

Burrow Architecture of the Spionid Polychaete *Polydora villosa* in the Corals *Montipora* and *Porites*

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Pi-Jen Liu and Hwey-Lian Hsieh (2000) Burrow architecture of the spionid polychaete *Polydora villosa* in the corals *Montipora* and *Porites*. *Zoological Studies* 39(1): 47-54. The spionid polychaete, *Polydora villosa*, is found only in living corals in the Penghu Archipelago, Taiwan. *Polydora villosa* builds burrows inside the coral skeleton and secretes mucus to form fragile mud-tubes in the burrows with openings projecting approximately 2 mm above the coral surface. X-ray radiographs of sections of the branching-shaped corals, *Montipora angulata*, *M. hispita*, and *M. informis*, and of the massive-shaped corals, *Porites lichen*, *P. lobata*, and *P. lutea*, have revealed that the burrows consist of 2 parts: a narrow, U-shaped passage and several straight, elongated tunnels. The U-shaped passages are located at the dead ends of the burrows, and the straight elongated tunnels are at the free, open end. Longitudinal and transverse sections of the burrows reveal that the straight elongated tunnels are encircled by a thick layer of calcium carbonate, but the U-shaped passages are not. The U-shaped passages directly intersect the growth direction of the corals, and the surfaces of the passages show traces of etching as examined under a scanning electron microscope. This suggests that the U-shaped passages are formed initially by *Polydora villosa* through active boring into the coral. At a later stage, the elongated tunnels are formed when the corals grow concurrently with the tube construction of *Polydora villosa*, indicating that the formation of burrows is passive at this time. The straight elongated tunnels are simple in *Porites*, but are branched in *Montipora*, whereas tunnel lengths are shorter in *Porites* than in *Montipora*. The branched morph of *Montipora* is often inhabited by *Polydora villosa*. We speculate that interactions between the coral *Montipora* and the worms may result in modification of the growth form of *Montipora* from an encrusting or columnar morph to a branched one. In contrast, the shape of *Porites* is not affected by the worm and retains its original massive form.

Key words: Polydorid polychaete, Burrow morphology, Coral.

Boring polychaete species are found within the eunicids, lumbrinerids, dorvilleids, spionids, cirratulids, and sabellids (Hutchings 1986, Cairns and Zibrowius 1997). Some species are efficient bioeroders and affect the infrastructure and strength of coral reefs by removing calcium carbonate as they excavate burrows in corals or coralline algae (White 1979, Bailey-Brock and Hartman 1987, Cairns and Zibrowius 1997).

Members of the spionid genera, *Polydora* and *Dipolydora*, are commonly associated with calcareous substrates and are considered either commensal with corals (Okuda 1937, Light 1970a) or erosive to corals and coralline algae (Hartman 1954, Lewis

1998). Many polydorids are able to bore into the shells of bivalves and gastropods, whereas *Dipolydora armata* bores into the hydrozoan *Millepora complanata* (Lewis 1998). There are various types of burrows, such as surface fouling burrows, U-shaped burrows, complex burrows, and mud-blisters. The U-shaped type has 2 parallel, closed arms and is formed by penetrating the structure of shells (Blake and Evans 1973). In terms of the boring processes, Blake and Evans (1973) summarize 3 mechanisms in *Polydora*: a chemical mechanism, where special glands secrete acid solutions to dissolve substrates; a mechanical mechanism, where the enlarged modified setae on the 5th setiger

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abrade the substrates; and a combined chemical and mechanical mechanism. However, direct evidence as to how *Polydora* bores into shells is still lacking (Blake and Evans 1973, Sato-Okoshi and Okoshi 1993).

Five polydorid species have been reported to bore into corals. They are *P. alloporis* (Light 1970a), *P. armata* (= *Dipolydora armata*) (Okuda 1937, Woodwick 1964, Blake 1996, Lewis 1998), *P. pacifica* (Takahashi 1937), *P. tridenticulata* (= *Dipolydora tridenticulata*) (Woodwick 1964, Blake 1996), and *P. wobberi* (Light 1970b). Among these, *P. alloporis* forms paired burrow-openings in the coenosteum of the hydrocoral *Allopora californica*; *P. wobberi* builds a U-shaped burrow in the white gorgonian *Lophogorgia* sp.; and *D. armata* forms complex burrows in the hydrocoral *Millepora complanata*. The remaining polydorids have not been studied in detail with regard to their burrow morphology, fine architecture, and boring mechanisms.

Polydora villosa is a new species and is found only in living coral colonies (Radashevsky and Hsieh submitted). In the shallow fringe coral reefs of the Penghu Archipelago, located in the middle of the Taiwan Strait, this polydorid species infects 29 out of 40 coral species examined. The infection rates of coral colonies vary with species and range from 15% to 100%. Infectious densities on the coral colonies range from 0.4 to 9 polydorid individuals/100 cm² (Liu 1996). Colonies of the corals, *Favites abdita*, *Porites lichen*, *Porites lobata*, and *Porites lutea*, are the most frequently infected, with 10% to 24% of their colonies discovered to have the polydorids (Liu 1996). *Polydora villosa* builds burrows inside the coral skeleton but with mud-tubes lining the burrows which extend approximately 2 mm above the coral surface. Since the presence of the burrows in the coral skeletons may weaken the strength of the coral skeletons, the purpose of our present study was to examine both the burrow morphology and fine architecture of the burrows of *Polydora villosa* in the corals *Montipora* and *Porites*.

MATERIALS AND METHODS

Polydora villosa is a newly described species (Radashevsky and Hsieh submitted). The type specimens are deposited at the Institute of Zoology, Academia Sinica, Taiwan. This polydorid species inhabits a variety of corals including the branched *Montipora angulata* Lamarck 1816, *M. hispita* Dana 1846, and *M. informis* Bernard 1897, and the massive *Porites lichen* Dana 1846, *P. lobata* Dana 1846,

and *P. lutea* Edwards and Haime 1860. These coral species were collected from Chin Bay (23°31'48"N; 119°33'E) of Penghu by scuba diving between May 1994 and April 1995. Coral colonies were cut into platy pieces of 2-3 mm in thickness with a grinding machine or a multi-drilling machine.

The general morphology of the burrows of *Polydora villosa* in coral pieces was examined by X-ray (Softex Coflex CMB-2). The inner surface of the burrows was exposed by grinding, dried in air, and then examined with a dissecting microscope. Coral pieces of *Montipora* and *Porites* containing the worm burrows were also coated with gold by the standard procedure, and then examined under a scanning electron microscope (Hitachi S-2500).

RESULTS

Polydora villosa builds burrows inside coral skeletons and secretes mucus to form fragile mud-tubes in the burrows with openings projected approximately 2 mm above the coral surface (Figs. 1, 12). X-ray radiographs and light microscopy show that the burrows of *Polydora villosa* are located inside the skeletons of living corals of *Montipora* and *Porites* and consist of 2 parts: a narrow U-shaped passage, and 2 or more straight, elongated tunnels (Figs. 2, 13). The U-shaped passage is at the dead end of the burrow, and the straight, elongated tunnel has opening to the outside (Figs. 2, 3, 13, 14). The following descriptions of the morphology and fine structure of the U-shaped passage are mainly based on worm burrows found in the coral *Porites*, whereas those of the elongated tunnels are from burrows in the coral *Montipora*.

U-shaped passage

The U-shaped passage is about 5 to 12 mm in length and consists of 2 arms which are parallel and separated by a very thin wall (Figs. 4, 5). The U-shaped passages are parallel to or inclined with growth bands of the corals, and thus they interrupt the depositional infrastructure of the coral skeleton (corallites and coenosteum) (Figs. 4, 5). The growth direction (depositional direction) of the corals is directly intersected (Fig. 4), indicating that the coral skeleton was already formed before the polydorids built the passages.

The inner surface of the U-shaped passages is characterized by exposed coral skeleton (Figs. 4-6) with no mud. The fine architecture of the surface of passages differs from that of the adjacent coral

skeleton. The wall of the U-shaped passages consists of broken and fragmented rod-shaped crystals (Figs. 7, 8); however, the intact coral skeleton consists of smooth, straight, and pointed rod-shaped crystals (Figs. 9, 10), indicating that erosion has occurred in the passage. The broken, fragmented features differ from those caused by a grinding process, which produces powder-like particles on the surface (Fig. 11). Such comparisons show that the characteristics of the surface of the U-shaped passages are not artifacts resulting from the grinding process.

Elongated tunnels

The straight, elongated tunnels extend from the arms of the U-shaped passages at various angles

and are simple in *Porites* (Fig. 2), but branched in *Montipora*, and are located at the center of the branches in *Montipora* (Fig. 13). In general, lengths of elongated tunnels are shorter in *Porites* (5 to 20 mm in length) than in *Montipora* (up to 50 mm in length). Hollow chambers filled with mud sometimes occur at the tips of the elongated tunnels in *Montipora*, whereas other chambers appear in the lower portions of the coral (Fig. 13). The burrow openings are scattered on the surface of *Porites* (Fig. 1), whereas they are located on the central tips of the terminal branches of *Montipora* (Figs. 12, 13). Coral corallites grow around the openings of the burrows in both coral species (Figs. 3, 14).

The elongated tunnels run perpendicular to the growth bands of the corals, and are parallel to the

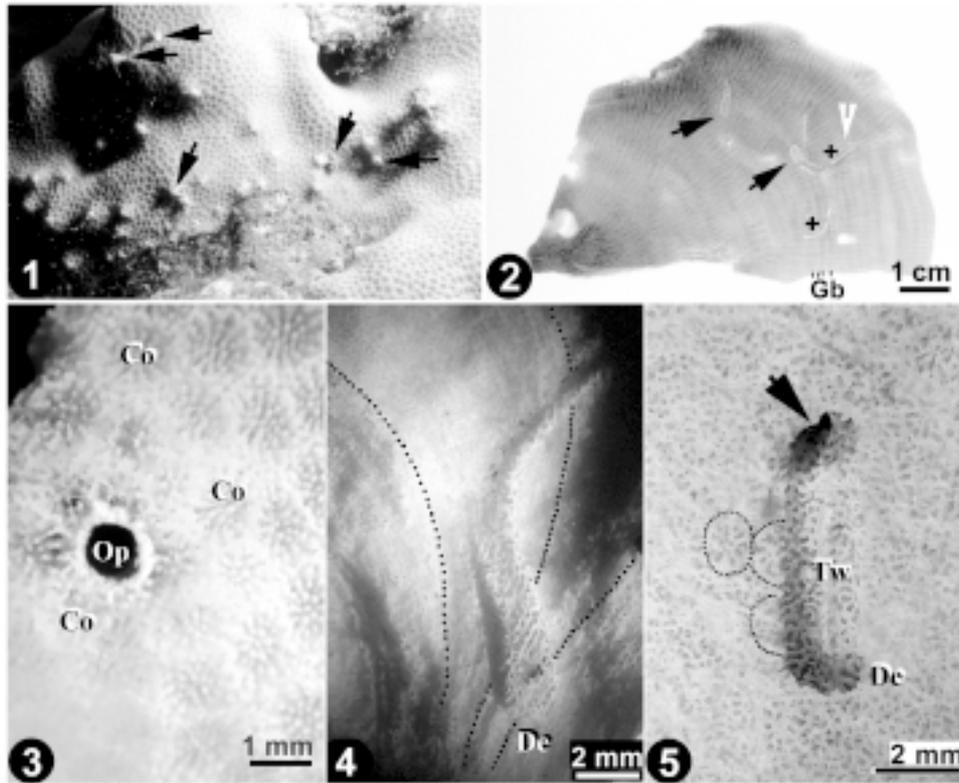


Fig. 1. Burrow openings (arrows) of *Polydora villosa* on the surface of the coral *Porites*.

Fig. 2. X-ray radiograph of the skeleton of *Porites* showing the burrows of *Polydora villosa*. Notice the intersections between the U-shaped passage (arrows) and the coral growth bands (Gb). The elongated tunnel (arrowhead) is perpendicular to the coral growth bands and is parallel to the depositional direction of the coral skeleton. The coral growth bands are disrupted when they meet the tunnels (crosses).

Fig. 3. Burrow opening of *Polydora villosa* on the surface of the coral *Porites*. Co: corallites, Op: burrow opening.

Fig. 4. Longitudinal section of the U-shaped passage of *Polydora villosa* in the skeleton of *Porites* sp. Notice that the U-passage cuts across the depositional direction (dotted lines) of the coral skeleton. De: dead end of the U-passage.

Fig. 5. Longitudinal section of the U-passage of *Polydora villosa* showing a thin wall (Tw) in the coral *Porites* sp. Notice the intact corallite (full stippled circle) which is adjacent to the worm's U-passage and the destroyed corallites (half stippled circles) which are cut through by a worm's U-passage. The coral growth bands run horizontally with the section plane. Elongated tunnels are extended from the open end of the U-passage (arrow). De: dead end of the U-passage.

direction of skeletal deposition. At the elongated tunnels in *Porites*, the direction of the coral growth bands changes where the bands meet the tunnels (Fig. 2), whereas in *Montipora*, the coral growth bands encircle the longitudinal axis of the tunnels (Fig. 15). In both cases, the coral skeleton is not intersected by the elongated tunnels. In addition, the layer of calcium carbonate lining the burrows grades into the coral skeleton proper (Figs. 15, 16), and the texture of the lining layer is similar to that on the basal plates of corals. These characteristics indicate that the coral skeleton is built at the same time as when the elongated tunnels are formed.

The inner surface of the straight, elongated tun-

nels of *Polydora villosa* differs from that of a U-shaped passage in which the former is coated with a secondary layer of calcium carbonate (Figs. 15, 16). This CaCO_3 layer is thicker in *Montipora* than in *Porites* (0.29 to 0.59 vs. 0.06 to 0.12 mm in thickness). The surface of the elongated tunnels (the surface of CaCO_3 lining) consists of numerous tightly packed fusiform crystals of calcium carbonate (Figs. 17-19).

DISCUSSION

The present results reveal that the spionid

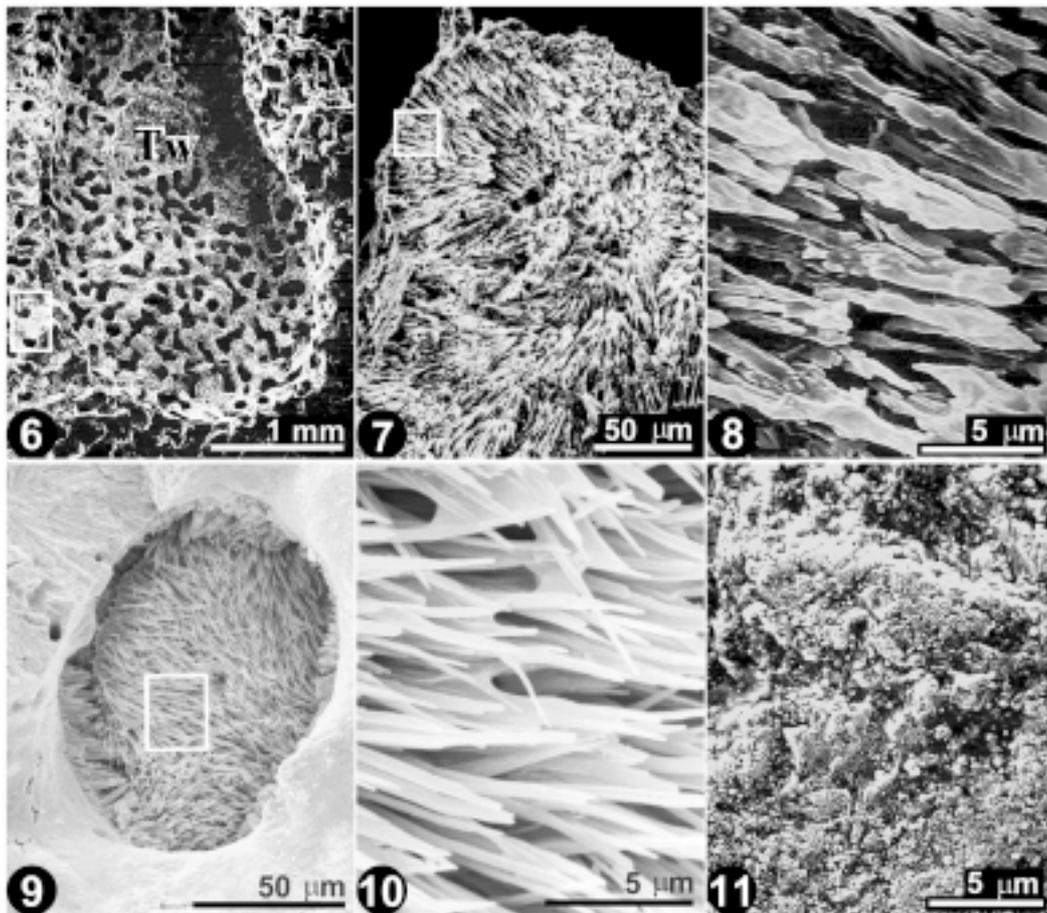


Fig. 6. SEM at low magnification showing surface structures of the U-shaped passage of *Polydora villosa* in *Porites*. Tw: thin wall. Enlargement of insert is shown in Fig. 9.

Fig. 7. SEM high magnification of Fig. 6 showing the loosely packed crystals within the coral skeleton of the coral *Porites*. Enlargement of insert is shown in Fig. 8.

Fig. 8. SEM high magnification of Fig. 7 showing etched, broken, and fragmented coral crystals of *Porites*.

Fig. 9. SEM at low magnification showing fine structure of intact coral skeleton of *Porites* adjacent to a U-shaped passage of *Polydora villosa*. Enlargement of insert is shown in Fig. 10.

Fig. 10. SEM high magnification of Fig. 9 showing complete and pointed rod-like crystals.

Fig. 11. SEM photograph revealing the effects of machine grinding on the surface of the coral skeleton adjacent to a U-shaped passage of *Polydora villosa* in the coral *Porites*. Notice many small granular particles on the surface.

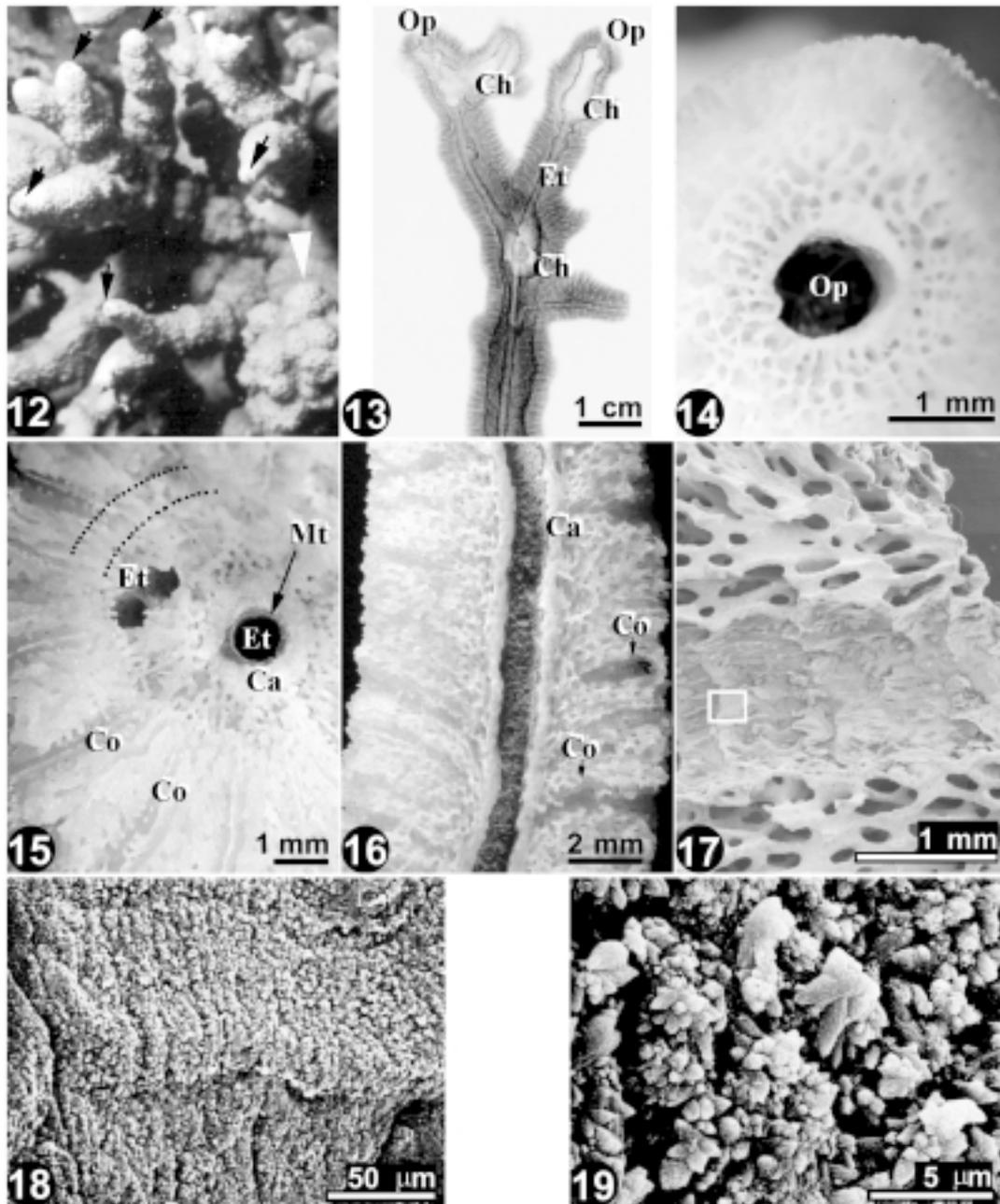


Fig. 12. Burrow opening (arrows) of *Polydora villosa* on branches of *Montipora*. Notice that *Montipora* is not branched (arrowhead) when it is not infested by polydorids.

Fig. 13. X-ray radiograph of the skeleton of *Montipora* showing the straight, elongated tunnels (Et) of *Polydora villosa*. The tunnels are situated on the central axis of the coral skeleton with several openings (Op) at the tips of the coral branches. Ch: mud chamber.

Fig. 14. Burrow opening of *Polydora villosa* on the branch tip of the coral *Montipora*. Op: burrow opening.

Fig. 15. Cross-section of elongated tunnels of *Polydora villosa* in the coral *Montipora* showing an old (Et, right) and 2 newly branched (Et, left) tunnels. The large, long cavities with corallites (Co) are indicative of the pre-existence of polyps. The dotted lines at the upper left corner depict the direction of the coral growth bands. Mt: mud tube.

Fig. 16. Longitudinal section of elongated tunnel of *Polydora villosa* in the coral *Montipora* showing the layer of CaCO_3 (Ca) lining the tunnel. Co: corallite.

Fig. 17. Surface structures of elongated tunnel of *Polydora villosa* in *Montipora* shown by SEM at low magnification. Enlargement of insert is shown in Fig.18.

Fig. 18. SEM high magnification of Fig. 17 showing the surface of the CaCO_3 layer on the elongated tunnel of *Polydora villosa* in the coral *Montipora*.

Fig. 19. SEM high magnification of Fig. 18 showing numerous fusiform clusters of CaCO_3 crystals of the coral *Montipora*.

Polydora villosa inhabits living corals in U-shaped passages and straight elongated tunnels, and that burrows are formed in 2 stages. In the initial stage, the spionid bores into the coral skeleton to form a U-shaped passage; then, at the latter stage, the growing coral deposits its skeleton using the worm's mud-tubes as a template, thus forming elongated tunnels. It is at the latter stage that interactions occur between the polydorids and the corals which modify the growth form of the coral. The changes are more distinct in the coral *Montipora* than in the coral *Porites*. Although the burrows in the 2 different coral genera exhibit a great deal of common morphology, some structures are distinctive and reflect characteristics of the host coral species.

U-shaped passage

The U-shaped passages of *Polydora villosa* in coral are similar to those made by other *Polydora* species in molluscan shells (Blake and Evans 1973). However, burrows in molluscan shells lack elongated tunnels, and grow into multiple U-shaped complexes (Blake and Evans 1973). Since the molluscan mantle secretes calcium carbonate materials and deposits them on the outer margins of the shells, not on the tops of old shells where *Polydora* lives, the openings of the polydorid burrows are not sealed by the mollusks, and thus elongated tunnels are not formed.

The fine architecture on the inner surface of the U-shaped passages exhibits characteristics of abrasion made by *Polydora villosa*. Another *Polydora* species, *P. websteri*, mainly uses a chemical mechanism (Haigler 1969), and *P. ciliata* larvae use both chemical and mechanical mechanisms (Hannerz 1956) to bore into calcareous substrates. The rough characteristics, such as abrasion pitting and etching seen in the inner surface of the U-shaped passages in *Polydora villosa* are similar to those found in coral skeletal crystals that have been dissolved by hydrochloric acid, acetic acid, or EDTA (Williams and Margolis 1974). Traces of scratches of the type reportedly made by the setae of 3 species of *Polydora* by boring into scallop and oyster shells (Sato-Okoshi and Okoshi 1993) were not found in the present study. We speculate that *Polydora villosa* secretes acids to erode the coral skeleton. However, it also can not be ruled out that the roughness is caused by the coral's recrystallization rather than by the worm's etching. It has been reported that in foraminifera, symbiotic algae change their respiratory and photosynthetic activities and thus result in alteration of original crystallization (MacIntyre and Reid 1995

1998).

When adults of *Polydora villosa* were extracted from their tubes in the laboratory, the worms could not bore into coral substrates again (authors' pers. observ.), indicating that the adults lack boring ability. The larvae or post-larvae of *P. ciliata* and *P. websteri* are able to bore into molluscan shells (Hemple 1957, Haigler 1969), and juveniles of *P. socialis* also can bore into a shell, excavate a burrow, and construct a mud tube (Blake 1969). In *Polydora villosa*, it is likely that the larvae settle on the corals, then metamorphose into juveniles, and finally bore into the coral and form the initial U-shaped passage.

The U-shaped passage is common in polydorid species living in corals and molluscan shells (Davis 1967, Evans 1969). The passages are characterized by an extension of a pair of parallel, closely adjacent tunnels. During the boring period, *Polydora* might curve its body, allowing minimum exposure to sea water, thus preventing the acid from being diluted. Forming a narrow burrow also reduces risk, since the larger the burrow is made, the longer the individuals are exposed to danger such as predation or stings by coral. Another advantage is that because the worms live in hard substrates, a U-shaped burrow allows them to turn around inside the coral and allows branched tunnels to open on the surface of the corals, thereby, improving the circulation within the burrows or increasing feeding sites, as is seen in many tube dwelling species like terebellids (Hsieh 1994) and chaetopterid polychaetes (Lutz 1985).

Elongated tunnels

There are no reports that *Polydora* is able to secrete calcium carbonate. However, the polydorids can collect calcium carbonate debris to fill their burrows as seen in *P. concharum* and *P. websteri* (Evans 1969). The calcium carbonate layer of the elongated tunnels in *Polydora villosa* is not structured the same as the calcium carbonate debris, but rather, its morphology and texture are similar to those of the basal plates of the corals *Porites* and *Montipora*.

The process of coral growth includes extension and accretion. The lower epidermis of coral polyps produces calcium carbonate skeleton continuously in the upward and outward directions. Some of the skeletons are cemented to new substrates as basal plates from which the polyps grow. Mud collected and cemented by the worms in the burrows may serve as a mold so that the skeletal materials are deposited, and basal plates are formed. In the field, a colony of the coral *Acropora* growing over a rope

produced a layer of basal plate. The coral *Montipora* also produces a basal plate that covered a toothpick which we used to mark the growth of the colonies. These observations support our conclusion that the calcium carbonate layer is produced by the corals, further indicating that the straight, elongated tunnels are formed by the coral in response to the presence of the polydorid.

Association between worm burrows and corals

In the present study, branched portions are mainly found to harbor the polydorids in *Montipora* (author's pers. observ., see Fig. 12). In addition, mud chambers are present at the branched regions of the worm's elongated tunnels, suggesting that *Polydora villosa* may cause the coral to branch out at the regions where the coral polyps are smothered by too much silt, and consequently, the coral growth direction is altered. This kind of modification of coral growth form due to polychaete inhabitation is not uncommon. For example, the syllid polychaete *Typosyllis* sp. makes its burrows that highly modify the morphology of the faviid corals, resulting in numerous grooves and tubes on the surface of the coral (Randall and Eldredge 1976). In this case, the syllids induce the corals to secrete basal plate-like structures. Spiny projections occur in the calcareous hydrozoan *Millepora complanata* as the coral host responds to the infestation of the polydorid *Dipolydora armata* (Lewis 1998). Another quite common phenomenon is found when crustaceans bore into live corals and the polyps deposit additional skeletal material to seal off the borer (Cairns and Zibrowius 1997).

The associations between the spionid *Polydora villosa* and the corals *Montipora* and *Porites* differ in several features. First, the presence of *Polydora villosa* may modify the morphology of *Montipora* from encrusting or columnar morphs to branched ones. However, the polydorids do not affect the morphology of *Porites* which has a slow growth rate and a more compact skeleton (Liu 1996). Second, since the burrows in *Montipora* are branched, 1 burrow may have multiple openings in *Montipora*, whereas it has only 2 in *Porites* (Liu 1996). Third, the differences in the growth rates of the corals may also cause the elongated tunnels to be longer in *Montipora* than in *Porites*. Fourth, the secondary CaCO₃ layer lining the elongated tunnels of the burrows is thicker in *Montipora* than in *Porites*. In brief, these differences can be attributed to different responses of coral host species.

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多毛類才女蟲在表孔珊瑚和微孔珊瑚內之蟲穴結構

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在澎湖青灣海域的珊瑚礁，管棲性的青灣才女蟲 (*Polydora villosa*) 棲息在活珊瑚體內，開口突出於珊瑚表面。珊瑚骨骼切片及 X-rays 照相顯示，團塊形微孔珊瑚 (*Porites* spp.) 和樹枝形表孔珊瑚 (*Montipora* spp.) 內的蟲穴可分成兩部份：U 形的蟲槽和直條形的延伸蟲道。由縱切和橫切的骨骼標本顯示，延伸蟲道有一層碳酸鈣壁包覆泥質蟲管，但 U 形蟲槽只有珊瑚的網狀骨骼。由 U 型蟲槽和延伸蟲道周圍的珊瑚骨骼結構及鈣質骨骼堆積的連續性和同質性的分析，以及在解剖顯微鏡和電子顯微鏡下的觀察顯示，U 型蟲槽具有蝕刻的痕跡，研判 U 型蟲槽是蟲體鑽入珊瑚所形成，而延伸蟲道則是珊瑚附著在蟲體所築的泥質蟲管上生長所形成。此外，蟲穴的構造在不同的珊瑚種類上亦有差異，包括延伸蟲道的分枝數目，延伸蟲道的長度及碳酸鈣壁的厚薄等。這些差異是導因於宿主珊瑚種類的不同。

關鍵詞：才女蟲多毛類，蟲穴形態，珊瑚。

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