Kern, J.P., Grimmer, J.C., & Lister, K.H,
1974

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Reprinted from JOURNAL OF PALEONTOLOGY
Vol. 48, No. 5, September 1974
pp. 978–982
Made in United States of America

JOURNAL OF PALEONTOLOGY, V. 48, NO. 5, P. 978–982, 2 TEXT-FIGS., SEPTEMBER 1974

A NEW FOSSIL SPIONID TUBE, PLIOCENE AND PLEISTOCENE OF CALIFORNIA AND BAJA CALIFORNIA

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ABSTRACT—*Polydora commensalis* (Polychaeta, Spionidae) and closely related species construct characteristic tubes in gastropod shells occupied by hermit crabs (Crustacea, Paguridae). Similar tubes are common as trace fossils, herein named *Helicotaphrichnus commensalis*, in Pliocene and Pleistocene strata of California and Baja California, and they provide fossil evidence for the persistence of the spionid-pagurid commensal relationship at least from Pliocene time to the present.

INTRODUCTION

ONE or more living species of the polychaete annelid genus *Polydora* (Family Spionidae) inhabit characteristic tubes that they construct in the columella and adjacent internal chamber wall of gastropod shells occupied by hermit crabs (Family Paguridae). Such tubes are constructed by the widely distributed species *Polydora commensalis* Andrews, 1891, and apparently by at least two other species—the closely related *P. bioccipitalis* Blake and Woodwick, 1972, and an unidentified species in Norway (Samuelsen, 1970, p. 40). Similar tubes occur as trace fossils in Pliocene and Pleistocene gastropods from California and Baja California. However, because of the similarity of the tubes of extant species, the fossil tubes cannot with certainty be attributed to any one of them. This paper describes the morphology of the fossil tubes, herein assigned to the new ichnogenus and ichnospecies *Helicotaphrichnus commensalis*, and summarizes their known fossil occurrence.

ACKNOWLEDGMENTS

This study was supported in part by a grant from the San Diego State University Foundation. The photographs were made by Takeo Susuki. The ichnogeneric name was suggested by Nicholas Genovese.

SYSTEMATIC PALEONTOLOGY

Genus HELICOTAPHRICHNUS n. gen.

Name.—The generic name is derived from the Greek words *helix*, meaning twisted, and *taphros*, meaning trench.

Type species.—*Helicotaphrichnus commensalis* n. sp.

Diagnosis.—*Helicotaphrichnus* is a partly excavated, partly deposited fossil tube that is found only in the columellar wall of gastropod shells. The tube may be single, or it may double back on itself once or twice to form tight "U" or "S" shapes, but it always follows the helical path of the chamber of the gastropod shell.

HELICOTAPHRICHNUS COMMENSALIS n. sp.
Text-figures 1, 2

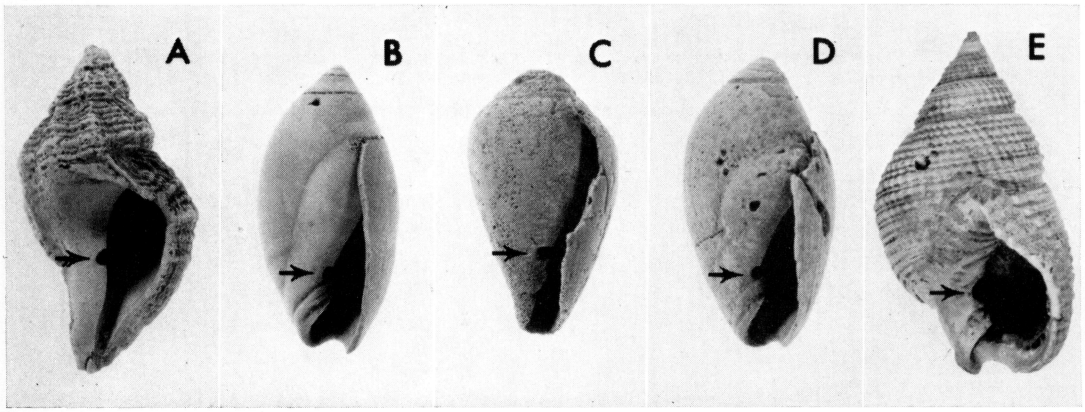
Name.—The specific name refers to the commensal relationship between the tube-building spionid and its pagurid host.

Types.—Holotype, UCLA Department of Geology no. 48143, Text-figure 1D; paratype, UCLA 48144, Text-figure 1E. Further data on types in caption to Text-figure 1.

Diagnosis.—As for genus.

Description.—The tube is constructed in the columellar wall of the gastropod shell. Only the aperture of the tube is visible on the inner lip of intact shells (Text-figs. 1A-E), and in some modern shells even this is not visible (Blake, 1969, p. 816). The outer wall of the gastropod shell must be removed to observe the tube inside the shell (Text-fig. 2A).

The initial part of the tube is perpendicular to the axis of the shell and consists of a groove excavated deeply into the columella and roofed over with a thin wall of calcium carbonate. Approximately three-fourths of the wall of the tube is excavated and one-fourth is deposited (Text-fig. 2A). The deposited wall is very thin and usually is worn or broken away. Berkeley and Berkeley (1936, p. 470) gave a similar description for tubes of *Polydora commensalis* in British Columbia, but Andrews (1891, p. 27) described this part of the tube



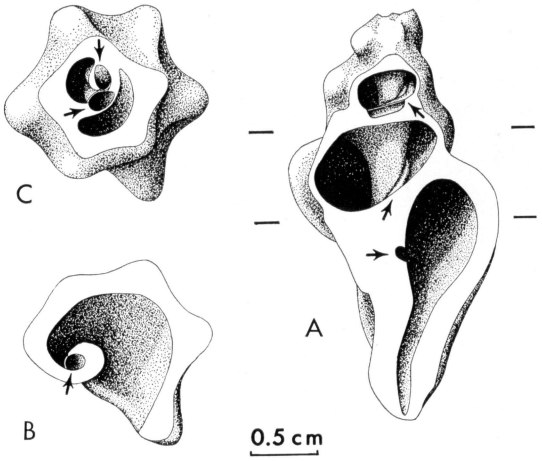
TEXT-FIG. 1—*Helicotaphrichnus commensalis* n. gen., n. sp. and tubes of modern *Polydora commensalis*. All ×2.0. A, UCLA Department of Geology no. 48140; tube of *P. commensalis* in *Ceratostoma nuttallii* (Conrad, 1856); intertidal, San Diego, California. B, UCLA 48141; tube of *P. commensalis* in *Olivella biplicata* (Sowerby, 1825); intertidal, San Diego, California. C, UCLA 48142; tube of *P. commensalis* in *Conus californicus* Hinds, 1944; intertidal, San Diego, California. D, UCLA 48143; holotype; *H. commensalis* in *Olivella biplicata*; Pleistocene Bay Point Formation, Pacific Beach, California. E, UCLA 48144; paratype; *H. commensalis* in *Nassarius grammatus* (Dall, 1917); Pliocene San Diego Formation, Pacific Beach, California.

as being excavated entirely within the columella of shells from the east coast of North America.

Beyond the first few millimeters the tube of *Helicotaphrichnus* turns sharply toward the apex of the shell and follows the helical course of the columellar wall. At the turn the tube commonly emerges somewhat more from the columella so that only about one-half of the wall is excavated and one-half is deposited, and beyond this point increasingly more of the wall may be deposited and less excavated. The specimens illustrated in Text-figure 2 do not show this progressive emergence of the tube from the columella.

Some tubes extend only a short distance toward the shell apex, but longer tubes turn back on themselves and closely follow their initial helical course back toward the first turn inside the inner lip, thus forming a "U" shape. However, this form differs from the characteristic U-shaped tubes made by some species of *Polydora*, in that it has only one aperture rather than two, and it is increased in length by excavation at the distal end of the tube, rather than at the elbow of the "U." Some tubes turn back again toward the shell apex and are thus S-shaped. The longest tubes observed have three full courses and are approximately 30 mm in length.

The tube apertures are smaller than 1.0 mm in diameter, and most are larger than 0.5 mm (Text-figs. 1A-E). The diameter of the tube increases with the distance from the aperture,



TEXT-FIG. 2—Three cross-section views showing the position and morphology of *Helicotaphrichnus commensalis* in *Ocenebra foveolata* (Hinds, 1844). These are composite drawings based on several specimens. A, Axial section exposing the interior of the shell in each of three whorls. Exposed in the body whorl is the initial segment of the tube near its aperture, where the deposited part of its wall is broken away. Only the ascending tube is present in the next whorl, but in the third whorl the ascending tube is partially hidden behind the descending tube, which is cut by the plane of the section. The broken apex of this specimen has no relationship to the presence of the tube. Horizontal lines indicate the approximate positions of the transverse sections shown in B and C. B, Transverse section in anterior part of shell where only ascending tube is present. C, Transverse section in posterior part of shell showing both ascending (above) and descending (below) portions of tube.

TABLE 1—The Department of Geology invertebrate fossil collections at the University of California, Los Angeles (UCLA) and San Diego State University (SDSU) contain Pleistocene specimens of *Helicotaphrichnus commensalis* from the localities and gastropods indicated. Most localities are in unnamed upper Pleistocene terrace deposits. They are arranged from south to north.

Localities	*Acanthina spirata* (Blainville 1832)	*Macron lividus* (A. Adams, 1855)	*Megasurcula stearnsiana* (Raymond, 1905)	*Mitrella carinata* (Hinds, 1844)	*Mitra idae* Melvill, 1893	*Nassarius mendicus* (Gould, 1849)	*Nassarius* sp.	*Ocenebra foveolata* (Hinds, 1844)	*Ocenebra interfossa* Carpenter, 1864	*Ocenebra poulsoni* (Carpenter, 1864)	*Olivella biplicata* (Sowerby, 1825)	*Olivella pedroana* (Conrad, 1855)	*Ophiodermella incisa* (Carpenter, 1864)
Bahia San Quintin, Baja California, UCLA 2411, SDSU 1670				x	x		x				x	x	
Rio Rosario, Baja California, UCLA 2723											x		
Punta Descanso, Baja California, UCLA 2715-2717	x										x		
Rio Morro, Baja California, UCLA 3162											x		
Rosarito Beach, Baja California, UCLA 3160											x		
Point Loma, San Diego County, California, UCLA 3605		x									x		
Pacific Beach, San Diego County, UCLA 3606, SDSU 1724	x										x		x
Torrey Pines, San Diego County, UCLA 3457											x		
San Clemente, Orange County, UCLA 2774	x	x						x	x		x		
Laguna Beach, Orange County, no locality number				x									
Newport Beach, Orange County, UCLA 2831	x									x	x		
San Pedro, Los Angeles County, UCLA 2381, 8153	x	x	x			x					x		
Playa del Rey, Los Angeles County, UCLA 2413											x		
Pacific Palisades, Los Angeles County, UCLA 3225											x		
Anacapa Island, UCLA 4883, 4884											x		
Cayucos, San Luis Obispo County, UCLA 3393, 3386, 3389											x		

and the greatest diameter observed is 1.5 mm. The tube is circular in cross-section throughout, and the walls are regular and smooth (Text-figs. 2A-C).

Occurrence.—We know of no previous reports of such tubes as fossils, though we have found them in shells from Pliocene and Pleistocene strata at a number of localities on the west coast of North America (Tables 1, 2). The minimum Pleistocene range, as indicated by these records, is from Bahia San Quintin, Baja California, to Cayucos, California, 30° to 35.5° north latitude, the Pliocene range from San Diego to Arcata, California, 33° to 41° north latitude.

Discussion.—*Helicotaphrichnus* differs in both form and origin from fossil U-shaped tubes that have been assigned to the genera *Polydora* Bosc, 1802, *Polydorites* Douvillé, 1908, and *Meandropolydora* Voigt, 1965, in that (1) the former has only one aperture instead of two, and (2) increase in length of the tube is accomplished by excavation only at its distal end rather than at both ends or at the elbow of the "U." These differences between *Helicotaphrichnus* and other fossil tubes thought to have been constructed by species of *Polydora* also reflect the taxonomic separation of the animals that construct the modern tubes, as Blake (1971, p. 17) has indicated that *P.*

TABLE 2—The invertebrate fossil collections at the University of California, Los Angeles (UCLA) and San Diego State University (SDSU) contain Pliocene specimens of *Helicotaphrichnus commensalis* from the localities and gastropod shells indicated.

Localities	*Cancellaria tritonidea* Gabb, 1866	*Nassarius grammatus* (Dall, 1917)	*Nucella lamellosa* (Gmelin, 1798)	*Olivella biplicata* (Sowerby, 1825)	*Shaskyus festivus* (Hinds, 1844)
Pacific Beach, San Diego County, San Diego Formation, SDSU 221, 222		x		x	
Ventura County, formation not indicated, UCLA 1934, SDSU 233	x			x	
Kettleman Hills, Fresno County, Etchegoin Formation, UCLA L-683					x
Arcata, Humboldt County, formation not indicated, no locality number			x		

commensalis should be assigned to a different genus. *Helicotaphrichnus* also is readily distinguished from these and all other fossil tubes by its unique form and occurrence.

Modern tubes of *Polydora commensalis* are indistinguishable from fossil *Helicotaphrichnus commensalis*. We have not seen modern tubes of *P. bioccipitalis*, but they apparently are similar to those of *P. commensalis*. Preserved specimens of the former were described as being covered only with silt and mucous (Blake and Woodwick, 1972, p. 77), but it is possible that they originally were covered also with calcium carbonate (J. A. Blake, written commun., January, 1973). Blake also feels that *P. commensalis* tubes from which the calcium carbonate wall is broken probably are indistinguishable from tubes of related species. An unidentified third species of *Polydora* reported by Samuelsen (1970, p. 40) from Norway may also construct similar tubes.

The known modern species that construct these tubes have only been found living commensally with hermit crabs (Blake, 1971, p. 17; 1972, p. 77; Samuelsen, 1970, p. 40), and it seems likely that fossil tubes also were constructed and inhabited only in the presence of pagurids. This spionid-pagurid commensal relationship thus has persisted at least from Pliocene time to the present. A somewhat different form of spionid commensalism indicated by Paleozoic fossil tubes has been described by Cameron (1969, p. 700–701). We have found *Helicotaphrichnus commensalis* in the shells of many different gastropod species (Tables 1, 2). Similarly, living *Polydora commensalis* construct tubes in the shells of probably dozens of gastropods (for example, see Hatfield, 1965, p. 357; Blake and Evans, 1973, table 3), and *P. bioccipitalis* occurs with at least four species (Blake and Woodwick, 1972, p. 77). However, both modern and fossil tubes are most common in shells in which the internal chamber is high and narrow in cross-section, with a constricted, trough-like junction of the outer shell wall and the columella (for example, *Olivella, Acanthina, Conus*). Such constricted chambers may provide greater security for the outer wall of the tube by restricting movement of the pagurid in that region.

Polydora commensalis lives today on both coasts of North America and the Pacific coast of Asia (Blake, 1971, p. 20; present study). It is common in the intertidal zone and reaches depths of at least 100 m in Sagami Bay, Japan. *P. bioccipitalis* apparently is known only from the coast of southern California (Blake and Woodwick, 1972, p. 77). We have not attempted to determine the total geographic and depth ranges of these species, because the possibility that other species construct similar tubes limits the usefulness of such information.

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MANUSCRIPT RECEIVED JUNE 19, 1973.
REVISED MANUSCRIPT RECEIVED DECEMBER 14, 1973.