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Mitinokuidrilus excavatus n. g., n. sp., a Marine Tubificid (Oligochaeta) with a Unique Mode of Reproduction

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ABSTRACT—*Mitinokuidrilus excavatus* n. g., n. sp. is described from shallow subtidal coarse sands in northern Japan (NW Pacific). The species is characterized by a unique mode of sexual reproduction. Each of the two types of mature worms represents the opposite sex: “male” worms have testes, seminal vesicles, male ducts and small spermathecae; “female” individuals possess clitellum, ovaries, ovisac, female ducts and fully developed spermathecae. No mature worms with intermediate sexual condition were collected. The taxonomic position and the possibility of consecutive hermaphroditism of the present species are discussed.

INTRODUCTION

Worms in the Class Oligochaeta are known to show an exclusive functional hermaphroditism with both male and female reproductive organs mature at the same time. Although the reciprocal sperm transfer, which is demonstrated by the deposition of the concopulant sperm in the spermathecae, is observed only in some large terrestrial species (Brinkhurst, 1982), almost all oligochaetes are believed to copulate in the same manner because of the virtually identical organization of reproductive organs throughout the class. There are, however, some deviations from this basic pattern. For example, uniparental reproduction (Gavrilov, 1935) including parthenogenesis (Cernosvitov, 1927; Christensen, 1961; Poddubnaya, 1984) is known in some species. A wide variety of sperm transfer is expected especially in the marine Tubificidae, which contains many species with modified reproductive systems: *Inanidrilus bulbosus* Erséus, 1979 has a dorsal spermathecal opening and an extremely long, peculiarly bended penial seta with a small sheath at its tip, and the species is suggested to deposit sperm to its own spermatheca (Giere and Milligan, 1989). Most of the members of *Aktedrilus* Knöllner and some other species in the subfamily Phallo-drilinae, as well as in the Limnodriloidinae, have spermathecal openings dorsally, which probably make the ordinary reciprocal sperm transfer difficult. Species of *Jamiesoniella* Erséus and some species of *Aktedrilus* and *Thalassodrilides* Brinkhurst and Baker lack spermathecae. This makes the mode of sperm transfer of these species enigmatic.

During early summer of 1997, the first author collected tubificid worms representing a new genus from the Otsuchi-Bay, Iwate prefecture, northern Japan. The species shows a

unique sexual condition. In the present paper, *Mitinokuidrilus excavatus* n. g., n. sp. is described together with the discussion on its taxonomic position and possibility of consecutive hermaphroditism.

MATERIAL AND METHODS

The material used in this study was collected during a short stay at the Otsuchi Marine Research Center, Ocean Research Institute, Tokyo University (8–14 May 1997). Specimens were extracted from grab samples by using decanting and sieving techniques. Following narcotization by dropping in a small amount of ethanol, worms were fixed in 70% ethanol, dehydrated by an ethanol series, cleared by xylene, and mounted whole in Canada balsam. Mounted specimens were observed with an Olympus BH-2 Nomarski differential interference contrast microscope. Measurements were made for 12 specimens of the type series. Body length was measured on a Power Macintosh 6300 computer using the public domain NIH Image program (developed at the U. S. National Institutes of Health and available from the Internet by anonymous FTP from zippy.nimh.nih.gov or on floppy disk from the National Technical Information Service, Springfield, Virginia, part number PB95-500195GEI).

Since none of the specimens has both male and female reproductive organs simultaneously but only one of them, each state is described as “male” or “female” phase, respectively.

Type material is deposited in the Zoological Museum, Division of Biological Sciences, Graduate School of Science, Hokkaido University (ZIHU), Sapporo, Japan.

Abbreviations used in Figs. 1–2

cl	clitellum
de	ventral depression
eca	ectal part of atrium
ena	ental part of atrium
fd	female duct
mf	muscle fibers
ov	ovary
pp	pseudopenis
pr	prostate gland
ps	penial seta
sf	sperm funnel

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st	spermatheca
sta	spermathecal ampulla
std	spermathecal duct
tes	testis
umd	undifferentiated male duct
vd	vas deferens
vs	vestigial seminal vesicle

TAXONOMY

Mitinokuidrilus n. g.

Definition. Somatic setae all bifid. Penial setae 2-4 per bundle, single-pointed. Normal alimentary canal present. Spermathecal pores in line with ventral setae. Spermathecae with duct and, when fully developed, large oval ampulla. Atrium elongated, bipartite: ental part heavily muscular, without granulated inner epithelium; ectal part not heavily muscular, but with granulated inner epithelium. Prostate gland one per atrium, stalked, attached to ectal part of atrium. Atrium terminating into eversible pseudopenis. Both male and female reproductive organs not developing simultaneously in one individual. Marine.

Etymology. The name is derived from Mitinoku, the traditional name of the district from which the present genus is described, and *drilos* (G.), worm.

Type species. *Mitinokuidrilus excavatus* n. sp., by original designation.

Mitinokuidrilus excavatus n. sp. (Figs. 1, 2)

Material examined. Holotype: ZIHU 1172, a whole-mounted specimen. Type locality: Akaiwa, Otsuchi Bay, Iwate prefecture, Japan; subtidal (about 1 m depth), gravel (8 May 1997). Paratypes: ZIHU 1173-1183, 11 whole-mounted specimens; data as for holotype. Other material examined: 91 whole-mounted specimens; data as for holotype.

Etymology. The species epithet is derived from *excavo* (L.), to hollow out, referring to the large ventral depression in XI of worms in male phase.

Description

Somatic characters

External features. Length 9.6-12.5 mm, width 0.27-0.33 mm at segment XI; number of segments 38-53. Prostomium blunt conical, 156-170 μ m long, 120-140 μ m wide. Body wall smooth; secondary annulations absent.

Setae (Fig. 1A). All bifid, 40 (in II) - 70 (in VI, VII) μ m long, 3-4 μ m wide at node; setal bundle consisting of three (sometimes two or four) setae in II-IX, two (sometimes three) thereafter. Setae similar in shape throughout body, with upper tooth slightly shorter and thinner than lower; teeth relatively small, with upper teeth slightly thinner and shorter than lower; subdental ligament weakly developed on lower teeth. Nodes at about ectal 3/5 of the setae. Ventral setae of XI modified into penial setae in male phase, or absent in female phase.

Alimentary canal. Pharynx in I-III. Pharyngeal pad dorsally in pharynx, slightly concave in shape; epithelium bearing dense microvilli. Pharyngeal glands present in IV-VI. Chloragogen tissue starting from VI; chloragogen cells forming a small mass on mid-ventral part of intestine anteriorly in X, between testes and/or spermathecae.

Coelom. Coelomocytes generally absent, but in one specimen (with total no. of segments 51), many coelomocytes observed in segments 40-49.

Nephridia. Unpaired or sometimes paired in each segment in posterior 1/3 of the body. Nephrostome present. Funnel small and tubular, penetrating septum and entering into postseptal nephridial tube. Postseptal part simple, not winded. Nephridiopore in the segment behind that bearing the funnel, in line with and slightly anterior to ventral setae.

Reproductive characters in male phase

Body wall. Large depression present on ventral surface of XI. Muscle fibers connecting depression to dorso-lateral part of body wall.

Penial setae (Fig. 1B, D). Ventral setae of XI modified into penial setae, 2-3 (rarely 4; 5-6 in one specimen) per bundle. Penial setae single-pointed, 43-52 μ m long, 2.6-3.2 μ m wide at node; nodes at ectal 1/4 of setae; ectal tips of setae vended. Penial bundles situated between male ducts, protruding into large ventral depression.

Septa in genital segments. Septa 9/10 and 10/11 projecting anteriorly and posteriorly to form anterior and posterior seminal vesicles, respectively. The former ending anteriorly in IX; the latter posteriorly in XIII-XV.

Gonads. Testes paired in X, about 100-160 μ m long, 50-90 μ m wide, simple, not lobed, connected to posterior surface of septum 9/10 ventro-laterally. Ovaries paired in XI, small, about 40-70 μ m long, 15-30 μ m wide, connected to septum 10/11; proliferating egg not observed.

Male ducts (Fig. 1C, D). All structures paired. Sperm funnel on septum 10/11, up to 80 μ m long. Vas deferens 60-80 μ m long, 12-20 μ m wide, with ciliated inner lumen, entering into atrium apically; peritoneal layer covering the vas deferens. Atrium bipartite, consisting of: (1) ental part, spindle-shaped, 125-160 μ m long, 40-70 μ m wide, with ciliated and poorly granulated inner epithelium (12-20 μ m thick) and outer muscular layer (8-20 μ m thick) composed of muscle fibers which run spirally around the inner epithelium but cross each other forming a diagonal pattern (see fig. 1C, ena); and (2) ectal part, 80-120 μ m long, about 15 μ m wide at the connection to the ental part of atrium, up to 65 μ m at broadest part, with heavily granulated inner epithelium and thin outer muscular lining, joining subapically to the ental part of atrium. Prostate gland entering into ectal part of atrium (see Fig. 1C). Atrium terminated in eversible pseudopenis, 45-55 μ m long, 50-70 μ m wide. Male pore posteriorly in XI, in line with ventral setae. **Spermathecae** (Fig. 1D). A pair in X; tubular, 90-120 μ m long, 30-45 μ m wide, sometimes divided into a duct-like part and a small, undeveloped, ampulla. Each spermatheca may open to exterior immediately posterior to the septum 9/10 in line

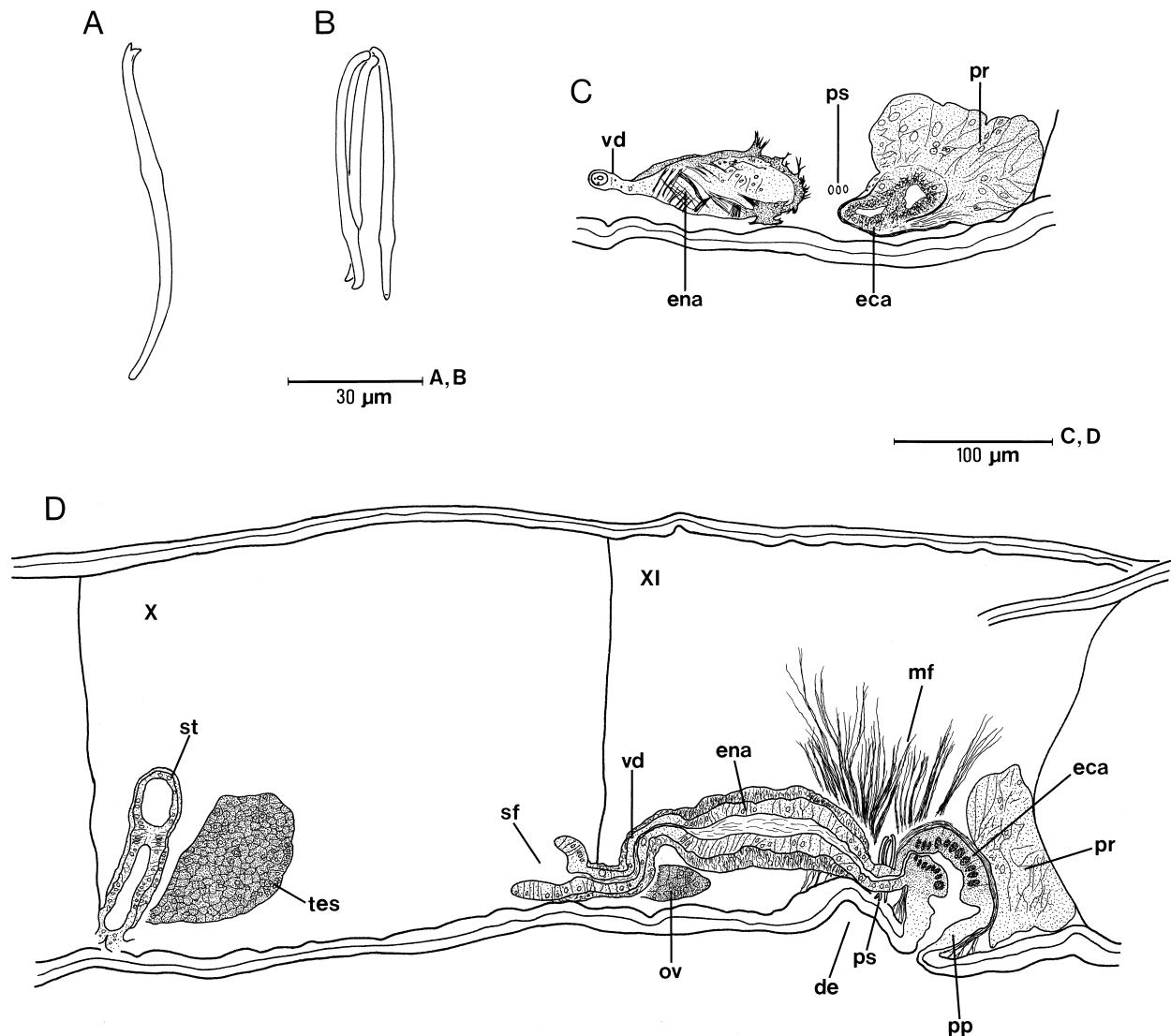


Fig. 1. *Mitinokuidrilus excavatus* n. g., n. sp. (A) somatic seta of VIII (holotype); (B) penial setae (holotype); (C) atrium and prostate gland showing connection between ectal part of atrium and prostate gland (paratype, ZIHU 1173); (D) reproductive organs in male phase (holotype). Seminal vesicles are not shown in D.

with ventral setae, but spermathecal pores not confirmed. Sperm in spermathecae absent.

Reproductive characters in female phase (Fig. 2)

Body wall. Clitellum extending over 1/3X-XII, completely ring-shaped, present only in female phase.

Septa of genital segments. Septum 11/12 modified into egg sac, ending posteriorly in XIII-XV. Loose vesicular structure (Fig. 2, vs) attached on anterior surface of septum 9/10 and posterior surface of septum 10/11.

Gonads. Ovaries paired in XI, 100-220 μm long, 40-120 μm wide. Proliferated eggs often attached to end of ovary. Testes absent.

Gonoducts. Inconspicuous paired female ducts present on septum 11/12. Undifferentiated, simple male ducts (Fig. 2, umd) present; each duct with ciliated sperm funnel and narrow lumen.

Spermathecae. A pair in X; each consisting of (1) ovoid ental ampulla 140-230 μm long, 90-130 μm wide and; (2) ectal duct 100-120 μm long, 40-60 μm wide. Ental part of a duct composed of tall, columnar cells. Spermathecal vestibules absent. Spermathecal pores immediately posterior to septum 9/10, in line with ventral setae. Sperm in spermathecae forming one or two bundles.

REMARKS

None of the specimens observed in this study possesses both male and female reproductive organs together. Instead, each worm has a male or female element only. Although this reproductive condition is uncommon in oligochaetes, *Mitinokuidrilus* n. g. clearly belongs to the family Tubificidae judging from the position and shape of the reproductive organs. Among the five subfamilies known in the Tubificidae,

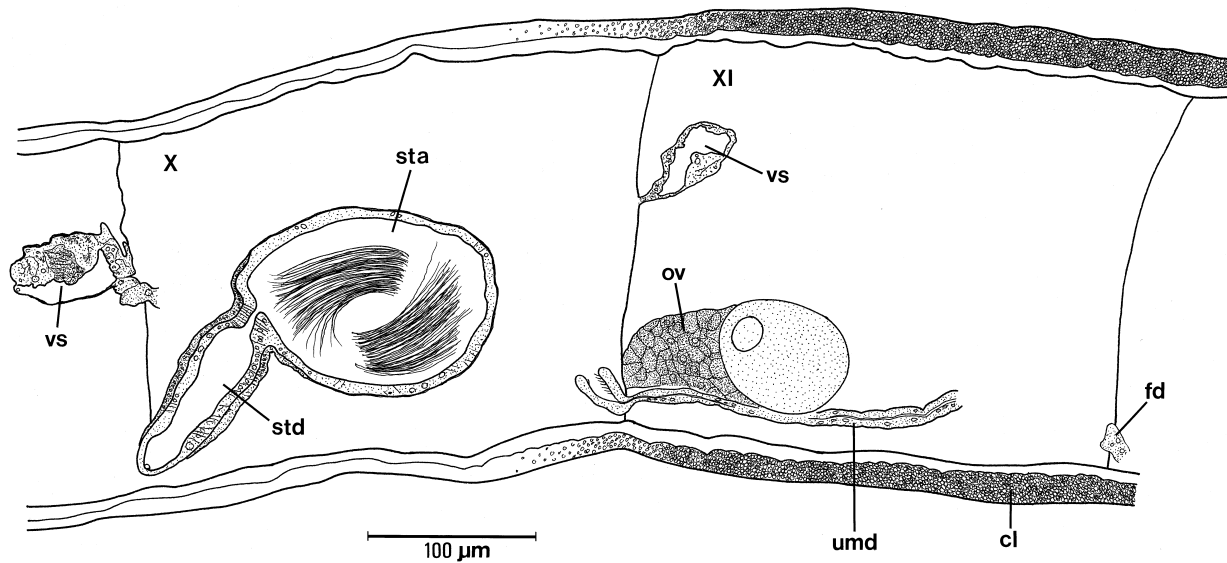


Fig. 2. *Mitinokuidrilus excavatus* n. g., n. sp. Reproductive organs in female phase (paratype, ZIHU 1179).

Mitinokuidrilus is encompassed in the Phallodrilinae because it possesses the stalked posterior prostate glands. *Mitinokuidrilus* shows the following characters known from Phallodrilinae: (1) prostate gland attached near ectal end of atrium; (2) absence of coelomocytes; (3) single-pointed penial setae with bended ectal tips; and (4) spermathecal pore situated in most anterior part of X.

Mitinokuidrilus is most similar to *Nootkadrilus* Baker, 1982: only these two genera in the Phallodrilinae share the bipartite atrium with a thick muscular ental part and an ectally attached prostate gland. *Mitinokuidrilus*, however, substantially differs from *Nootkadrilus* in the absence of glandular prostatic tissue on or around vas deferens. Moreover, *Mitinokuidrilus* has spermathecae with large ovoid ampullae and eversible pseudopenes, both of which are never seen in *Nootkadrilus*. There are no other genera in the Phallodrilinae comparable to *Mitinokuidrilus*.

In a recent phylogenetic analysis of phallodriline genera it was suggested that glandular vas deferens of *Nootkadrilus* developed independently of the anterior prostate gland of other phallodriline species (Erséus, 1992). It is, therefore, probable that *Nootkadrilus* and *Mitinokuidrilus* share an ancestor which lacked an anterior prostate gland.

DISCUSSION

Among 104 specimens examined here, there were 46 "male" and 58 "female" worms, but no individuals of an intermediate state of reproduction. Only the spermathecae in "female" worms are filled with sperm. From these facts it is apparent that simultaneous sperm transfer does not occur in *Mitinokuidrilus excavatus* n. g., n. sp. A question is whether this species is dioecious or a consecutive hermaphrodite with a short time of transition. The small spermathecae of "male" worms could be the rudiments of the muscular layer of the

developed spermathecae because they are entirely covered with the distinct peritoneal cells (Gustavsson and Erséus, 1997). In contrast, the fully developed spermathecae of "female" worms have very thin muscles, at least on the ampullae, instead of a peritoneal layer. It is, therefore, likely that the small spermathecae in "male" worms later continue to develop in "female" worms. Consequently, the present species is probably a protandric consecutive hermaphrodite with a rapid transition between the two phases in one individual. This view is supported by the presence of loose vesicular structures in "female" worms, i. e., structures that seem to be the vestiges of seminal vesicles in "male" worms.

Poddubnaya (1980) reported in three tubificid species that the development of testes precedes that of ovaries, and spermathecae are formed last during the morphogenesis of reproductive organs. It is also reported that ovaries persist longer than testes in *Tubifex tubifex* (Poddubnaya, 1984) and some species of the family Naididae (Lasserre, 1975). At least in some aquatic microdrilids, the male genital system tends to develop antecedently to the female genital system. This tendency may be expressed strongly in the present species. This view will be confirmed by further studies.

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