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SPIONID BORE HOLE *POLYDORICHNUS SUBAPICALIS* NEW ICHNOGENUS AND ICHNOSPECIES: A NEW BEHAVIORAL TRACE IN GASTROPOD SHELLS

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ABSTRACT—Identification of tracemakers is of primary importance for evaluating the biotic interactions inferred from bore holes in fossil shell assemblages. Domicile bore holes in the subapical whorls of gastropods produced by spionid polychaete *Dipolydora* sp., supposed to be commensal with hermit crabs, are common in dead gastropod assemblages from deepwater habitats in the Philippines. These holes exhibit unique features and support a new criterion for the interpretation of nonpredatory borings in fossil gastropods. Diagnostic of these bore holes are: small circular to elliptical outer opening, the presence of weak dissolution of the columella beneath the bore hole, and the presence of a hollowed tube composed of detritus held together with mucus within some gastropod whorls anterior to the hole. The two selection factors of subapical whorls and elongate shells are supplementary criteria for recognition of these holes. Bore holes are recognized here in a deepwater gastropod assemblage from the upper Pliocene Shinzato Formation of Okinawa, Japan, and named *Polydorichnus subapicalis* n. igen. and isp. These holes are identical to modern examples exhibiting similar site and species selectivity. *P. subapicalis* has its oldest fossil record in the upper Miocene of the Philippines, was common in offshore assemblages from the Miocene onward, and is a good indicator of occupation by a hermit crab and for commensalism between polychaetes and hermit crabs.

INTRODUCTION

A WIDE variety of organisms bore holes into shelled invertebrates for the sake of predation and habitation (e.g., Bromley, 1981, 1993; Taylor et al., 1983; Boucot, 1990; Kabat, 1990; Kowalewski, 1993). These holes provide indirect evidence for understanding the behavior and ecological interactions among ancient organisms. For example, fossil predatory bore holes have attracted particular attention over the past three decades because they offer quantifiable data on various evolutionary aspects of predator-prey interactions through geologic time, mainly with reference to evaluating the ‘‘Mesozoic marine revolution’’ hypothesis and the escalation model of evolution (Vermeij, 1977, 1987; see also reviews by Brett and Walker, 2002; Walker and Brett, 2002; Kase and Ishikawa, 2003; Kelley and Hansen, 2003).

Nonpredatory bore holes are also common in fossil and modern shell assemblages. The holemakers include clionid sponges (Bromley, 1970), spionid polychaetes (Cameron, 1969b; Zottoli and Carriker, 1974; Kern et al., 1974; Kern, 1979), boring bivalves (Carter, 1978), homing patellogastropod and hipponicid gastropods (e.g., Kase et al., 1994, 1995, 1998; Vermeij, 1998), and barnacles (Seilacher, 1969), among others. Such holes can usually be determined by assessment of their shape, size, and unique boring pattern.

In practice, however, we often encounter simple circular holes in shelled organisms for which it is difficult to interpret origins. A number of bore holes still cannot be identified with particular holemakers, particularly in Mesozoic and Paleozoic faunas (e.g., Ausich and Gurrola, 1979; Smith et al., 1985; Harper et al., 1998; Baumiller et al., 1999). Carriker and Yochelson (1968) and Kowalewski (2002) cautioned against implicit identification of these holes, even when they occur together with potential holemaking organisms. The correct identification of holemakers is indispensable for evaluating ecological interactions related to bore holes but is not always possible (Bromley, 1981).

This study deals with domicile bore holes produced by the nonpredatory, commensal spionid polychaete *Dipolydora* sp. in the subapical whorls of gastropod shells. We follow Overstreet (1983) and Williams and McDermott (2004) in defining commensalism.

A description of a new fossil ichnogenus and ichnospecies *Polydorichnus subapicalis* is proposed. Williams (2000) recently discovered bore holes made by spionid polychaetes in the subapical part of gastropod shells occupied by hermit crabs from shallow waters of the tropical northwestern Pacific. Some authors also cited spionid borings in the apical and subapical whorls and columellas of deep-sea gastropods (e.g., Quinn, 1991; Walker and Voight, 1994; Kohn and Arua, 1999); however, these traces have never been named systematically or recorded in the fossil record. This ichnofossil will present important information on the taphonomy of gastropod shells and possibly present the history of commensalism between polychaetes and hermit crabs.

MATERIALS

We examined a total of 246 modern, dead gastropod shells occupied by hermit crabs and 166 living gastropods for bore holes of commensal spionids. These shells were sequentially collected from 2000 to 2005 by tangle nets at two sites, ‘‘Alabaster Point’’ (9°29′05N, 123°43′09E; 300–400 m in depth) and ‘‘Epitonium Point’’ (9°30′42N, 123°41′49E; 100–200 m in depth), named by local fishermen, from a muddy bottom off the southern coast of Panglao Island, Bohol Province, the Philippines. The specimens were fixed in 10% formalin, rinsed in tap water, and stored in 70% ethanol. The crustaceans and polychaetes specimens are registered as NSMT Cr16768–16793 and NSMT-Pol. H 477 in the Department of Zoology of the National Science Museum, Tokyo and the living gastropod specimens are deposited in the Department of Geology of the same museum, as an unregistered reference collection.

We also examined fossil shells from the upper Pliocene Shinzato Formation on the Miyagishima islet along the central part of Okinawa Island, southern Japan. These shells came from an exposure (26°21′33N, 127°58′43E; loc. 87-21 of Noda, 1988) that is the most prolific in fossil shells on the Miyagishima islet (Fig. 1). The strata at this site consists of bioturbated sandy mud, and the exposure is about 20-m thick and thought to have been deposited at upper bathyal depths (200–400 fathoms, according to MacNeil, 1960). In the outcrop, the shells have no signs of postmortem transportation by bottom currents or fragmentation by sediment compaction. However, there is abundant evidence that hermit crabs occupied the gastropod shells (e.g., ichnofossil *Helicotaphrichnus commensalis* Kern et al., 1974, which is identical to the borings that were produced by an obligate commensal polychaete of hermit crabs) and transported them across the bottom (see Walker, 1992; Walker and Voigt, 1994). The sediment is very easily removed from the fossil shells by soaking them in water, so that even the delicate traces of epi- and endobionts can be seen clearly. For these reasons, shells from this exposure are suitable for this study.

In total, 6,095 Pliocene gastropod specimens belonging to 153 species within 29 families were obtained by washing denuded

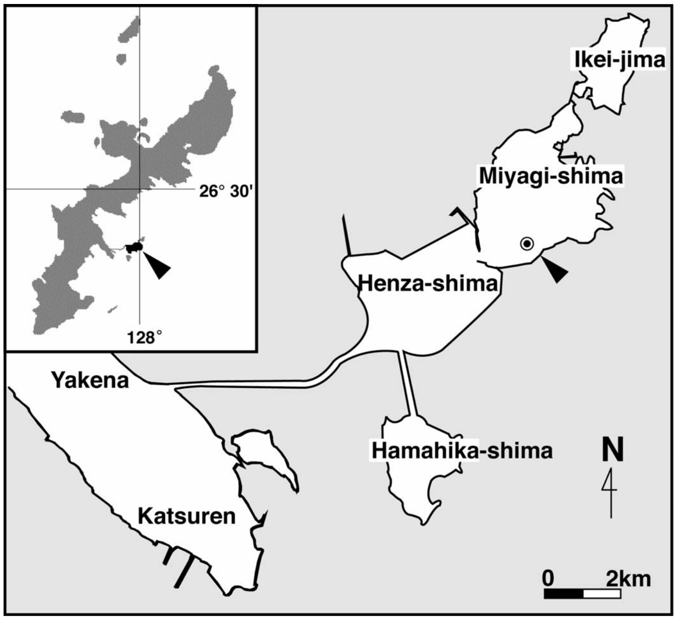

FIGURE *1*—Pliocene fossil locality (arrowhead) in Miyagi-shima Island, Okinawa, Japan (inset).

residue through a 2 mm sieve with water. We examined all specimens for bore holes under a dissecting microscope. We identified five types of holes based on the criteria of Carriker and Yochelson (1968), Robba and Ostinelli (1975), Kern et al. (1974), and Kern (1979), including predatory bore holes made by naticids, muricids, and octopi, nonpredatory bore holes made by spionid polychaetes (*Helicotaphrichnus commensalis*), and the new bore holes discussed in this study. All the specimens from the Shinzato Formation examined in this paper are deposited in the Department of Geology, the National Science Museum, Tokyo (NSM PM17381–17533).

OBSERVATIONS OF MODERN SPIONID BORE HOLES

Bore-hole morphology.—The following description of commensal spionid bore holes is based mainly on those in *Gemmula kieneri* (Doumet, 1840) and *Cerithium matukense* Watson, 1880, as these taxa best preserve the bore holes (Fig. 2). The outer opening of the hole is circular to elliptical in shape, and very small in size (<3 mm). The hole penetrates the whorl surface between the sutures straight or at an angle slightly oblique to and oriented toward the coiling direction (i.e., clockwise). The outer margins of the larger bore holes are sometimes jagged, especially when the gastropod shells have strong sculpture (Fig. 2.2). However, these holes are circular when they are small in size (<1 mm), and such holes are difficult to distinguish in outside view from typical predatory holes produced by muricid gastropods. In *G. kieneri*, the size of bore-hole openings ranges from 0.1 to 2.0 mm in horizontal axis (HA) and 0.1 to 1.2 mm in vertical axis (VA), and in *C. matukense* the HA ranges from 0.4 to 1.2 mm and the VA ranges 0.3 to 1.1 mm (detailed measurements see Table 1). Like muricid bore holes, they are cylindrical holes with an almost straight and smooth inner-wall surface, but the larger bore holes have an elliptical outer opening that is quite variable in shape, unlike those produced by naticid and muricid gastropods (Fig. 2.2).

There is a coiled hollow tube made of organic mud that fills two to three whorls anterior to the bore-hole opening (Fig. 2.3), and a unique feature associated with these holes is the presence of a small, flat area on the columella of gastropod shells, just beneath the bore-hole opening (Fig. 2.4, 2.5). This feature is only discernible when organic mud within the subapical whorls has been completely removed. This flattened area may have resulted from a mechanical boring process that occurs when the worm expands its dwelling, because a similar occurrence is found in *Dipolydora commensalis* (Andrews, 1891) as it expands its tube along the columella of inhabited shells (Williams, personal commun. 2005).

These holes occur only on the subapical whorls of the gastropods. For example, in *G. kieneri*, the bore-hole openings are distributed from the first to fourth teleoconch whorls and are mostly adjacent to the lower suture (Fig. 2.2). However, their relative position in the shell largely depends upon the morphology of the shells. The holes are present more anteriorly on elongate shells (with smaller apical angles) than on robust shells (with larger apical angles); in other words, the interior volume of the whorls in elongate shells is smaller and increases at a much slower rate than in robust shells (Fig. 2.1, 2.6), suggesting that the worms selected a site upon the shell whorl that may allow them space to conduct their boring activities.

Spionid polychaetes.—Williams (2001a) systematically studied 10 species of *Polydora* Bosc, 1802 and related genera in the family Spionidae, in intertidal and shallow-subtidal waters (<5 m) in the Philippines and Indonesia, of which seven species are borers into gastropod shells as well as commensals of hermit crabs. Above all, *Dipolydora commensalis* produces a unique U-shaped boring on the columella of gastropods, and its trace-fossil examples are well known as *Helicotaphrichnus commensalis*. This ichnospecies has been widespread from the Eocene onward and indicates a long-shared history between hermit crabs and polydorids (Walker, 1992). The borings of *D. commensalis* are initiated on the columella near the outer lip and wind around the apex where the worm can access the lumen (Kern et al., 1974; Williams and McDermott, 2004), but these distinctly differ from our trace.

The spionid worms discussed in this study are most probably borers into the subapical whorls of gastropod shells inhabited by hermit crabs (Fig. 2.1). Of the reported seven spionid species that are commensal on hermit crabs studied by Williams (2001a), *Polydora robi* Williams, 2000 is the only one that bores into the subapical whorls of dead gastropod shells inhabited by hermit crabs (Williams, 2001a). M. Imajima of the National Science Museum, Tokyo, and W. Sato-Okoshi of Tohoku University (personal commun. 2003 and 2005, respectively), however, have shown that the borers from off Panglao, Philippines, belong to a single species of the genus *Dipolydora* Verrill, 1879 and have suggested that the species may represent a new species.

Like *P. robi*, *Dipolydora* sp. stays in a lumen within a coiled hollow tube in detrital material that consists of organic-rich mud with many tests of foraminifers (Figs. 2.3, 3). Zottoli and Carriker (1974) showed that *Polydora websteri* Hartman in Loosanoff and Engle, 1943, collected detrital material and formed a tube that it held together with secreted mucus. The worms of *Dipolydora* sp. stay in the tube, with their anterior region near the bore-hole opening, and extend their palps outward from the hole opening, which suggest at least a suspension/deposit-feeder mode for this animal which is characteristic for most spionids (Fig. 3). Williams (2000, 2001a, 2001b, 2002) reported that *P. robi* are able to reverse direction in their tubes as they switch their feeding mode. *P. robi* and *D. commensalis* captured food particles by manipulating a pair of peristomial palps extending outward from the bore-hole opening, and also fed on the eggs of hermit crabs associated with the same gastropod shell (Williams and McDermott, 1997, 2004; Williams, 2000, 2001a, 2002). We have not observed whether or not *Dipolydora* sp. also feeds on the eggs of associated hermit crabs. Further observation is needed to analyze feeding behavior of *Dipolydora* sp.

Williams (2000) also observed that up to five worms inhabited one shell, typically with one large female and one small male within the hermitted shells in shallow water. We also sometimes

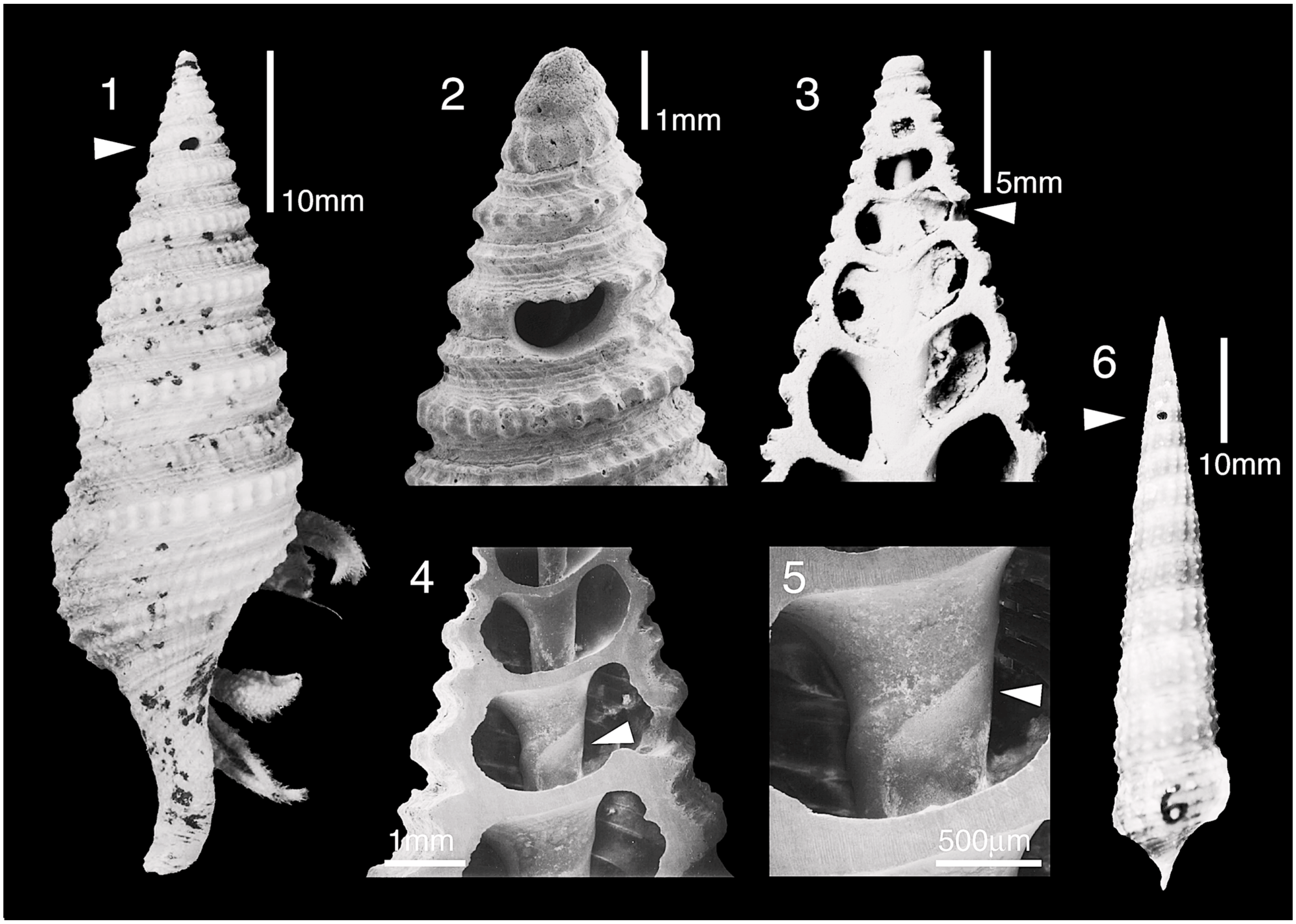

FIGURE 2—Modern domicile bore holes produced by *Dipolydora* sp. in *Gemmula kieneri* (Doumet, 1840) and *Cerithium matukense* Watson, 1880 from a sea bottom off Panglao Island, Bohol Province, the Philippines. *1*, *G. kieneri*, occupied by the hermit crab *Paguristes* aff. *palythophilus* Ortmann, 1892. A domicile bore hole is seen in the shell's subapical part (arrowhead); *2*, enlargement of the apical part of *G. kieneri*, showing the elliptical domicile bore hole oriented slightly obliquely to the shell coiling direction. The right margin of the opening is jagged; *3*, cross-sectional view of *G. kieneri*, showing the presence of a mud/detrital tube held together with mucus anterior to the bore-hole opening (arrowhead), along with a hollow tube inside the sediment; *4*, whorl section of *G. kieneri*, sediment removed, shows the columella eroded by the spionid (arrowhead); *5*, enlargement of the eroded columella in *4*; *6*, a small domicile bore hole (arrowhead) produced by *Dipolydora* sp. in *C. matukense*. Note that the opening is positioned more anteriorly than in *G. kieneri* and is not elliptical in shape.

observed one large female and one small male present in hermitted shells from off Panglao.

Hermit crabs and hermitted shells.—Dipolydora sp. is commensal with a wide variety of hermit crabs, all of which represent different species from those commensal with *P. robi* from shallow water reported by Williams (2000, 2001a, 2001b, 2002). The 246 individuals of hermit crabs examined here belong to 16 species, eight genera, and three families (Appendix 1, supplemental data archive at www.journalofpaleontology.org). Many of these species are difficult to identify, because hermit crabs at this depth have not been thoroughly investigated in the tropical western Pacific, including the Philippines; in fact, several species may be new (M. Osawa, personal commun. 2003). Species of Diogenidae are most dominant and make up over 75% of the total number of species, of which *Paguristes* aff. *palythophilus* Ortmann, 1892 is the most dominant. Species of Paguridae add up to less than 20% of the total number of species, and Parapaguridae species are less than 5%.

Gastropod shells occupied by hermit crabs collected from "Alabaster Point" consist of 30 species belonging to 23 genera and

TABLE *1*—Morphology of spionid bore holes in subapical part of the shells in two gastropod species from the "Alabaster point," Bohol Island, Philippines (Recent) and two gastropod species from the Shinzato Formation, Miyagishima Island, Okinawa, Japan (Pliocene).

Species (Age)	Number of specimens examined	Number of bore holes examined	Mean size of bore hole opening (mm ± SD) Horizontal axis (HA)	Mean size of bore hole opening (mm ± SD) Vertical axis (VA)	Mean VA/HA ratio
Gemmula kieneri (Recent)	42	42	0.99 ± 0.50	0.65 ± 0.28	0.72 ± 0.22
Cerithium matukense (Recent)	20	20	0.82 ± 0.26	0.69 ± 0.23	0.86 ± 0.13
Gemmula granosa (Pliocene)	54	66	0.77 ± 0.49	0.56 ± 0.33	0.77 ± 0.12
Ancilla (*Turrancilla*) *chinenensis* (Pliocene)	39	39	0.68 ± 0.44	0.43 ± 0.20	0.74 ± 0.23

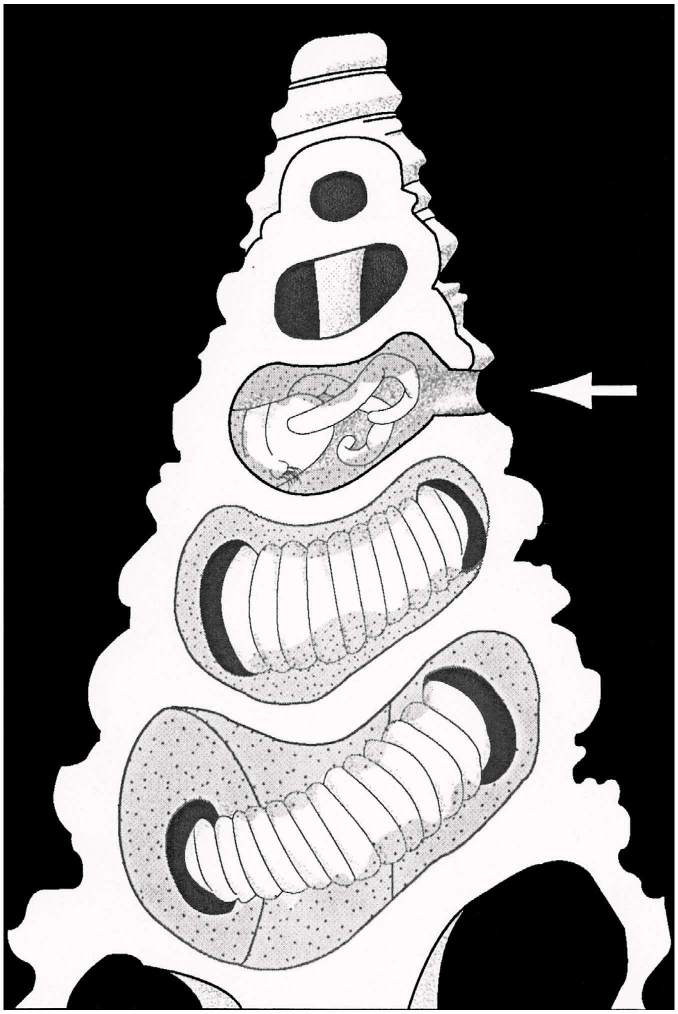

FIGURE *3*—Schematic drawing of *Dipolydora* sp. positioned as in life within *Gemmula kieneri*, showing that the spionid worm inhabits a mucus-mud tube within the shell whorl and faces toward the bore-hole opening (arrow).

12 families (Appendix 1, Supplemental Data archive at www.journalofpaleontology.org). Of the 30 species, *Dipolydora* bore holes are found in 18 species that belong to 15 genera and nine families. Bore holes frequently occur in elongate shells such as Turridae (the bore-hole occurrence = 80%, N = 66), Colubrariidae (61%, N = 38), Cerithiidae (59%, N = 34), and Olividae (50%, N = 14). In contrast, bore holes have rarely been identified in shells with larger apical angle such as Muricidae (the bore-hole occurrence = 0%, N = 20), Naticidae, or trochiform shells (personal observation). We have observed that the apical whorls of elongate shells are situated close to the ocean bottom when the hermit crabs carry them, with their apertures almost parallel to the bottom as when the shells were alive (Fig. 4.1). In contrast, the hermit crabs carry rounded and trochiform shells with their apices variably raised above the bottom, depending on the robustness of the body whorl (Fig. 4.2). A possible interpretation is that these rounded and trochiform shells are not suitable for feeding by *Dipolydora* sp., because the raised apices would prevent them from accessing the food in bottom sediments. This interpretation is only possible if the worms obtain foods mainly from bottom sediments, but we have not yet confirmed their feeding habits.

In contrast, Voight and Walker (1995) reported a high rate of infestation by spionid polychaete in trochiform living gastropods of the genus *Gaza* Watson, 1879 from the northern coast of South America and the Gulf of Mexico. The bore holes are present not in the subapical whorls but at the shell's apex, and penetrate through the protoconch (see also Quinn, 1991; Walker and Voight, 1994). The holemaker is as yet an undescribed spionid, and the worm's body is right next to the snail's living tissue (Walker, personal commun. 2005). We herein examined a total of 166 living gastropods that were collected by tangle nets from Alabaster Point during March and June 2005 and from Epitonium Point in June 2005. A total of 50 living gastropod specimens belonging to 24 species within 19 genera and 10 families were collected from Alabaster Point, and 116 living gastropod specimens belonging to 22 species within 19 genera and 14 families were collected from Epitonium Point (see Appendix 2, supplemental data archive at www.journalofpaleontology.org). None of them have spionid boring on their subapical part, although the hermitted shells from the same points were highly infested by *Dipolydora* sp. It is quite probable that *Dipolydora* sp. is a commensal of hermit crabs.

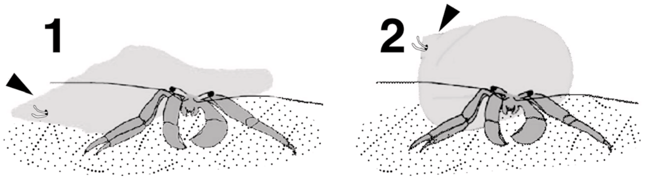

FIGURE *4*—Difference in shell tilt when carried by a hermit crab. *1*, tilt in elongated shell and position of bore hole (arrowhead). Spionids extend their palps outward from the bore-hole opening; *2*, tilt in rounded shell and position of bore hole (arrowhead).

SYSTEMATIC ICHNOLOGY

POLYDORICHNUS new ichnogenus

Diagnosis.—Very small hole (usually less than 2 mm) with circular to elliptical outer opening, suggested to be commensal in origin and present only in subapical whorls of gastropod shells. Axis of hole usually slightly oblique to substrate surface (mostly toward clockwise coiling direction of whorl). Boring associated with detrital mud tube, if preserved, in anterior two or three whorls of gastropod, and small abraded area on columella just beneath bore-hole opening.

Discussion.—*Polydorichnus* is morphologically most similar to the ichnogenus *Oichnus* Bromley, 1981 as redefined by Nielsen et al. (2003) when only dealing with holes. The emended diagnosis of *Oichnus* by Nielsen et al. (2003) includes a variety of holes (completely penetrated) and pits (incompletely penetrated) ranging from circular to rhomboidal shape of the outer-opening shape. It is often difficult to separate *P. subapicalis* from *Oichnus simplex* Bromley, 1981 by merely comparing the shape of the outer-opening. However, it is easier to differentiate *Polydorichnus* from *Oichnus* by considering the presence of associated erosion on the shell columella.

Etymology.—From the polydorid, polychaete, that makes such traces.

Type species.—*Polydorichnus subapicalis* new ichnospecies.

Occurrence.—From the Miocene to Recent, widespread in warm temperate to tropical, shallow to bathyal soft-bottomed deposits. It is mostly common in subtropical to tropical bathyal deposits (see Table 2).

POLYDORICHNUS SUBAPICALIS new ichnospecies
Figure 5

Diagnosis.—As for the ichnogenus.

Description.—*Polydorichnus subapicalis* has an overall morphology comparable to modern commensal bore holes produced by *Dipolydora* sp. Following description of holes based mainly on those in *Gemmula granosa* (Helbling, 1779) and *Ancilla* (*Turrancilla*) *chinenensis* MacNeil, 1960 from upper Pliocene Shinzato Formation on Miyagishima islet along central part of Okinawa Island, southern Japan, as these taxa at site are abundant and best preserve bore holes (Fig. 5). Like modern examples, it is basically a cylindrical hole, with elliptical outer opening that is circular when size of bore-hole opening relatively small. In *G. granosa*, size of bore-hole openings ranges

TABLE 2—The fossil records of *Polydorichnus subapicalis* n. igen. and isp. Sample depository (abbreviations): Naturhistorisches Museums Wien (NMW); National Science Museum, Tokyo (NSM); U.S. National Museum of Natural History (NMNH); Mizunami Fossil Museum (MFM); National Museum of Natural History Natularis (RGM); Mines and Geosciences Bureau, Quezon City, Philippines (MGB); Shizuoka University (SU).

Age	Formation and/or area	Environment	Number of specimens with *P. subapicalis*	Number of specimens examined	Depository
Late Cretaceous	Gosau, Austria	Tropical, shallow	—	1,072	NMW
Late Cretaceous	Coffee Sand; Mississippi, USA	Warm temperate, shallow	—	116	NSM
Late Cretaceous	Repley Formation; Tennessee, USA	Warm temperate, shallow	—	502	NSM
Late Cretaceous	Repley Formation; Tennessee, USA	Warm temperate, shallow	—	>100	NMNH
Paleocene (Thanetian)	Chalons-sur-Vesle, Marne, France	Subtropical, shallow	—	437	RGM
Paleocene (Thanetian)	Various localities, Marne, France	Subtropical, shallow	—	57	RGM
Paleocene	Montian, Hainoit, Belgium	Subtropical, shallow	—	72	RGM
Early Eocene (Ypresian)	Gan, Pyrénées Atlantique, France	Subtropical, shallow	—	244	RGM
Early Eocene (Ypresian)	Cuise-la-Motte, Oise, France	Subtropical, shallow	—	425	RGM
Early Eocene (Ypresian)	Aizy-Jouy, Liancourt, Rethevil, France	Subtropical, shallow	—	45	RGM
Early Eocene (Ypresian)	St. Gobain, Aisne, France	Subtropical, shallow	—	188	RGM
Middle Eocene	Kosciusko Formation; Mississippi, USA	Tropical, shallow	—	40	NSM
Middle Eocene	Cook Mountain Formation; Mississippi, USA	Tropical, shallow	—	212	NSM
Middle Eocene (Lutetian)	Cressay, Yvelines, Paris Basin, France	Subtropical, shallow	—	5,293	NSM
Middle Eocene (Lutetian)	Bende Ameki, Nigeria	Subtropical, shallow	—	264	RGM
Middle Eocene (Bartonian)	Ver-sur-Launette, Oise, France	Subtropical, shallow	—	451	RGM
Middle Eocene (Bartonian)	Isles-les-Meldeuses, Seine et Marne, Paris Basin, France	Tropical, shallow	—	4,140	NSM
Late Eocene (Priabonian)	Grimmertingen, Belgium	Subtropical, shallow	—	416	RGM
Late Eocene	Dnepropetrovsk, North-East Ukraine	Subtropical, shallow	—	113	NSM
Early Oligocene (Ruperian)	Keistraat, Klein Spouen, Belgium	Subtropical, shallow	—	309	RGM
Early Oligocene	Headon Hill Formation; Isle of Wight, UK	Subtropical, shallow	—	1,441	NSM
Early Oligocene	Red Bluff Formation; Mississippi, USA	Warm temperate, moderately deep	—	251	NSM
Late Oligocene (Chattian)	Söllingen, Niedersachsen, Germany	Subtropical, shallow	—	36	RGM
Late Oligocene (Chattian)	Duisburg, Nordrhein-Westfalen, Germany	Subtropical, shallow	—	409	RGM
Late Oligocene	Byram Formation; Mississippi, USA	Warm temperate, shallow	—	313	NSM
Early Miocene	Chipola Formation; Florida, USA	Warm temperate, shallow	—	3,842	NSM
Middle Miocene	Dnepropetrovsk, North-East Ukraine	Subtropical, shallow	—	181	NSM
Middle Miocene	Akeyo Formation; Gifu, Japan	Subtropical, shallow	—	>100	MFM
Late Miocene	Dingle Formation; Panay, Philippines	Tropical, moderately deep	17	455	NSM
Early Pliocene	Barili Formation; Cebu, Philippines	Tropical, moderately deep	1	587	NSM
Early Pliocene	Merida Formation; Leyte, Philippines	Tropical, moderately deep	28	139	NSM, MGB
Early Pliocene	Tartaro Formation; Luzon, Philippines	Tropical, shallow	1	251	NSM
Late Pliocene	Cabatuan Formation; Panay, Philippines	Tropical, shallow	—	225	NSM
Late Pliocene	Takanabe Formation; Miyazaki, Japan	Subtropical, bathyal	105	535	NSM
Late Pliocene	Hijikata Formation; Shizuoka, Japan	Subtropical, bathyal	40	272	NSM
Late Pliocene	Ananai Formation; Kochi, Japan	Subtropical, moderately deep	39	1,103	NSM
Late Pliocene	Shinzato Formation; Okinawa, Japan	Tropical, bathyal	850	6,095	NSM
Late Pliocene	Minebari Formation; Miyako-jima, Okinawa, Japan	Tropical, bathyal	1	60	SU
Plio-Pleistocene	Mandog Formation, Davao, Philippines	Tropical, moderately deep	5	302	NSM, MGB
Early Pleistocene	Calooshatchee Formation; Florida, USA	Subtropical, shallow	36	1,325	NSM
Middle Pleistocene	Shibikawa Formation; Akita, Japan	Cold temperate, shallow	—	424	NSM
Late Pleistocene	Katanishi Formation; Akita, Japan	Cold temperate, shallow	—	544	NSM
Late Pleistocene	Yabu Formation; Makuta, Chiba, Japan	Warm temperate, shallow	5	286	NSM
Late Pleistocene	Wan Formation; Kikaigashima, Kagoshima, Japan	Tropical, shallow	13	271	NSM
Holocene	Moeshima Formation; Kagoshima, Japan	Warm temperate, moderately deep	—	78	NSM

from 0.1 to 2.1 mm in horizontal axis (HA) and 0.1 to 1.3 mm in vertical axis (VA). In *A.* (*T.*) *chinenensis*, HA ranges from 0.2 to 2.0 mm and VA ranges from 0.2 to 0.9 mm (detailed measurements see Table 1). Right margin of openings on right-coiled gastropods sometimes jagged (Fig. 5.2, 5.6). Weak abrasion on columella close to bore hole (Fig. 5.3, 5.4, 5.7, 5.8). Whorls anterior to bore hole sometimes filled with matrix, which indicates presence of detrital mud deposited by borer and hollow tube in matrix where borer lived. Matrix readily recognizable, since is sometimes stained red with iron oxide and contains many more foraminifer tests than does sediment that entered through aperture during or after burial. However, mud tube not always preserved. Bore holes occur only on subapical whorls of gastropods. In *G. granosa*, bore-hole openings distributed from second protoconch to fourth teleoconch whorls and are mostly adjacent to next whorl (Fig. 5.2). In contrast, bore holes do not show clear site selectivity within a whorl, but slightly tend to open at either apertural or adapertural side. Judging from good agreement of modern and fossil bore-hole characters, *P. subapicalis* most likely handiwork of commensal spionid polychaetes of hermit crabs, probably identical to or closely related to *Dipolydora* sp. from off Panglao Island.

Of 153 gastropod species belonging to 29 families from Shinzato Formation, *P. subapicalis* found in 78 species belonging to 17 families and 13.9% of total number of individual gastropods (850 out of 6,095 shells examined, Appendix 3, Supplemental Data archive at www.journalofpaleontology.org). *P. subapicalis* most common in elongate shells such as Turridae (borings are present in 27.2% of total specimens), Fasciolariidae (50.6%), and Olividae (19.9%). In contrast, *P. subapicalis* has not been found in cap-shaped shells [*Cocculina loochooensis* MacNeil, 1960 and *Sabia* cf. *conica* (Schumacher, 1817)] and very rare in round and trochiform shells such as Naticidae (2.5%) and Trochidae (1.3%) (Appendix 3, Supplemental Data archive at www.journalofpaleontology.org). Shell shape (represented by shell width divided by height in largest specimen collected) correlates with *P. subapicalis* infestations ($r^2 = 0.189$; Table 3, Fig. 6.1). It may be result of position of apical part when shells carried by hermit crabs (see Fig. 4). *P. subapicalis* also has not been found or very uncommon on small-sized adult shells. Figure 6.2 shows relationship between frequency of shells with *P. subapicalis* and shell size for 29 common species (Table 3). Shell size (represented by height of largest specimen obtained) positively correlates with *P. subapicalis* infestation

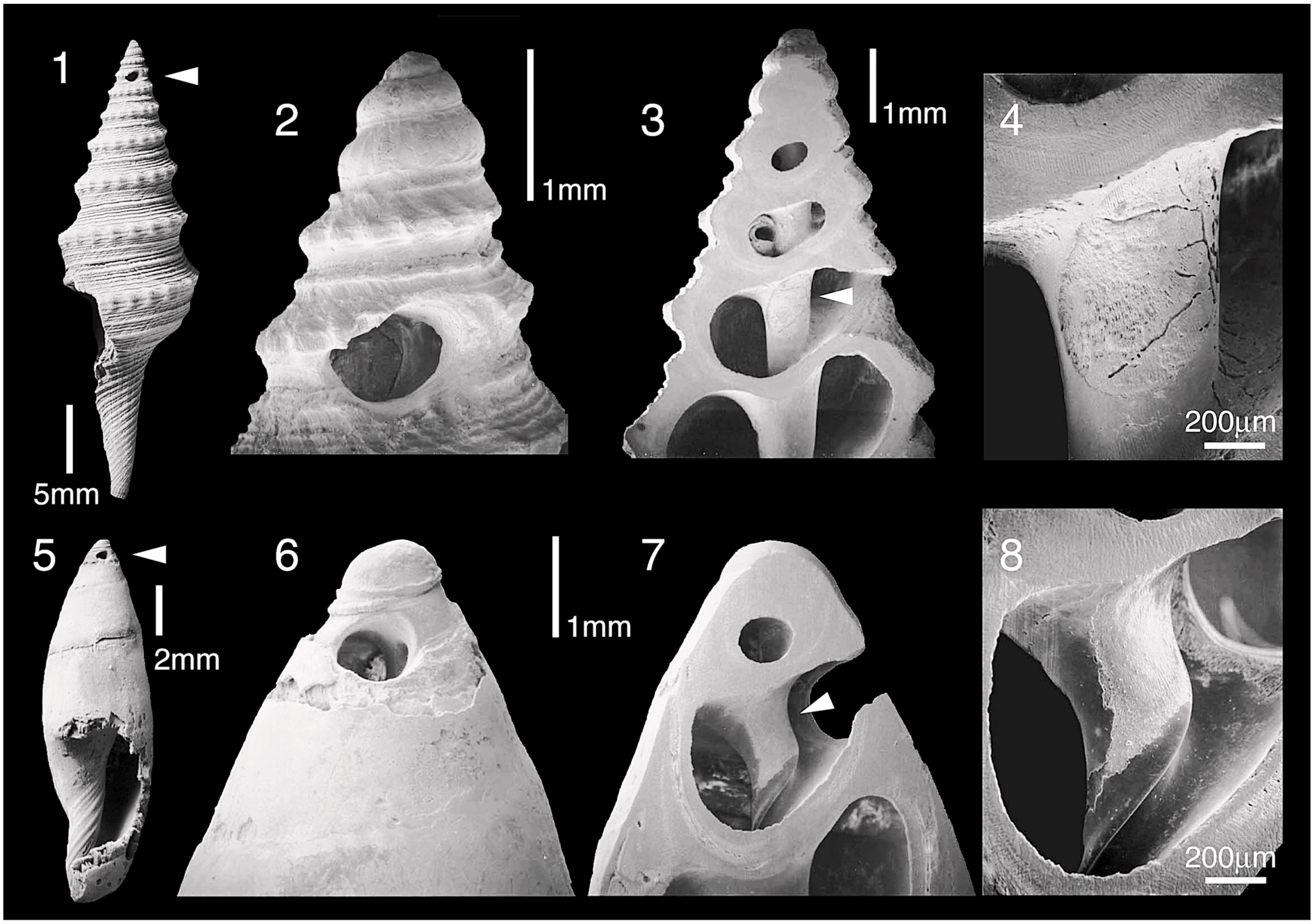

FIGURE 5—*Polydorichnus subapicalis* n. igen. and isp. in gastropod shells from the upper Pliocene Shinzato Formation of Okinawa, Japan. *1*, NSM PM16969, holotype in *Gemmula granosa* (Helbling, 1779), showing *P. subapicalis* in the subapical part (arrowhead); *2*, details of *P. subapicalis* in *1*, showing a somewhat obliquely penetrated bore hole. The right margin of the hole opening is jagged; *3*, whorl section of *G. granosa* shows the eroded columella beneath the bore-hole opening (arrowhead); NSM PM16970; *4*, details of the eroded columella in *3*; *5*, *P. subapicalis* (arrowhead) in *Ancilla* (*Turrancilla*) *chinenensis* MacNeil, 1960; NSM PM16971; *6*, details of *P. subapicalis* in *5*; *7*, whorl section of *A.* (*T.*) *chinenensis* shows the eroded columella beneath the bore-hole opening (arrowhead); NSM PM16972; *8*, details of the eroded columella in *7*.

(r^2 = 0.634; Table 3, Fig. 6.2). It is interesting to note that *Polydorichnus subapicalis* is found in more than 70% of shells infested by *Helicotaphrichnus commensalis* (trace fossil commensal of hermit crabs), while only less than 8% in shells without this trace fossil (see Table 3), suggesting high probability that *P. subapicalis* is also trace fossil commensal of hermit crabs.

Etymology.—The species name refers to the subapical position on gastropod shells, where the bore holes are present.

Type.—NSM PM16969 (holotype); NSM PM16970–16972 (referred specimens).

Occurrence.—As for the ichnogenus.

Fossil record of Polydorichnus subapicalis.—Although *P. subapicalis* is represented by a rather featureless and simple, elliptical to rounded hole when viewed from outside the shell, the erosion of the columella just beneath the bore hole and concentration of the holes mostly on the subapical whorls, make them easy to recognize in fossil shells. The presence of a hollowed, muddy filling originally with high organic content is another feature for discrimination although it will not always be preserved. The preference of *P. subapicalis* for elongate shells is also a supplementary criterion for recognition. We have assessed the fossil record of *P. subapicalis*, although preliminarily, by examining large collections of Cretaceous and Cenozoic mollusks stored in the National Science Museum, Tokyo, and other museums (see Table 2).

Despite our survey, we have not found any examples of Cretaceous, Paleocene, Eocene, or Oligocene *P. subapicalis* (Table 2). The oldest example of *P. subapicalis* we have found is from the upper Miocene of the Panay Island, Philippines, which suggests that such bioerosion had begun at least by Miocene time. The overall characteristics of the Miocene bore holes are nearly identical to Pliocene *P. subapicalis* and to modern examples (Fig. 7.1–7.3).

Among the Cenozoic material examined for this study, *P. subapicalis* is uncommon in shallow-water and common in deepwater molluscan assemblages (see Table 2). Williams (2000) reported another kind of subapical boring by commensal spionids *Polydora robi* in intertidal and subtidal, shallow-water, hard bottoms in the tropical Western Pacific, however, we unfortunately do not have hard-bottom fossil shells assemblages.

DISCUSSION

The documentation of domicile bore holes made by spionids in modern gastropod shells and *Polydorichnus subapicalis* n. igen. and n. isp. in fossil gastropods has important paleoecological implications for three reasons.

First, it provides a new trace fossil in modern and Cenozoic gastropods. Second, *P. subapicalis* may be good indicator of the activities of hermit crabs in the fossil record. The presence of *P. subapicalis* in fossil gastropods suggests that the shells were occupied by a hermit crab(s), even if the occupant was not preserved

TABLE 3—Distribution of *Helicotaphrichnus commensalis* and *Polydorichnus subapicalis* n. igen. and isp. in 29 dominant (>50 individuals) gastropod species from the Pliocene Shinzato Formation, Miyagishima Island, Okinawa, Japan.

Species	Family	Number of specimens	Shell height (mm)	Shell width/height ratio	Number of specimens with bore hole(s)		Infestation rate of *P. subapicalis*	
					Helicotaphrichnus commensalis	*Polydorichnus subapicalis*	Specimen with *H. commensalis*	Specimen without *H. commensalis*
Solariella cf. *albalitus*	Trochidae	58	7.5	0.88	0	2	0/0	2/58
Solariella sp. 1	Trochidae	86	7.9	0.87	0	0	0/0	0/86
Trochocerithium shikoensis	Cerithiidae	332	11.2	0.47	5	12	1/5	11/327
Argyropeza cf. *divina*	Cerithiidae	122	10.5	0.30	0	7	0/0	7/122
Euspira cf. *pallida*	Naticidae	621	12.5	0.89	9	15	2/9	13/612
Euspira sp.	Naticidae	66	9.5	0.88	0	0	0/0	0/66
Natica sp.	Naticidae	69	20.0	1.05	4	1	0/4	1/65
Naticarius cf. *niasensis*	Naticidae	112	16.4	0.98	1	6	0/1	6/111
'Balcis' chinenensis	Eulimidae	66	7.7	0.40	0	0	0/0	0/66
Profundinassa babylonica	Nassariidae	358	9.3	0.51	3	16	0/3	16/355
Profundinassa sp. 1	Nassariidae	110	8.1	0.46	1	8	0/1	8/109
Profundinassa sp. 2	Nassariidae	82	7.6	0.45	0	0	0/0	0/82
Hindsia (*Nihonophos*) *solida*	Buccinidae	80	22.5	0.50	13	11	8/13	3/67
Ancilla (*Turrancilla*) *chinenensis*	Olividae	922	35.1	0.36	114	193	81/114	112/808
Uromitra noharai	Mitridae	139	24.1	0.26	4	20	4/4	16/135
Cancellaria yonabaruensis	Cancellariidae	161	11.7	0.60	4	3	0/4	3/157
Gemmula granosa	Turridae	326	46.8	0.33	119	185	104/119	81/207
Gemmula cassinella	Turridae	144	33.1	0.33	26	46	17/26	29/118
Splendrillia incompta	Turridae	58	12.1	0.34	1	2	1/1	1/57
Splendrillia aff. *incompta*	Turridae	92	15.1	0.34	0	6	0/0	6/92
Splendrillia sp.	Turridae	58	20.8	0.31	17	30	11/17	19/41
Etrema hayasakai	Turridae	55	13.3	0.35	0	2	0/0	2/55
Lioglyphostoma tobaruensis	Turridae	119	19.1	0.26	13	19	6/13	13/106
Lioglyphostoma sp.	Turridae	60	18.6	0.32	2	2	1/2	1/58
Propebela belelloidea	Turridae	136	14.5	0.41	1	1	0/1	1/135
Daphnella ryukyuensis	Turridae	98	30.0	0.33	10	17	7/10	10/88
Pupa cf. *reussi*	Acteonidae	145	12.1	0.50	1	5	1/1	4/144
Ringicula sp.	Ringiculidae	291	7.5	0.69	0	4	0/0	4/291
Abderospira puncturata	Cylichnidae	62	7.0	0.80	0	0	0/0	0/62
Total		5,028			348	613	244/348 (70.1%)	369/4,680 (7.9%)

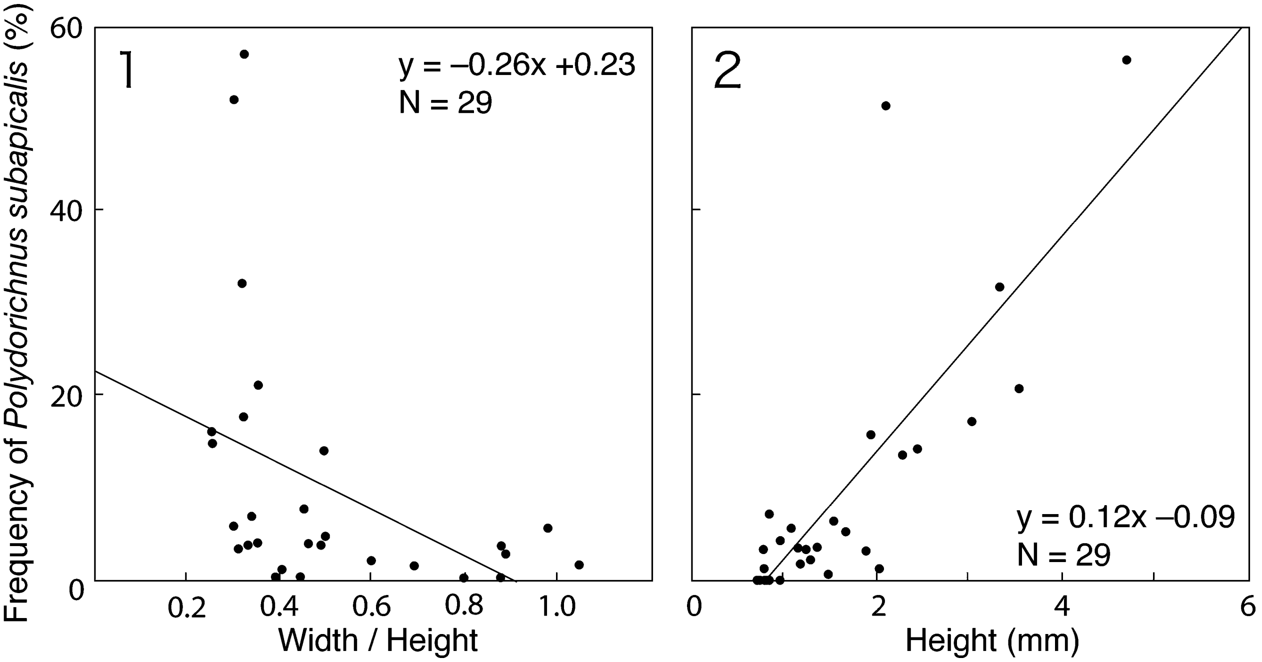

FIGURE *6*—Frequency of *Polydorichnus subapicalis* n. igen. and isp. in fossil gastropod shells having different shell shapes among 29 dominant (>50 individuals) species in the Pliocene Shinzato Formation, Okinawa, Japan. *1*, plot of *P. subapicalis* frequencies against shell width/height ratio with regression lines by method of least squares (r^2 = 0.189); *2*, plot of *P. subapicalis* frequencies against shell height with regression lines by method of least squares (r^2 = 0.634).

in situ or in the same bed. Such ichnofossil occurrences document the history of taphonomic processes that the shells experienced after death (Seilacher, 1969; Walker, 1988, 1989, 1992, 2001; Ishikawa et al., 2004). Third, *P. subapicalis* may be additional evidence of a commensal-host relationship between polychaetes and hermit crabs. Hermit crabs (Anomura: Paguridae) themselves have a long fossil record, probably originating in the early Jurassic (Glaessner, 1969). Fraaije (2003) suggested that hermit crabs changed their shell preference from ammonites to gastropods during the Cretaceous, based on the discovery of a fossil hermit crab preserved in situ in the body chamber of an Early Cretaceous ammonite from Speeton, United Kingdom. The utilization of shells by hermit crabs was considered initially developed for concealment and protection of the abdomen, and it also allows them to use gastropod lumen space during reproduction (McLaughlin, 1983). Hermit crabs seem to provide a new niche for epibiotic and endobiotic organisms in the marine ecosystems from the Middle Jurassic onward (Walker, 1992; Williams and McDermott, 2004).

The origin of polychaetes is much older than that of hermit crabs, probably dating back to the Cambrian (Morris, 1989). The endolithic lifestyle of polychaetes is a strategy that evolved in their long history (see Cameron, 1969a, 1969b). Ichnogenera attributed to borings by polychaetes are *Caulostrepsis* Clarke, 1908; *Clionoides* Fenton and Fenton, 1932; *Helicotaphrichnus* Kern et al., 1974; *Meandropolydora* Voigt, 1965; *Ostreoblabe* Voigt, 1965; *Ramosulichnus* Hillmer and Schulz, 1973; *Trypanites* Mägdefrau, 1932 and *Vermiforichnus* Cameron, 1969a. The oldest example among them is *Trypanites* from the Cambrian period, although determinations of the exact culprits are difficult except for rare cases (see Häntzschel, 1975; Taylor and Wilson, 2003). Cameron (1969a) reported a fossil polychaete that resembles living members of the family Spionidae preserved in situ in its bore hole *Vermiforichnus clarkei* Cameron, 1969a on a bivalved shell from the middle Devonian of central New York, USA.

Boring spionids have used a variety of substrates from sandy bottom to calcareous substrates in their evolutionary history. Gastropod shells occupied by hermit crabs would have appeared as a new attractive niche to the spionids, because the shells can provide many additional benefits for associated spionids (e.g., for protection from burial or predation, increased food resources, and exposure to favorable environmental conditions by migration of crabs; see Williams and McDermott, 2004). The hermit crab-commensal spionid bore hole *Helicotaphrichnus commensalis* first appeared during the Eocene in the Atlantic and Gulf Coastal Plain of the United States (Walker, 1992), suggesting a new niche for boring spionids during the epoch.

CONCLUSIONS

1. Domicile bore holes in the subapical whorls of dead gastropod shells are common in deep waters of the Philippines, where they are produced by an unnamed spionid species of the polydorid genus *Dipolydora* that may be a commensal of hermit crabs. The bore holes exhibit: 1) cylindrical geometry; 2) perpendicular to slightly oblique penetration; 3) circular to elliptical outer openings, sometimes with a jagged outer margin in larger openings (usually right side of openings in right-coiled gastropods); 4) a slightly dissolved shell columella beneath the bore hole; 5) the presence of an organic-rich, muddy filling with a hollow tube on some whorls anterior to the bore hole; 6) a strong site preference for the subapical whorls; and 7) species preference for elongate shells.

2. An examination of deepwater gastropods from the upper Pliocene Shinzato Formation of Okinawa, Japan, shows that bore holes with these characteristics are widespread, and are described here as *Polydorichnus subapicalis* n. igen. and isp.

3. A preliminary survey of Cretaceous and Cenozoic gastropod assemblages shows that the oldest *P. subapicalis* is from the upper Miocene, whereas the first appearance of another hermit crab-associated spionid bore hole (*Helicotaphrichnus commensalis*) in gastropod shells is from the Eocene of Atlantic Gulf Coastal Plain (Walker, 1992).

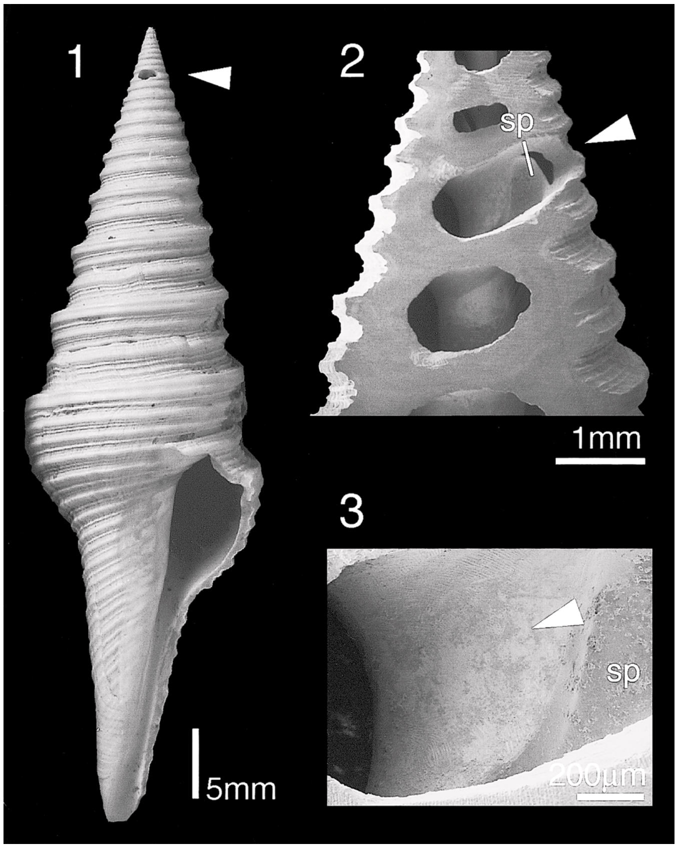

FIGURE 7—The oldest example of *Polydorichnus subapicalis* n. igen. and isp. from the upper Miocene Dingle Formation on Panay Island in the Philippines. *1*, *Gemmula* (*Unedogemmula*) *butonensis asanoi* Shuto, 1969, showing *P. subapicalis* in the subapical whorls (arrowhead); NSM PM16973; *2*, whorl section of *1* shows the eroded columella beneath the bore-hole opening (arrowhead) and its anterior whorl. sp, septum of shell; *3*, details of eroded columella (arrowhead) in *2*.

4. *Polydorichnus subapicalis* may also indicate of shells once occupied by hermit crabs in fossil gastropod assemblages, and of commensalism between polychaetes and hermit crabs in the fossil record, even though the two shell occupants are not preserved in the sediment. Therefore, these bore holes are useful for evaluating the taphonomic histories of fossil gastropod shells (Walker, 1992; Ishikawa et al., 2004).

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