterns, and ecophenotypic responses along the commisure of the brachiopod *Tichosina* strongly suggested that epizoic foraminifera benefit from feeding currents generated by their host (ZUMWALT and DELACA, 1980). Access to increased or accumulated food resources may thus be a key factor for adopting an epizoic lifestyle and appears to be particularly advantageous for attached foraminifera with a limited grazing radius. Indeed, the largest number of epizoic foraminifera recorded so far are often represented by attached species (*e.g.*, HAYWARD and HAYNES, 1976; MULLINEAUX and DELACA, 1984). Additional benefits derived from an epizoic lifestyle have been reported to include the provision of a permanent

Table 1. *Epizoic foraminifera and general features of host organisms.*

Host Species	Host Group	Feeding Strategy	Depth	Location	Foraminifera	Reference
Ostrea edulis	Pelecypod	Filter feeding	5 m	North Sea	*Crithionina*	KORRINGA, 1951
Chlamys septemradiata	Pelecypod	Filter feeding	>70 m	off Scotland	*Crithionina* *Rhabdammina* *Planorbulina* *Cibicides* *Hyperammina*	ALLEN, 1953
Ascidia obliqua	Tunicate	Filter feeding	40–50 m	Gullmar Fjord	*Cibicides*	NYHOLM, 1961
Ascida mentula	Tunicate	Filter feeding	40–50 m	Gullmar Fjord	*Cibicides*	
Lima angolensis	Pelecypod	Filter feeding	951 m	Gulf of Guinea	*Rosalina* *Cibicides* spp. ?*Verrucina* *Trochammina* ?*Sangenina* ?*Placopsilina*	TODD, 1965
Crassinella lunulata	Pelecypod	Filter feeding	?	off Florida	unnamed sp.	HARRY, 1966
Notocorbula operculata	Pelecypod	Filter feeding	?	Gulf of Mexico	*Hanzawaia*	BOCK and MOORE, 1968
Unnamed sp.	Mollusks	?	0–20 m	off California	*Rosalina*	DELACA and LIPPS, 1972
Unnamed sp.	Crustaceans	?	0–20 m	off California	*Rosalina*	
Siliceous sponge	Porifera	Filter feeding	[fossil]	Poland	*Tolypammina*	KAZMIERCZAK, 1973
Unnamed sp.	Barnacles	Susp. feeding		Oxfordian		
Sertularia argentea	Hydroid	Filter feeding	>102 m	Irish and Malin Sea	17 species	DOBSON and HAYNES, 1973
Abietinaria abietina	Hydroid	Filter feeding				
Sertomma tamarisca	Hydroid	Filter feeding				
Lafoea gracillima	Hydroid	Filter feeding				
Lafoea gracillima	Hydroid	Filter feeding				
Lafoea dumosa	Hydroid	Filter feeding				
?*Aequoria* sp.	Hydroid	Filter feeding				
Diphasia pinaster	Hydroid	Filter feeding				
Sertularella polyzonias	Hydroid	Filter feeding				
Sertularella gayi						
Diopatra ornata	Polychaete	Filter feeding	0.3–12 m	off California	*Glabratella* *Elphidium* spp. *Bucella*	LIPPS and RONAN, 1974
Chlamys opercularis	Pelecypod	Filter feeding	40–56 m	off England	51 species	HAYWARD and HAYNES, 1976
Placopecten magel.	Pelecypod	Filter feeding		off Newfoundl.	unnamed spp.	
Pecten maximus	Pelecypod	Filter feeding		off NW Europe	unnamed spp.	
Tichosina floridensis	Brachiopod	Filter feeding	100–200	off Oregon and off Florida	*Sporadotrema* *Homotrema* *Carpenteria*	ZUMWALT and DELACA, 1980

Table 1. *Continued.*

Host Species	Host Group	Feeding Strategy	Depth	Location	Foraminifera	Reference
					Cibicides *Rosalina* *Biarritzina*	
Astacilla longicornis	Isopoda	Filter feeding	24–31 m	off Scotland	*Lobatula*	MOORE, 1985
Adamussium colbecki	Pelecypod	Filter feeding	20–27 m	Antarctica	*Cibicides*	ALEXANDER and DELACA, 1987
Polydora ciliata	Polychaete	Filter feeding	<30 m	Kiel Bight	*Ammotium*	LINKE and LUTZE, 1993
Bathycrinus sp.	crinoid	?	2,000 m	Norwegian and Greenland Sea	*Cibicidoides*	
Potamethus mahngreni	Polychaete	Filter feeding	?		unnamed sp.	
Aphroditidae sp.	Polychaete	?	?		unnamed sp.	
Achelia echinata	Pantopod	?	?		unnamed sp.	
Unnamed sp.	Hydrozoa	?	?		unnamed sp.	
Unnamed sp.	Porifera	?	?		unnamed sp.	

hard substrate for attachment and the protection from turbulence and silting (ZUMWALT and DELACA, 1980; HAYWARD and HAYNES, 1976; ALEXANDER and DELACA, 1987).

Our observations indicate that epizoic foraminifera derive similar benefits from the association with the amphipod *Oligochinus lighti.* Its agglutinated tube simultaneously provides attachment surface and protection from oversilting for epizoic foraminifera. Most importantly, however, *Oligochinus* apparently accumulates sufficient food resources by filter feeding to support individual epizoic foraminifera.

Selection of an elevated, epizoic microhabitat above an otherwise nutrient-rich sedimentary habitat may also be considered advantageous in terms of predator avoidance. Potential predatory organisms living in and on the sediments are abundant and include taxa like the neogastropod *Olivella biplicata,* the dominant macroinvertebrate along the coast of California (HICKMAN and LIPPS, 1983). Foraminifera living with hydroids have been reported not to be harmed by the host's nematocysts (DOBSON and HAYNES, 1973) that otherwise function as effective protection against potential predators. Preferential site selection on elevated substrates may also be useful to avoid scaphopods, well known predators on foraminifera that live in the sediment (BILYARD, 1974; POON, 1987; SHIMEK, 1990).

Foraminifera/crustacean associations have been previously reported to be rather rare (MOORE, 1985). Although little is known about the role of foraminifera in crustacean diets, at least three reports have shown that asellote isopods and tanaid crustaceans prey on foraminifera (WILSON and THISTLE, 1985; ALEXANDER and DELACA, 1987; SVAVARSSON *et al.*, 1993). This may explain why certain crustaceans are rarely used as hosts. Conversely, however, BARNARD (1969a) reports that among the 155 amphipod species present in the Californian intertidal, 58 species are tube dwellers. The present report on foraminifera living epizoically on tubes of a smaller, filter-feeding amphipod suggests that foraminifera/crustacean associations may be more widespread than previously thought.

CONCLUSIONS

Agglutinated tubes of the amphipod *Oligochinus lighti* in mud flats of San Francisco Bay are commonly populated by individual specimens of epizoic foraminifera. Five species of foraminifera including one attached form have been identified in life positions on the outer tube wall. No evidence has been found that the amphipod is affected by or preys on its epizoans. Foraminifera appear to benefit from increased food resources accumulated by the amphipods' feeding currents, suggesting a commensal relationship. While in most foraminifera/invertebrate associations the provision of hard substrate provides protection against turbulence and oversilting, in some instances the selection of elevated hard substrate may also provide protection against potential predators. The widespread abundance of tubicolous amphipods suggests that foraminifera/crustacean associations may be more common than previously thought.

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LITERATURE CITED

ALEXANDER, S.P. and DELACA, T.E., 1987. Feeding adaptations of the foraminiferan *Cibicides refulgens* living epizoically and parasitically on the antarctic scallop *Adamussium colbecki*. *Biological Bulletin*, 173, 136–159.

ALLEN, J.A., 1953. Observations on the epifauna of the deep-water muds of the Clyde Sea area with special reference to *Clamys septemradiata* (Muller). *Journal of Animal Ecology*, 22, 240–260.

BARNARD, J.L., 1969a. Gammaridean amphipoda of the rocky intertidal of California: Monterey Bay to La Jolla. *Bulletin of the United States National Museum*, 258, 1–230.

BARNARD, J.L., 1969b. The families and genera of marine gammaridean amphipoda. *Bulletin of the United States National Museum*, 271, 1–535.

BARNARD, J.L.; BOWERS, D.E., and HADERLIE, E.C., 1980. Amphipoda: The amphipods and allies. *In:* MORRIS, R.H.; ABBOTT, D.P., and HADERLIE, E.C., (eds.), *Intertidal Invertebrates of California*. Stanford: Stanford University Press, pp. 559–566.

BERNHARD, J.M. and BOWSER, S.S., 1992. Bacterial biofilms as a trophic resource for certain benthic foraminifera. *Marine Ecology Progress Series*, 83, 263–272.

BILYARD, G.R., 1974. The feeding habits and ecology of *Dentalium entale stimpsoni* Henderson, (Mollusca; Scaphopoda). *The Veliger*, 17(2), 126–138.

BOCK, W.D. and MOORE, D.R., 1969. A commensal relationship between a foraminifer and a bivalve mollusk. *Gulf Research Reports*, 2, 273–277.

DELACA, T.E. and LIPPS, J.H., 1972. The mechanism and adaptive significance of attachment and substrate pitting in the foraminiferan *Rosalina globularis* (d'Orbigny). *Journal of Foraminiferal Research*, 2, 68–72.

DOBSON, M. and HAYNES, J., 1973. Association of foraminifera with hydroids on the deep shelf. *Micropaleontology*, 19(1), 78–90.

HARRY, H.W., 1966. Studies on the bivalve mollusks of the genus *Crassinella* in the Northwestern Gulf of Mexico: Anatomy, ecology and systematics. *Texas University Publications*, 11, 65–89.

HAYWARD, J.J.B. and HAYNES, J.B., 1976. *Clamys opercularis* (Linneaus) as mobile substrate for foraminifera. *Journal of Foraminiferal Research*, 6, 30–38.

HICKMAN, C. and LIPPS, J.H., 1983. Foraminiferivory: Selective ingestion of foraminifera and test alterations produced by the neogastropod Olivella. *Journal of Foraminiferal Research*, 13(2), 108–114.

KAZMIERCZAK, J., 1973. *Tolypammina vagans* (Foraminiferida) as inhabitant of the Oxfordian siliceous sponges. *Acta Paleontological Polonica*, 18(1), 95–115.

KORRINGA, P., 1951. The shell of *Ostrea edulis* as a habitat (Mollusca Bivalvia). *Archives Néerlandaises de Zoologie*, 10, 32–152.

LANGER, M.R., 1992. Biosynthesis of glycosaminoglycans in foraminifera: A review. *Marine Micropaleontology*, 19(3), 245–255.

LANGER, M.R. and GEHRING, C., 1993. Bacteria farming: A possible feeding strategy of some smaller, motile foraminifera. *Journal of Foraminiferal Research*, 32(1), 40–46.

LANGER, M.R.; HOTTINGER, L., and HUBER, B., 1989. Functional morphology of low diverse benthic Foraminifera from the tidal flats of the North Sea. *Senckenbergiana Maritima*, 20(3/4), 81–99.

LEE, J.J. and ANDERSON, O.R., 1991. Symbiosis in Foraminifera, *In:* LEE, J.J. and ANDERSON, O.R. (eds.), *Biology of Foraminifera*. London: Academic Press, pp. 157–220.

LINKE, P. and LUTZE, G.F., 1993. Microhabitat preferences of benthic foraminifera—A static concept or a dynamic adaptation to optimize food acquisition. *In:* LANGER, M.R. (ed.), Foraminiferal microhabitats. *Marine Micropaleontology*, 20, 215–234.

LIPPS, J.H., 1983. Biotic interactions in benthic foraminifera. *In:* TEVESZ, M.J.S. and MCCALL, P.L. (eds.), *Biotic Interactions in Recent and Fossil Communities*. New York: Plenum Press, pp. 331–376.

LIPPS, J.H. and RONAN, T.E., 1974. Predation on the foraminifera by the polychaete worm *Diopatra*. *Journal of Foraminiferal Research*, 4(3), 139–143.

MOORE, P.G., 1985. *Cibicides lobatulus* (Protozoa: Foraminifera) epizoic on *Astacilla longicornis* (Crustacea: Isopoda) in the North Sea. *Journal of Natural History*, 19, 129–133.

MORRIS, D.P.; ABBOTT, D.P., and HADERLIE, E.C., 1980. *Intertidal Invertebrates of California*. Stanford: Stanford University Press, 690p.

MULLINEAUX, L.S. and DELACA, T.E., 1984. Distribution of Antarctic benthic foraminifers settling on the pecten *Adamussium colbecki*. *Polar Biology*, 3, 185–189.

NYHOLM, K.G., 1961. Morphogenesis and biology of the foraminifer *Cibicides lobatulus*. *Zoologiska Bidrag fran Uppsala*, 33, 157–196.

POON, P.A., 1987. The diet and feeding behaviour of *Caudulus tolmiei* Dall, 1897. (Scaphopoda: Siphonodentalioida). *Nautilus,* 101, 88–92.

SHIMEK, R.L., 1990. Diet and habitat utilization in a northeastern Pacific Ocean scaphopod assemblage. *American Malacological Bulletin,* 7(2): 147–169.

SUMNER, F.B.; LOUDERBACK, G.D.; SCHMIDT, W.L., and JOHNSON, E.C., 1914. A report upon the physical conditions in San Francisco Bay, based upon the operations of the United States steamer Albatross during the years 1912 and 1913. *California University Publications, Zoology,* 14, 1–198.

SVAVARSSON, J.; GUDMUNDSSON, G., and BRATTEGARD, T., 1993. Feeding by asellote isopods (Crustacea) on foraminifers (Protozoa) in the deep sea. *Deep-Sea Research,* 1, 40(6), 1225–1239.

TODD, R., 1965. A new *Rosalina* (Foraminifera) parasitic on a bivalve. *Deep-Sea Research,* 12, 832–837.

UNITED STATES COAST AND GEODETIC SURVEY, 1973. *Tide Tables West Coast, North and South America.* Washington: United States Printing Office.

WILSON, G.D.F. and THISTLE, D., 1985. *Amuletta,* a new genus for *Ilyarachna abyssorum* Richardson, 1911 (Isopoda: Asellota: Eurycopidae). *Journal of Crustacean Biology,* 5(2), 350–360.

ZUMWALT, G.S. and DELACA, T.E., 1980. Utilization of brachiopod feeding currents by epizoic foraminifera. *Journal of Paleontology,* 54, 477–484.