

## Species of the Genus *Polydora* (Polychaeta, Spionidae) from the Middle Kurile Islands

By

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**Abstract** Five previously described *Polydora* species, *Polydora* sp., *P. quadrilobata* JACOBI, *P. alborectalis* RADASHEVSKY, *P. curiosa* RADASHEVSKY and *P. trilobata* RADASHEVSKY, are reported from the Middle Kurile Islands. Adult morphology and ecology of a new species, *Polydora vulcanica*, are described. The species inhabits mud tubes in the intertidal and subtidal zones. Large settlements of *P. vulcanica* (with density of up to 100,000 individuals per 1 square metre) were recorded in the craters of two volcanoes on the Middle Kurile Islands. It occurs also near southeastern Kamchatka and off the Shumagin Islands, the Aleutian Islands.

Unusual marine ecosystem in the flooded crater of Ushishir Volcano (Kraternaya Bight of Yankich Island, the Kurile Islands) which has arisen and is functioning under the influence of gaso-hydrothermal vents was recently found and investigated during expeditions of the Institute of Marine Biology, Vladivostok (IMBV) (review: ZHIRMUNSKY & TARASOV, 1990; Shallow-water . . . , 1991). Macrobenthos from the intertidal and subtidal zones of Kraternaya Bight is described by KOSTINA (1991) and KAMENEV (1991). The polychaete species off the coast of Yankich Island are described by BUZHINSKAJA (1990).

In June–July 1988 the author took part in an expedition of the IMBV to Kraternaya Bight organized aboard the R/V “Berill”. Besides the bight, the shallow-water zone off adjacent islands of the Middle Kuriles, Simushir Is., Ketoi Is., Rasshua Is., and Matua Is., were also investigated. In the present paper, six *Polydora* species (Polychaeta, Spionidae) are reported from the region examined. Of these, three species are reported from Kraternaya Bight, and one new species is described. All the species are widely distributed; there are no endemic species.

Subtidal samples were obtained by the author with SCUBA. Spionid collection deposited in the IMBV, and additional materials from Kraternaya Bight provided by Vladimir I. KHARLAMENKO (IMBV), from southeastern Kamchatka provided by Alexander V. RZHAVSKY, Pacific Institute of Geography, Petropavlovsk-Kamchatsky, and from the Aleutian Islands kindly loaned by Nora R. FOSTER, University of Alaska Museum, Fairbanks (UAMF), were also examined. The collection localities mentioned in the text are shown in Fig. 1.

The type and representative materials are deposited in the IMBV, in the Zoological Institute, St. Petersburg (ZISP), in the National Science Museum (Nat. Hist.),

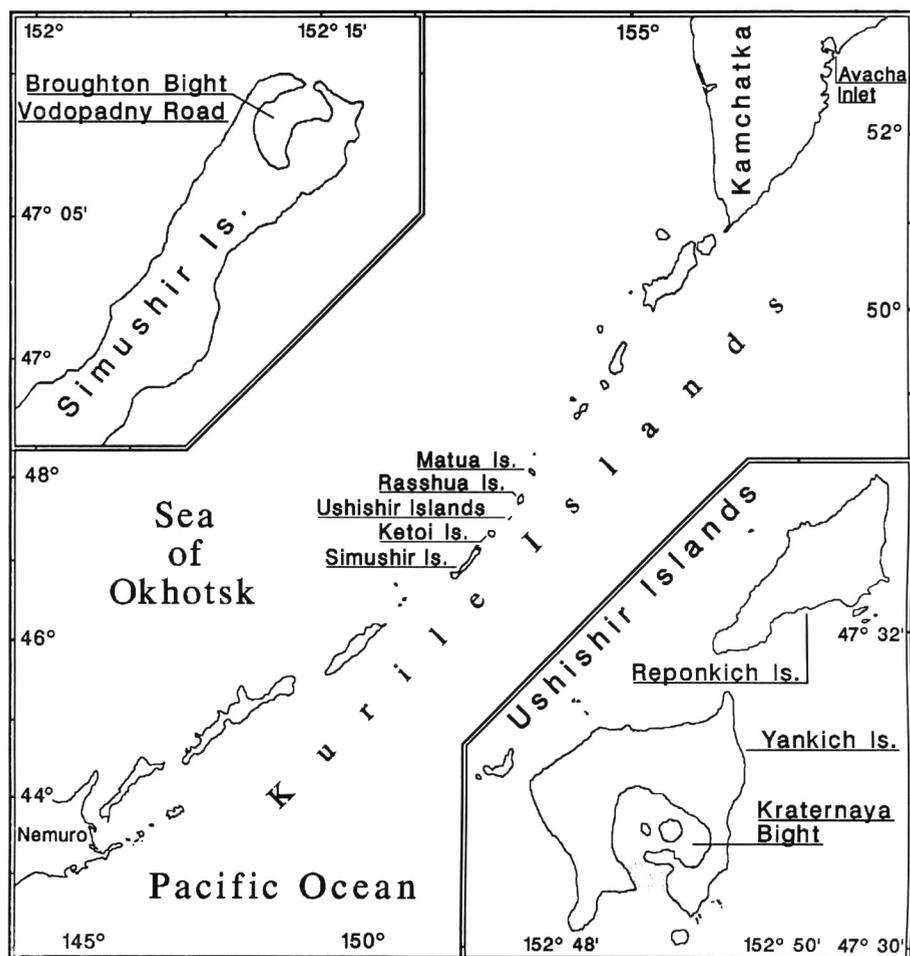


Fig. 1. Map showing collection localities mentioned in the text.

Tokyo (NSMT), and in the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

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*Polydora* sp.

*Polydora ciliata*: ANNENKOVA, 1938, p. 177; MORI *et al.*, 1975, pp. 371–380; RADASHEVSKY, 1986, pp. 36–43.

*Polydora ciliata ciliata*: USCHAKOV, 1955, p. 271, fig. 94 D; CHLEBOVITSCH, 1961, p. 200.

*Polydora* cf. *ciliata*: RADASHEVSKY, 1993, p. 12; MANCHENKO & RADASHEVSKY, 1993, p. 543.

Not *Polydora ciliata*: JOHNSTON, 1838, pp. 67–68, pl. 3, figs. 1–6.

*Material examined.* *Polydora* cf. *ciliata*: ZISP 24/48430, Broughton Bight of Simushir Is., intertidal, from shells of barnacle *Semibalanus cariosus* (PALLAS), 6 exs., coll. V. RADASHEVSKY, 12 July 1988; ZISP 25/48431, Broughton Bight of Simushir Is., 5–10 m, from shells of gastropod *Fusitriton oregonense* (REDFIELD), 10 exs., coll. V. RADASHEVSKY, 12 July 1988; Vodopadny Road of Simushir Is., 10 m, from coralline algae encrusting boulders, 2 exs., coll. V. RADASHEVSKY, 13 July 1988 (material not preserved). Extensive author's material from the North West Pacific.

*Description.* Specimens up to 21 mm long and 0.85 mm wide for 115 segments. Prostomium incised or nearly rounded anteriorly. Up to four eyes present or eyes absent. Caruncle continuing posteriorly to middle or to posterior end of setiger 2. Nuchal tentacle absent. Setiger 1 with only neurosetae. Posterior specialized noto-setae absent. Neuropodial bidentate hooks from setiger 7, with constriction on shaft, not accompanied by capillary setae. Setiger 5 with ventral and dorsal tufts of capillaries. Heavy spines falcate, with large lateral accessory tooth. Branchiae from setiger 7, being large at first, absent from posterior half of body or up to the caudal portion. Pygidium disc-like or cup-shaped, with dorsal gap or incision. Intertidal specimens with darkly pigmented palps, anterior and posterior ends, while subtidal specimens without black pigmentation.

*Remarks.* *Polydora* sp. was previously reported from the Far Eastern seas as *Polydora ciliata* (JOHNSTON, 1838) by many authors. It has been shown, however, that *Polydora* sp. and *P. ciliata* are sibling species differing in ecological characters (MANCHENKO & RADASHEVSKY, 1993). The first of them bores into calcareous substrata, while the latter inhabits mud tubes in sediment. Further investigations are required to clarify relationships between them and to identify *Polydora* sp.

### *Polydora quadrilobata* JACOBI, 1883

*Polydora quadrilobata* JACOBI, 1883, p. 3, 2 pls. — RADASHEVSKY, 1993, pp. 12, 18, fig. 9, synonymy.

*Material examined.* *Polydora quadrilobata*: ZISP 42/48427, between two islets of Kraternaya Bight, Yankich Is., 15 m, mud+shells, 3 exs., coll. V. RADASHEVSKY, 2 July 1988; ZISP 43/48428, southwestern part of Kraternaya Bight, 5–7 m, Yankich Is., muddy bottom, 30 exs., coll. V. RADASHEVSKY, 19 July 1988; ZISP 44/48429, southwestern part of Kraternaya Bight, Yankich Is., 10 m, muddy bottom, 17 exs., coll. V. RADASHEVSKY, 22 July 1988.

*Remarks.* In Kraternaya Bight, *P. quadrilobata* has been found subtidally together with *P. vulcanica* (see below). The population density of the species amounted from several ten to several hundred individuals per 1 square metre.

*Distribution.* Arctic Europe and Asia: from Baltic Sea and English Channel to the South Kurile Islands and Peter the Great Bay of the Sea of Japan; west coast of North

America: from the Aleutian Islands south to San Pedro Channel, southern California; east coast of North America: from Hudson Bay south to New England.

***Polydora alborectalis* RADASHEVSKY, 1993**

*Polydora alborectalis* RADASHEVSKY, 1993, pp. 12, 39, figs. 20–21.

*Material examined.* *Polydora alborectalis*: IMBV 3/12186, Broughton Bight of Simushir Is., 15 m, from shell of jingle shell *Pododesmus macrochisma* (DESHAYES), 6 exs., coll. V. RADASHEVSKY, 12 July 1988.

*Distribution.* Mainland coast of the Sea of Japan: from Chikhachev Bay south to Peter the Great Bay; Moneron Is.; Sakhalin Is.; the Kuriles; Sea of Okhotsk; southeastern Kamchatka; Bering Sea.

***Polydora trilobata* RADASHEVSKY, 1993**

*Polydora trilobata* RADASHEVSKY, 1993, pp. 12, 36, figs. 17 e–j, 18–19.

*Material examined.* *Polydora trilobata*: ZISP 4/48424, southwestern part of Kraternaya Bight, Yankich Is., 10 m, from shells of barnacle *Balanus rostratus* HOEK, 15 exs., coll. V. RADASHEVSKY, 30 June 1988; ZISP 5/48425, Broughton Bight of Simushir Is., intertidal, from shells of barnacle *Semibalanus cariosus*, 20 exs., coll. V. RADASHEVSKY, 12 July 1988; ZISP 6/48426, Broughton Bight of Simushir Is., 10 m, from shells of gastropod *Fusitriton oregonense* occupied by hermit crab *Pagurus* sp., 10 exs., coll. V. RADASHEVSKY, 12 July 1988.

*Distribution.* Mainland coast of the Sea of Japan: from Chikhachev Bay south to East Korean Bay; Oki Islands in the Sea of Japan; South Sakhalin; the Kuriles; southeastern Kamchatka; Bering Sea.

***Polydora curiosa* RADASHEVSKY, 1994**

*Polydora curiosa* RADASHEVSKY, 1994, pp. 121–136, figs. 2–5.

*Material examined.* *Polydora curiosa*: ZISP 10/48419, Vodopadny Road of Simushir Is., 10 m, from coralline algae encrusting boulders, 2 exs., coll. V. RADASHEVSKY, 13 July 1988.

*Distribution.* The Kuriles, from Simushir Is. south to Shikotan Is.; South Sakhalin; Moneron Is.; ? Vostok Bay of the Sea of Japan.

***Polydora vulcanica* sp. nov.**

(Figs. 2–3)

*Polydora* sp.: BUZHINSKAJA, 1990, p. 20; ZHIRMUNSKY & TARASOV, 1990, p. 100; KAMENEV, 1991; KOSTINA, 1991.

*Type material.* *Polydora vulcanica*: the holotype, ZISP 1/48420, southeastern

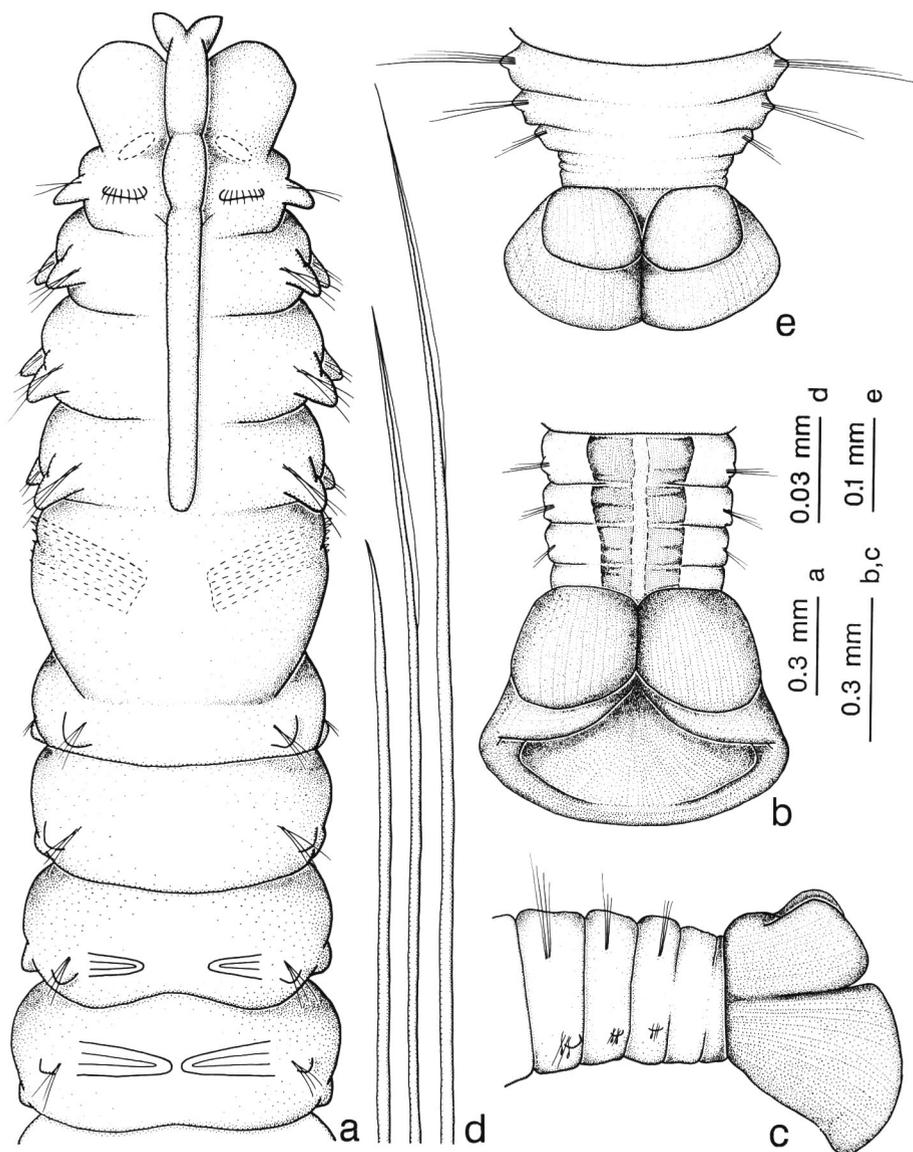


Fig. 2. *Polydora vulcanica* sp. n. — a, Anterior end, dorsal view, palps removed; b, posterior end, dorsal view; c, same, lateral view; d, unwinged and winged capillaries from posterior notopodia; e, posterior end, dorsal view; a-d, holotype; e, paratype IMBV 6/12194.

part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, coll. V. RADASHEVSKY, 21 July 1988; 22 paratypes, ZISP 2/48421, the same locality, coll. V. RADASHEVSKY, 27 June 1988; 10 paratypes, ZISP 3/48422, the same locality, coll. V. RADASHEVSKY, 21 July 1988; 16 paratypes, ZISP 4/48423, southwestern part of Kraternaya

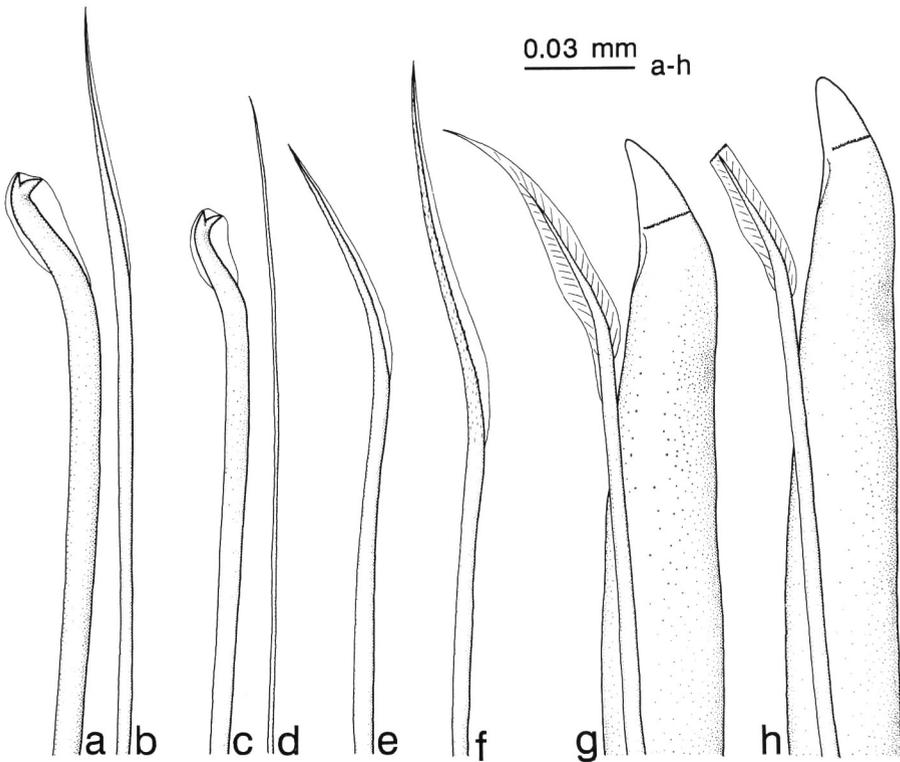


Fig. 3. *Polydora vulcanica* sp. n. — a, Neuropodial bidentate hooded hook of setiger 7; b, accompanying winged capillary neuroseta of setiger 7; c, neuropodial bidentate hooded hook from posterior setiger; d, accompanying unwinged capillary neuroseta from posterior setiger; e, neuroseta of setiger 5; f, notoseta of setiger 5; g-h, heavy spines and pennoned companion setae of setiger 5.

Bight, Yankich Is., 3 m, muddy bottom, coll. V. RADASHEVSKY, 4 July 1988; 24 paratypes, anterior ends, IMBV 1/12185, southeastern part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, coll. V. RADASHEVSKY, 27 June 1988; 10 paratypes, IMBV 2/12190, southeastern part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, coll. V. RADASHEVSKY, 21 July 1988; 8 paratypes, IMBV 3/12191, southwestern part of Kraternaya Bight, Yankich Is., 3 m, muddy bottom, coll. V. RADASHEVSKY, 4 July 1988; 13 paratypes, IMBV 4/12191, northern part of Kraternaya Bight, Yankich Is., 2–3 m, muddy bottom, coll. V. RADASHEVSKY, 22 July 1988; 34 paratypes, IMBV 5/12193, southeastern part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, coll. V. KHARLAMENKO, 25 June 1990; 1 paratype, IMBV 6/12194, southeastern part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, coll. V. KHARLAMENKO, 25 June 1990; many paratypes, IMBV 7/12195, southeastern part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, coll. V. KHARLAMENKO, 1 September 1992; 10 paratypes, NSMT-Pol. P 348, southeastern part of Kraternaya

Bight, Yankich Is., low intertidal, muddy sand, coll. V. RADASHEVSKY, 27 June 1988; 9 paratypes, USNM 148721, southeastern part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, coll. V. RADASHEVSKY, 27 June 1988.

*Representative material.* *Polydora vulcanica*: IMBV 8/12196, northern part of Kraternaya Bight, Yankich Is., 2–3 m, muddy bottom, many exs. in tubes, coll. V. RADASHEVSKY, 22 July 1988; IMBV 9/12197, southeastern part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, many exs. in tubes, coll. V. KHARLAMENKO, 1 September 1992; IMBV 10/12198, southeastern part of Kraternaya Bight, Yankich Is., 2.5–3 m, on surface of algae, many exs., coll. G. KAMENEV, 27 August 1986; IMBV 11/12199, southeastern part of Kraternaya Bight, Yankich Is., 2.5–3 m, gravel, many exs., coll. G. KAMENEV, 27 August 1986; IMBV 12/12200, southeastern part of Kraternaya Bight, Yankich Is., 6 m, gravel, 1 ex., coll. G. KAMENEV, 27 August 1986; IMBV 13/12201, eastern part of Kraternaya Bight, Yankich Is., 2 m, gravel, 1 ex., coll. G. KAMENEV, 30 August 1986; IMBV 14/12202, southeastern part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, many exs. in tubes, coll. V. RADASHEVSKY, 27 June 1988; IMBV 15/12203, southeastern part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, 5 exs., coll. E. KOSTINA, 3 July 1988; IMBV 16/12204, southeastern part of Kraternaya Bight, Yankich Is., low intertidal, muddy sand, many exs. in tubes, coll. O. KUSSAKIN, 26 August 1992; IMBV 17/12205, Broughton Bight of Simushir Is., 2–20 m, muddy sand, 11 exs., coll. V. RADASHEVSKY, 12 July 1988; IMBV 18/12206, Zapadny Point of Avacha Inlet, southeastern Kamchatka, 6 m, muddy bottom, many exs., in poor condition, coll. V. SHALUKHANOV, 16 September 1985; IMBV 19/12207, Zapadny Point of Avacha Inlet, southeastern Kamchatka, 6 m, muddy bottom, many exs. in tubes, coll. V. SHALUKHANOV, 16 September 1985; IMBV 20/12208, Mud Bay of Popov Is., Shumagin Islands, Aleutian Islands, 55°21.00'N 160°30.00'W, intertidal, muddy sand, 5 exs., 8 May 1985; *Polydora* sp.: UAMF 1987–7, Aleutian Islands, Shumagin Islands, Popov Is., Mud Bay, intertidal, muddy sand, 36 exs., 8 May 1985.

*Description of holotype.* Specimen measuring 23 mm long and 1.25 mm wide for 155 segments. Pigmentation absent. Prostomium distinctly bifid on anterior margin. Eyes absent. Caruncle continuing posteriorly to beginning of setiger 5. Nuchal tentacle absent (Fig. 2 a). Palps extending posteriorly to setigers 12–13.

Setiger 1 with well developed noto- and neuropodial lobes, both having capillary setae. Notosetae of setigers 2–4, 6, and following setigers arranged in three successive rows, those of each succeeding row being longer. Caudally, setae of anterior row losing wings, whereas those of posterior rows winged (Fig. 2 d). Specialized posterior notosetae absent. Winged neurosetae of setigers 2–4 and 6 arranged in two rows. Neuropodial bidentate hooded hooks from setiger 7, without constriction on shaft (Fig. 3 a, c), up to 10 in series. Two or three winged capillary setae accompanying hooks to setigers 12–13 (Fig. 3 b), then disappearing, and up to three slender unwinged capillaries appearing in far posterior setigers (Fig. 3 d).

Setiger 5 larger than preceding and succeeding setigers, with ventral tuft of 7

winged setae (Fig. 3 e), semicircular row of large heavy spines alternating with penoned companion setae (Fig. 3 g–h), and bundle of 5 dorsal setae (Fig. 3 f). Heavy spines falcate, 6 in series, with thin accessory shelf around tip.

Branchiae from setiger 8 to setiger 115, small anteriorly, reaching full size on setigers 10–11 and gradually diminishing in size after setiger 17.

Pygidium with large ventral lobe and two smaller dorsal ones, of white colour (Fig. 7 b–c).

Glandular pouches from setiger 6, small at first, the largest in setigers 8–15 and then diminishing in size.

Gizzard-like structure in digestive tract present, consisting of anterior transparent muscular part and posterior white, apparently secretory part. Rectum of white colour.

*Variability.* In Kraternaya Bight, largest specimens measure 70 mm in length, 1.3 mm in width and have up to 160 segments. The caruncle extends in small individuals to the middle of setiger 3, in large individuals to the middle of setiger 4, to the anterior border or rarely to the middle of setiger 5. Pigmentation and eyes absent in small and large specimens. Palps extending posteriorly up to setiger 25. The heavy falcate spines of setiger 5 with thin accessory shelf around tip, or occasionally accessory shelf is invisible. They are up to 9 in number, but usually 5 to 7. Branchiae usually from setiger 8 and rarely from setiger 7, being small anteriorly. They are absent from the posterior third or fourth of the body. A gizzard-like structure continues for two segments, beginning in setigers 12–28. Rectum white in posterior 5–10 segments. Majority of the specimens examined was large in size with three-lobed disc-like or cup-shaped pygidium. A few small, 35–55-segmented specimens had four-lobed pygidium (Fig. 2 e). Probably, as animal grew older, two ventral lobes are united into one and the pygidium becomes three-lobed. Similar metamorphosis was described by RADASHEVSKY (1993) in *Polydora cardalia*.

Specimens from Broughton Bight, Avacha Inlet and Popov Is. have the same morphology as the ones from Kraternaya Bight.

*Ecology.* *Polydora vulcanica* constructs mud tubes in sediment, on surface of stones and algae. The upper part of the tube is smooth, up to 1 mm in width, the lower one is rough, up to 2.5 mm in width, the total tube length is up to 12 cm.

In Kraternaya Bight, the species was found in low intertidal in the southeastern part of the bight near the area of intertidal and terrestrial gaso-hydrothermal vents, and subtidally on the peripheral regions of the bight down to 20 m depth. In the intertidal zone, it covered great area forming compact mats and separate aggregations. Those aggregations were up to 50 cm in diameter, were elevated at 5 to 8 cm above the bottom surface, and had density up to 100,000 tubes per 1 square metre. They form a shelter for up to 20 small invertebrate species: actinia, nematodes, polychaetes, bivalves, crustaceans, etc., hiding between the worm tubes. In the subtidal zone, the aggregations occurred along the peripheral regions of the bight at a depth of 1 to 5 m. The great number of them accumulated around gaso-hydrothermal vents. No aggregations but separate individuals of *P. vulcanica* were found below 5 m. They

occurred together with *P. quadrilobata*.

*Polydora vulcanica* appears to be the most numerous macrobenthic species in Kraternaya Bight, so that the bight might be called *Polydora*-land.

In Broughton Bight, also representing a flooded volcano's crater, the population density of the species was up to several thousand individuals per 1 square metre at a depth of 2 to 20 m.

*Differential diagnosis.* *Polydora vulcanica* is closely related to *Polydora socialis* (SCHMARDA, 1861) and *Polydora cardalia* BERKELEY, 1927, in adult morphology and ecology. They differ, however, in that *P. socialis* and *P. cardalia* have generally straight heavy spines with subterminal enlargement in setiger 5, while *P. vulcanica* has falcate spines with accessory shelf around the tip. *Polydora vulcanica* differs from *P. cardalia* also by lesser maximal size, up to 70 mm long for 160 segments but not 115 mm long for 250 segments, lesser number of spines in setiger 5, up to 9 but not 12 or more, and by the absence of specialized needle-like capillaries in posterior notopodia. Moreover, small individuals of *P. cardalia* usually have eyes and black pigmentation on anterior segments which are absent in small individuals of *P. vulcanica*.

*Polydora socialis* was primarily described from Chile but now is reported as a widespread and probably cosmopolitan species (BLAKE, 1979). *Polydora cardalia* was reported from British Columbia, the North Bering Sea, the Chukotsk Sea, south-eastern Kamchatka, the North Kuriles and the North Japan Sea (RADASHEVSKY, 1993). The author is of the opinion that the distribution of *P. socialis* is more restricted than generally believed and that many records may prove to belong to related species. Probably, the three mentioned *Polydora* species are vicariants. They form an aggregate or group of closely related vicarious species which replace one another along the Pacific coast or coexist in some areas.

*Etymology.* The specific name is Latin for volcanic. The species is named for its abundance in volcanic habitats.

*Distribution.* Middle Kurile Islands; southeastern Kamchatka; eastern Aleutian Islands.

## References

- ANNENKOVA, N., 1938. Polychaeta of the North Japan Sea and their horizontal and vertical distribution. *Reports of the Japan Sea hydrobiological expedition of the Zoological Institute of the Academy of Sciences of the USSR in 1934*, 1: 81–230. (In Russian, with English summary.)
- BLAKE, J. A., 1979. Revision of some polydorids (Polychaeta: Spionidae) described and recorded from British Columbia by Edith and Cyril BERKELEY. *Proc. biol. Soc. Wash.*, **92**: 606–617.
- BUZHINSKAJA, G. N., 1990. Polychaetes off the coast of Yankich Island (Ushishir Islands, Kurile Islands). *Proc. zool. Inst., Leningrad*, (218): 18–35. (In Russian, with English summary.)
- CHLEBOVITSCH, V. V., 1961. The polychaetous annelids of the tidal zone of the Kurile Islands. *Explor. Far East. Seas USSR*, 7: 151–260. (In Russian.)
- JACOBI, R., 1883. Anatomisch-histologische Untersuchung der Polydoren der Kieler Bucht. 35 pp. Inaug. Dissertation, Kiel.
- JOHNSTON, G., 1838. Miscellanea Zoologica. Aricidae. *Mag. Zool. Bot. Edinburgh*, **2**: 62–73.

- KAMENEV, G. M., 1991. Macrobenthos from the subtidal zone of Kraternaya Bight. Part 1. Quality data and species distribution. In: ZHIRMUNSKY, A. V., & V. G. TARASOV (eds.), Shallow-water Gaso-hydrothermal Vents and Kraternaya Bight Ecosystem (Volcano Ushishir, the Kurile Islands.) Vol. 2. Biota. Vladivostok. (In Russian, with English summary.)
- KOSTINA, E. E., 1991. Macrobenthos from the intertidal zone of Kraternaya Bight and Hot Beach (the Kurile Islands). In: ZHIRMUNSKY, A. V., & V. G. TARASOV (eds.), Shallow-water Gaso-hydrothermal Vents and Kraternaya Bight Ecosystem (Volcano Ushishir, the Kurile Islands.) Vol. 2. Biota. Vladivostok. (In Russian, with English summary.)
- MANCHENKO, G. P., & V. I. RADASHEVSKY, 1993. Genetic differences between two sibling species of the *Polydora ciliata* complex (Polychaeta: Spionidae). *Bioch. Syst. Ecol.*, **21**: 543–548.
- MORI, K., W. SATO, T. NOMURA & M. IMAJIMA, 1985. Infestation of the Japanese scallop *Patinopecten yessoensis* by the boring polychaetes, *Polydora*, on the Okhotsk Sea coast of Hokkaido, especially in Abashiri waters. *Bull. Jpn. Soc. sci. Fish.*, **51**: 371–380. (In Japanese, with English summary.)
- RADASHEVSKY, V. I., 1986. Reproduction and larval development of the polychaete *Polydora ciliata* in Peter the Great Bay of the Sea of Japan. *Mar. Biol., Vladivostok*, **6**: 36–43. (In Russian, with English summary.)
- 1993. Revision of the genus *Polydora* and related genera from the North West Pacific (Polychaeta: Spionidae). *Publ. Seto mar. biol. Lab.*, **36**: 1–60.
- 1994. Life history of a new species of *Polydora* (Polychaeta: Spionidae) from the Sea of Okhotsk and evolution of lecithotrophy in polydorid genera. *Ophelia*, **39**: 121–136.
- USCHAKOV, P. V., 1955. Polychaeta of the Far Eastern seas of the USSR. *Keys to the Fauna of the USSR*, **56**: 1–445. (In Russian.)
- ZHIRMUNSKY, A. V., & V. G. TARASOV, 1990. Unusual marine ecosystem in the flooded crater of Ushishir Volcano. *Mar. Ecol. Prog. Ser.*, **65**: 95–102.
- & V. G. TARASOV (eds.), 1991. Shallow-water Gaso-hydrothermal Vents and Kraternaya Bight Ecosystem (Volcano Ushishir, the Kurile Islands). Vols. 1–2. Vladivostok. (In Russian, with English summary.)