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A New Species of the Genus *Rhyacodrilus* Bretscher (Oligochaeta, Tubificidae) from Japanese Lakes

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ABSTRACT—A new tubificid oligochaete, *Rhyacodrilus hiemalis* sp. nov., is described from four lakes in central Japan. This species resembles *R. coccineus* (Vejdovsky), *R. sodalis* (Eisen) and their unclear relatives (the Far East Russian *R. sokolskajae* Semernoi and *R. sibiricus* Semernoi, the Chinese *R. sinicus* (Chen)), but is distinguished from these congeners by having many long hair chaetae, many long intermediate teeth on the dorsal pectinate chaetae, ventral pectinate chaetae, and masses of gland cells around the male pores. This species is an annual that breeds during the cold season but aestivates in deeper sediment in summer.

INTRODUCTION

Rhyacodrilus Bretscher is a large and cosmopolitan genus in the family Tubificidae (Oligochaeta). More than twenty *Rhyacodrilus* species are known in the world [2, 4], including several Far-Eastern forms [5, 6, 10, 11, 15–25, 27]. However, no taxonomic study of this genus exists in Japan, although it has been referred to in faunal records [9, 14]. Recent ecological studies have shown that a distinct *Rhyacodrilus* species dominantly occurs and breeds in winter in some central-Japanese lakes [12, 26, 28], but its taxonomic status has been left unclear. In this paper, I describe it as a new species. I also provide known information on the distribution and biology of the new species.

METHODS

For observation of external characteristics, fixed specimens were mounted whole in either Canada balsam or Amman's lactophenol. For anatomical study, some specimens were cut serially and stained with hematoxylin and eosin. A detailed observation of the chaetal structure was made with the aid of a scanning electron microscope (SEM). The type specimens are deposited in the Division of Biological Sciences, Graduate School of Science, Hokkaido University (ZIHU). In addition to the present species, the North American *Rhyacodrilus sodalis* (USNM 32645, neoparatype, and R. O. Brinkhurst collection) and *R. coccineus* (R. O. Brinkhurst collection) were examined for comparison with the present species.

To clarify the life history of the present species, quantitative samplings of worms and cocoons were performed monthly for 5 years from 1980 to 1985 at the type locality, the center of Lake Kitaura. Triplicate bottom samples taken with the aid of a basic type of Ekman-Birge bottom sampler were

immediately passed together through a screen with 0.25 mm mesh. Then the remainder was fixed in a 10% formalin solution, and worms and cocoons were sorted and counted. As an index of body size, the width of the eighth segment [13] was measured and the sexual maturity was determined for each fixed worm; the mature worm has a clitellum. The bottom water temperature was measured at every sampling.

DESCRIPTION

Subfamily Rhyacodrilinae Hrabě, 1963
(Japanese name: Nagare-itomimizu-aka, new)
Genus *Rhyacodrilus* Bretscher, 1901
(Japanese name: Nagare-itomimizu-zoku)

Rhyacodrilus hiemalis sp. nov.
(Japanese name: Fuyu-nagare-itomimizu, new)
(Figs. 1–5)

Rhyacodrilus sp. : Yasuda and Okino, 1987, p. 2 [28]; Narita, 1990, p. 35 [12]; Takada et al., 1992, p. 328 [26].

Rhyacodrilus sp. 1 : Ohtaka, 1993, p. 38 [14].

Types. Holotype: ZIHU-1003, a sagittally sectioned mature specimen, center of Lake Kitaura, Ibaraki Prefecture (36°01'N, 140°34'E; 6 m deep, mud): 14 Feb. 1981, A. Ohtaka collected. Paratypes: ZIHU-1004, a mature specimen from the type locality; anterior part of body sagittally sectioned and the rest whole-mounted: 5 Jan. 1985, A. Ohtaka collected. ZIHU-1005, a cross sectioned mature specimen from the type locality; 24 Dec. 1982, H. Kikuchi collected.

Other materials examined. Over a hundred mature specimens, Lake Kitaura (type locality): 16 Oct. 1980–17 June 1985, A. Ohtaka and H. Kikuchi collected. One mature and two immature specimens, Takahamairi Bay, Lake Kasumigaura, Ibaraki Prefecture (exact locality unknown): 6 Mar. 1982, T. Iwakuma collected. Three mature and ten immature specimens, Lake Suwa, Nagano Prefecture (36°02'N, 138°06'E, 2–4 m deep, mud): 21 Nov., 1 Dec. 1983, 14 June,

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1 Oct. 1984, K. Takada collected (see Yasuda and Okino [28]). Four mature specimens, off the Ecological Research Center, Kyoto Univ., the south basin of Lake Biwa, Shiga Prefecture (35°04'N, 135°54'E; 5 m deep, mud): 22 Feb. 1985, T. Narita collected (see Narita [12]). 15 mature specimens, off Ayame-hama, the north basin of Lake Biwa (35°04'N, 136°00'E; littoral with 5–10 m in depth, mud): 21 Dec. 1989–29 Jan. 1990, M. Nishino collected.

Description. In mature and fixed state, body 17–35 mm long, 0.5–1.2 mm wide in anterior segments, segments up to 190. Living worms up to 60 mm in length. Body light red when living, rectangular in cross section throughout. No pigments on body wall. Prostomium conical and well developed. No secondary annulations. Epidermis thick with several transverse furrows on each segment.

Chaetal bundles situated almost at middle position of segments preclitellarly, and at 2/3–3/4 from anterior septa of segments postclitellarly. Dorsal chaetal bundles consisted of smooth or hispid hair chaetae (Fig. 2A) and pectinate chaetae (Figs. 1A–D, 2B). Dorsal hairs in anterior segments 4–8 per bundle, up to 640 μm long, including 1–3 short ones. They become shorter, thinner, and decrease in number posteriorly: 1–3 per bundle in middle part of body, while wholly lost in a variable number of posterior segments. Dorsal pectinate chaetae weakly curved with nodules at 1/3

from distal end or more distally. In anterior segments, dorsal pectinate chaetae (Fig. 1A) 5–9 per bundle, 118–180 μm long, the distal end with a deep V-shaped notch in which the upper teeth 8.6–10.2 μm long, almost equal in length and thickness, or slightly longer and thinner than the lower teeth (8.2–9.9 μm long), and with 6–11 long and distinct intermediate teeth set in parallel between the upper and lower teeth (Fig. 2B). In middle and posterior segments, dorsal pectinate chaetae (Fig. 1B, C) 1–5 per bundle, 80–150 μm long, the upper teeth 6.1–7.8 μm long, longer and thinner than the lower (5.7–7.2 μm long) and the intermediate teeth 5–8 in number, short. Distal shape of the dorsal pectinate chaetae sometimes modified to have truncated and serrated tip in upper teeth (Fig. 1D). Ventral chaetae all pectinate with nodules at 1/3 from distal end; those in anterior segments (Figs. 1E, F, 2C) 6–8 per bundle, 120–162 μm long, the upper teeth 7.4–11.1 μm long, longer and almost as thick as the lower (5.3–7.0 μm long) and intermediate teeth 5–10 in number, fine and shorter than those on dorsal pectinate chaetae. In posterior segments, ventral chaetae 2–5 per bundle, 70–136 μm long, the intermediate teeth reduced in number and length, located mainly on proximal part of the lower teeth (Fig. 1G). Penial chaetae (Fig. 1H) 3–7 per bundle, 146–180 μm long, with the heads close together; the nodules situated at 1/3 to 1/4 from distal end and the distal

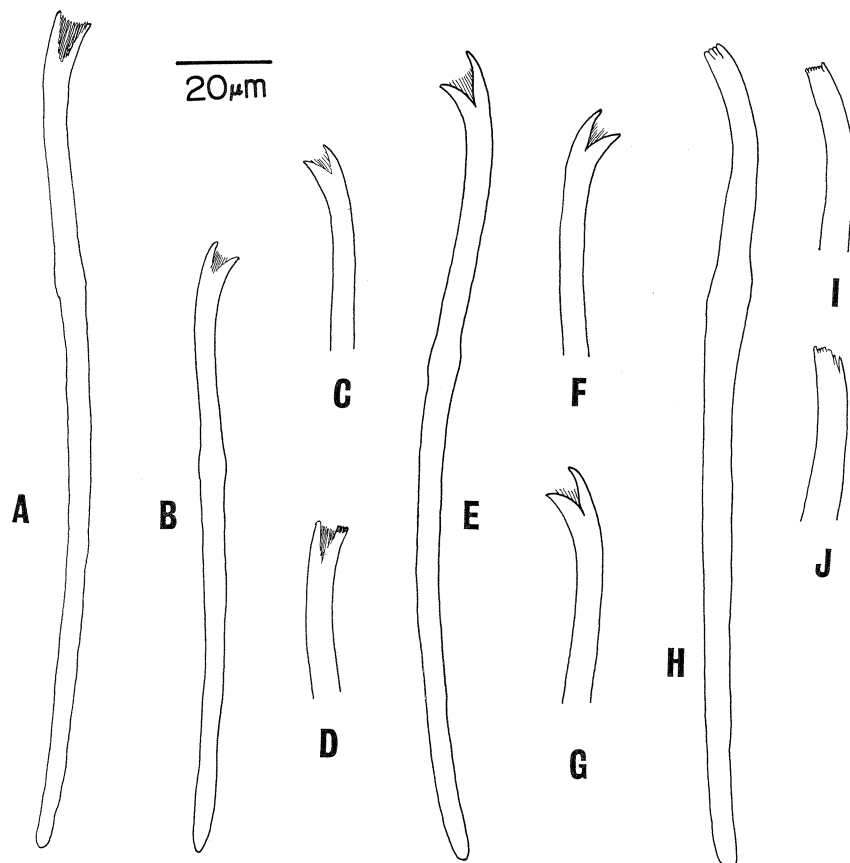


FIG. 1. Chaetae of *Rhyacodrilus hiemalis* from Lake Kitaura (type locality). A, dorsal pectinate chaeta in segment IX; B, the same in XXX; C, the same in XX; D, variation of dorsal chaeta in XX; E, ventral chaeta in VIII; F, the same in X; G, the same in a posterior segment; H–J, penial chaetae. Figures except for A, B, E and H showing only distal ends.

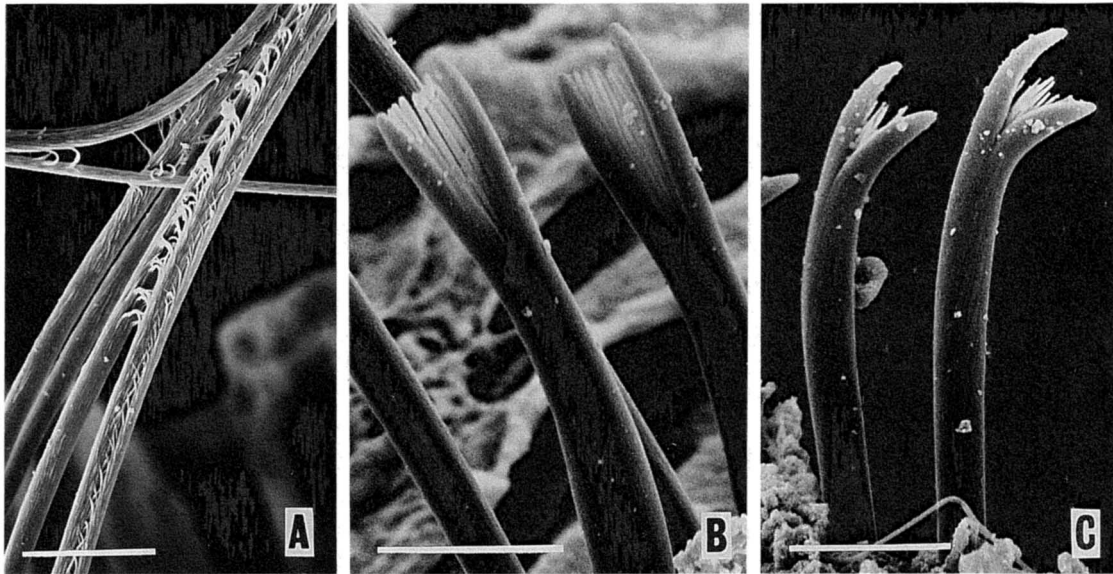


FIG. 2. SEM photomicrographs of chaetae in *Rhyacodrilus hiemalis* from Lake Kitaura. A, hair chaetae in an anterior segment; B, dorsal pectinate chaetae in an anterior segment; C, ventral chaetae in an anterior segment. Scales: 10 μm .

end split into some to several rudimentary teeth (Fig. 1I, J).

Clitellum whitish in outer appearance, from beginning of segment X to end of XII with several narrow transverse furrows on each segment; the epidermis thick (up to 95 μm high) and extremely glandular dorsally and laterally, while thin and depressed ventrally. Testes and ovaries in X and XI, respectively. Male funnels in X, 320 μm in diameter, thick and moderately large (Fig. 3). Vasa deferentia in XI, short (about 700 μm long), stout and not coiled, connected with atria subapically; both terminal junctions a little narrower than the other parts. Atria ovoid, 240 μm long by 130

μm , covered with pear-shaped prostate gland cells 48–80 μm in height; the inner epithelium thick and glandular. Pseudopenis protrusible, the lumen ciliated. Masses of diffused cells set around male pores (Figs. 3, 4); each cell up to 80 μm in height, pear-shaped and glandular, closely similar in shape and structure to prostate gland cell covering atrium. Male pores separately opening nearly at middle of segment XI, just lateral to penial chaetal bundles (Fig. 5A). Female funnels in XI, as large as male funnels. Spermathecae in X, opening ventrally immediately behind septum 9/10 (Figs. 3, 5B); the ampullae up to 600 μm long, large and spherical in

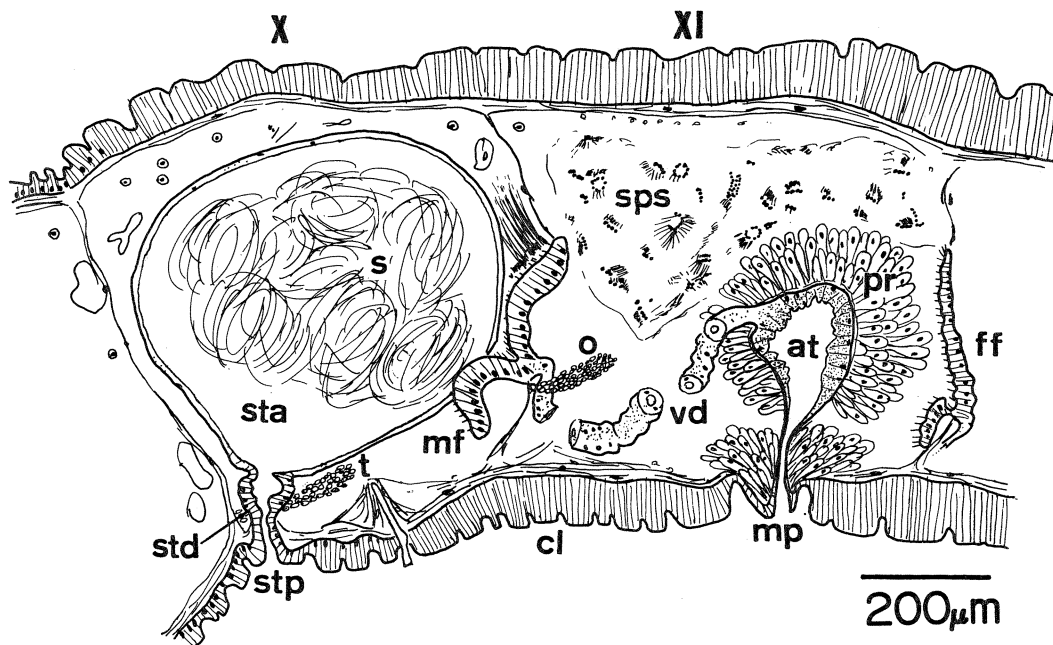


FIG. 3. Sagittal section of genital segments in *Rhyacodrilus hiemalis* from Lake Kitaura (holotype). at, atrium; cl, clitellum; ff, female funnel; mf, male funnel; mp, male pore; o, ovary; pr, prostate gland; s, sperm; sps, sperm sac; sta, spermathecal ampulla; std, spermathecal duct; stp, spermathecal pore; t, testis; vd, vas deferens.

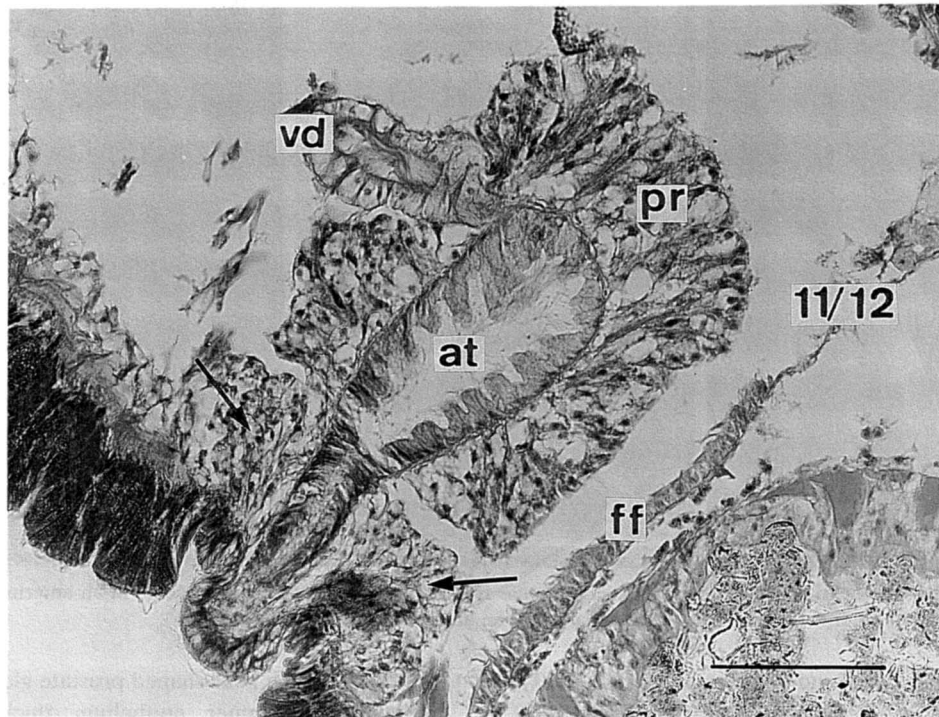


FIG. 4. Sagittal section of atrium in *Rhyacodrilus hiemalis* from Lake Kitaura. Arrows showing mass of gland cells around male pore. Scale: 100 μm .

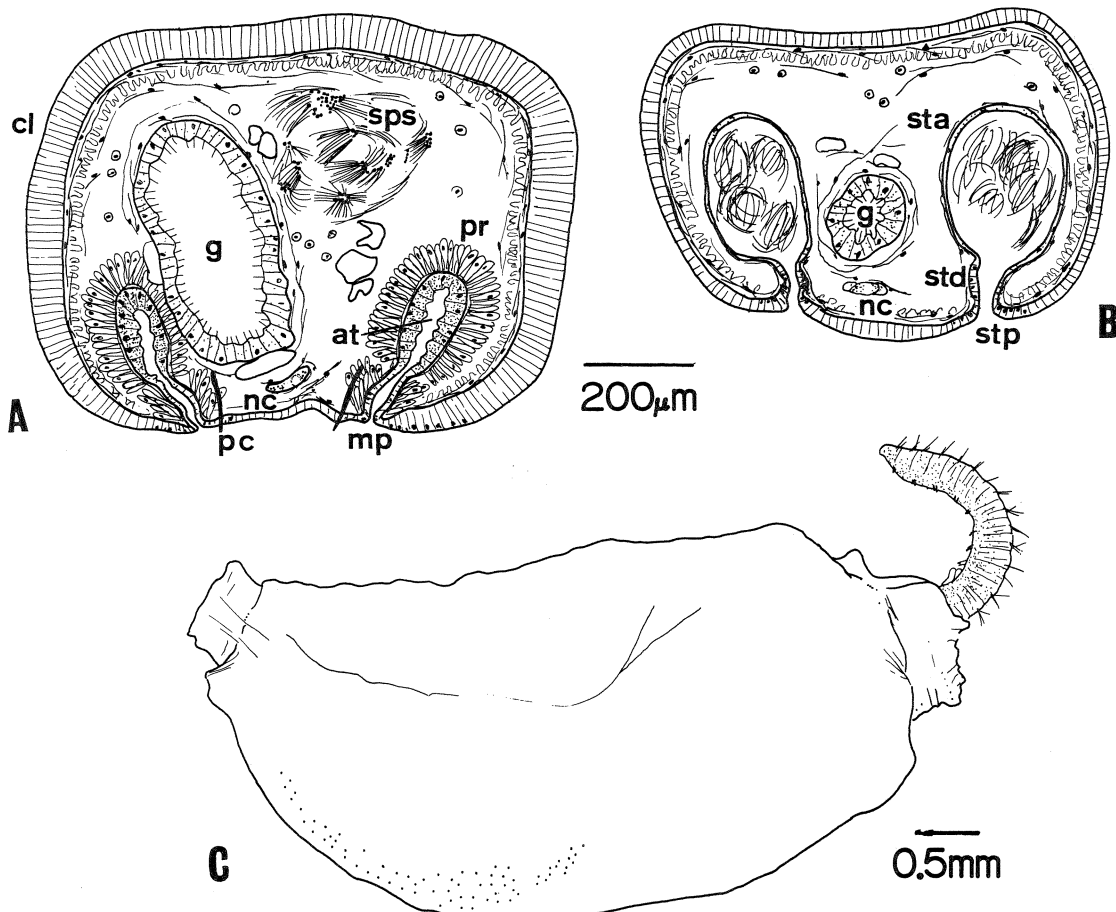


FIG. 5. *Rhyacodrilus hiemalis* from Lake Kitaura. A, cross section of segment XI at the line of male pores (paratype); B, the same of X at the line of spermathecal pores (paratype); C, cocoon together with a hatching worm. g, gut; nc, nerve cord; pc, penial chaeta.

shape, not connected with alimentary canal; the ducts 70–100 μm long, short and well marked off from the ampullae with a distinct distension near the ampulla. Loose sperm masses in spermathecal ampulla. Sperm sac from IX to XX and egg sac from XI to XVIII; both mainly occupying left side of coelom.

Coelomocytes especially abundant in anterior segments; each coelomocyte spherical in shape with a diameter of 12–18 μm . Large transverse vessels in 1/2VII, VIII and IX. Pharynx in II and III, the wall thick with pharyngeal glands dorsally. Oesophageal gland absent. Chloragogen cells from IV on, becoming abundant from VI. Alimentary canal widen from XII or XIII. Nephridia from VI on, but absent in X and XI in mature specimens.

Cocoon up to 5 mm long and 2.5 mm wide (Fig. 5C), in shape a weakly bent spindle with a concave side by which it adheres to solid materials, usually living or dead mollusc shells of any species (mostly the gastropod *Sinotaia quadrata histricus* (Gould) in L. Kitaura) or sometimes pieces of wood. Cocoon wall opaque, thick and soft, mixed with foreign matters. Up to seventeen embryos in a single cocoon. Young worms about to hatch out 2.0–2.5 mm long with 25–32 segments. Dorsal chaetal bundles of these pre-hatching worms with 2–3 hairs and 2–3 pectinates per bundle anteriorly, and 0–1 hairs and 1–2 pectinates posteriorly; the ventral chaete pectinate like mature worms: 1–2 per bundle anteriorly, single posteriorly.

Variation. No morphological difference was found be-

tween local populations in four lakes. The dorsal hair chaetae of the present species were usually distributed in the anterior half of the body (at least up to segment L), and became fewer or wholly absent in a variable number of posterior segments. In one specimen with 152 segments, the dorsal hairs were distributed sporadically until segment 135. This suggest that the dorsal hairs of the present species are easily lost in posterior bundles. In a specimen from Lake Kitaura, the position of the genital organs has been shifted anteriorly; the clitellum was in V–VII, the testes and spermathecae in V, and the ovaries and male pores in VI, but the shape of these organs was normal.

Life history. Figure 6 shows the seasonal changes in the occurrence of this species together with the bottom water temperature at the type locality, the center of Lake Kitaura. Every year, this species was predominant from autumn through spring when the bottom water temperature was below 15°C, but it was rarely obtained in summer months. The breeding was restricted to winter. The disappearance of this species in summer is probably caused by its migration into the deeper layer of sediment where the basic type of Ekman-Birge sampler (15 cm in height) cannot reach (see remarks for reasons). The cocoons were collected in spring, following the occurrence of mature worms. Monthly changes in the frequency distribution of the body size expressed by the width of the eighth segment (Fig. 7) indicates that this is an annual species. Worms quickly increased their size from October and attained sexual maturity in December, then disappeared

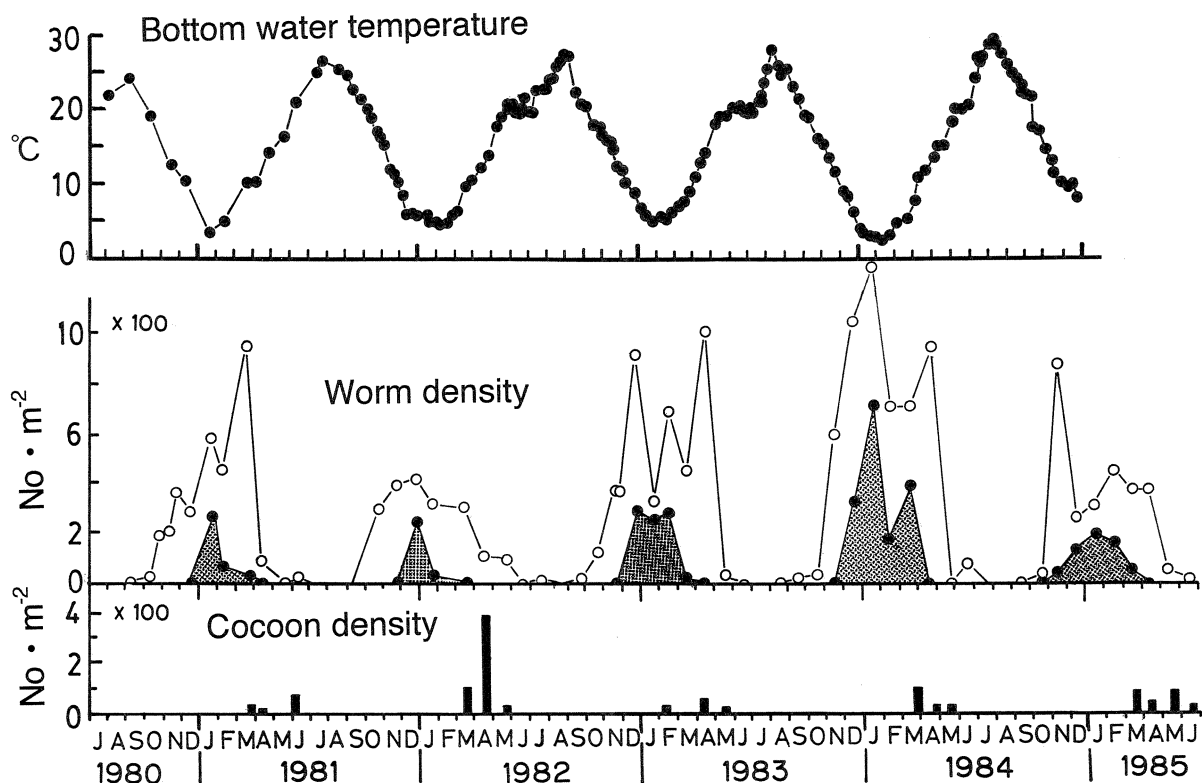


FIG. 6. Seasonal changes in density of worms (middle) and cocoons (bottom) of *Rhyacodrilus hiemalis*, and bottom water temperature (top) at the center of Lake Kitaura. Shaded parts indicate sexually mature individuals.

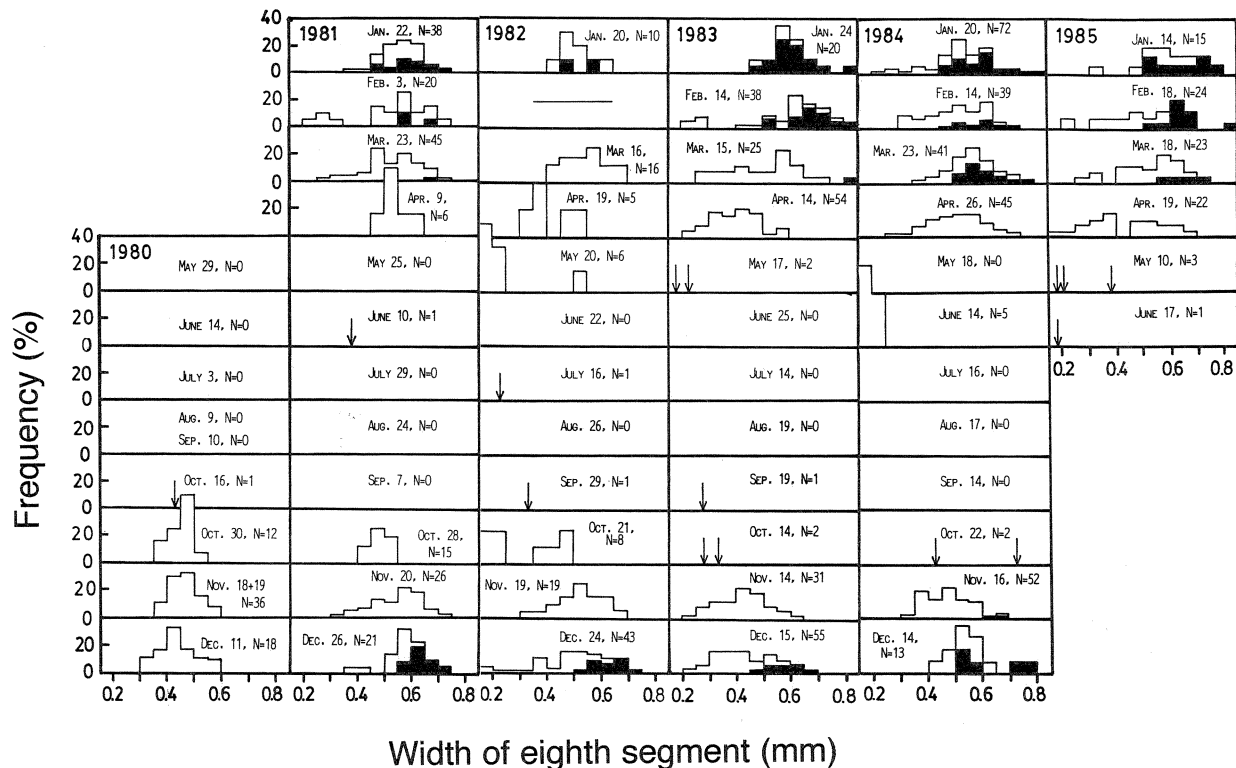


FIG. 7. Monthly changes in the frequency distribution of the width of eighth segment in *Rhyacodrilus hiemalis* at the center of Lake Kitaura. Solid parts indicate sexually mature individuals. When specimens were less than five at a single sampling occasion, the value is shown as arrow for each individual; the arrow individuals were all sexually immature.

by the next spring. Newly hatched small worms appeared from December to February.

Ethymology. The specific epithet is derived from the breeding habit of this species, i.e., its breeding is restricted to winter.

Distribution. So far, this species has been recorded from the following four lakes in central Japan: L. Kitaura, L. Kasumigaura, L. Suwa, and L. Biwa. In Lake Biwa, this species is distributed throughout the south basin (shallower than 6.5 m), but is restricted from littoral to upper profundal regions (up to 40 m deep) in the deeper north basin (Nishino *et al.*, unpubl.). It inhabits muddy bottoms.

Remarks. The status of several important characteristics of the present species is synoptically shown in Table 1 together with that of five other *Rhyacodrilus* species. The present new species has large masses of gland cells around the male pores (Fig. 4). Such a structure has never been described nor figured in previous descriptions of any other congeners. As shown in Figure 8 A and B, *R. coccineus* (Brinkhurst collection, collection data unknown) and *R. sodalis* (Brinkhurst collection from Oregon, USA) are actually devoid of it. Although I could not check the other congeners, it is most likely that this character is unique for this species because the structure is too distinct to have been overlooked by previous authors.

This species resembles the almost cosmopolitan *R. coccineus* (Vejdovsky, 1875) by sharing hair and pectinate chaetae with a V-shaped notch in the dorsal bundles and with

globular to ovoid atria. However, this species is distinctly different from *R. coccineus* in several important characteristics. That is, in this species the distal teeth of dorsal pectinate chaetae are long and almost parallel with long and distinct intermediate teeth, whereas they are relatively short and divergent with short and fine intermediate teeth in *R. coccineus*. In addition, as shown in Table 1, in this species the chaetae are greater in number and longer.

The distal form of the dorsal pectinate chaetae in this species, on the other hand, more resembles that of the North American *R. sodalis* (Eisen, 1879) [7]. According to the present examination of *R. sodalis* (paraneotypes from Lake Tahoe, California/Nevada, USA), the dorsal pectinate chaetae have markedly long (8.5–10.0 μ m) and almost parallel teeth with the upper ones being a little longer than the lower, and the intermediate teeth are few to several in number, and are short and very fine (Fig. 8C). Such a structure in *R. sodalis* is different from that of the present species in that the lateral teeth are longer, whereas the intermediate teeth are shorter and finer. In addition, the dorsal hairs and pectinate chaetae are distinctly fewer and shorter in *R. sodalis* (Table 1) than in this species.

The following species are also related to *R. coccineus* or *R. sodalis*: the Chinese *R. sinicus* (Chen, 1940) [6], the Far East Russian *R. sokolskajae* Semernoi, 1971 [17] and *R. sibiricus* Semernoi, 1971 [18]. Their specific entities are still unclear, and different opinions have been proposed about their taxonomic status [1, 2, 4, 27]. For the present, a

TABLE 1. Comparison of taxonomic characters in six *Rhyacodrilus* species

species Reference	<i>coccineus</i> [2], *[27] (present study)	<i>sodalis</i> [1], *[3] (present study)	<i>sinicus</i> [6]	<i>sokolskajae</i> [17]	<i>sibiricus</i> [18]	<i>hiemalis</i> present study
Body length (mm)	10–35, *5	5–10	80–150	20–22 (fixed)	–40	17–35 (fixed)
Number of segments	60–110, *51–52	33–100	42–56	45–70	–140	–190
Anterior dorsal hairs						
number per bundle	3–5, *1–2	1–2, *2–3 (0–3)	2–4	3–4	4–6	4–8
length (μm)	*170–180	(–380)	240–250	–470	–500	–640
Anterior dorsal pectinates						
number per bundle	–5, *2–4	2–3, *–6 (2–4)	2–4	4–5	5–7	5–9
length (μm)	*80	(–94)	70–100	165–179	127–132	118–180
intermediate teeth	fine	short, very fine	absent	fine	thin membrane	long, distinct
Anterior ventral chaetae						
number per bundle	3–5, *3–5	–6, *–6 (5–9)	3–6	4–7	6–10	6–8
length (μm)	*60–70	(–90)	70–100	144–150	177.5 (mean)	120–162
intermediate teeth	absent	absent	absent	absent	absent	present
Atrium						
form	globular	*globular-ovoid	ovoid-globular	ovoid	ovoid	ovoid
junction with vas deferens	subapical	*apical	apical	apical	subapical	subapical
Gland cells around male pore	(absent)	(absent)	absent	absent	absent	present

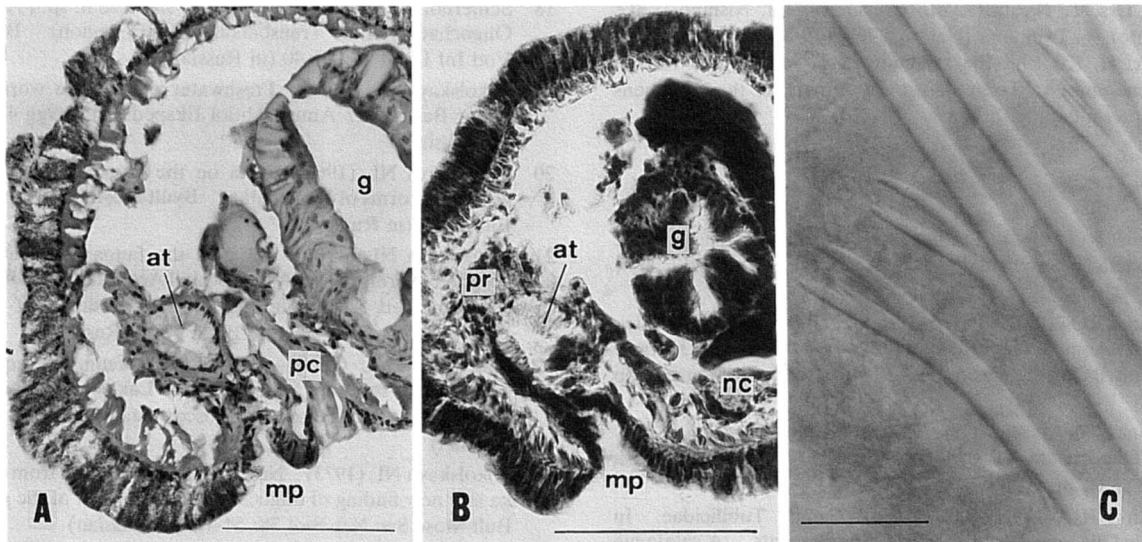


FIG. 8. A and B, cross section at the line of male pore in *Rhyacodrilus coccineus* (A) (R. O. Brinkhurst collection) and *R. sodalis* (B) (from Oregon, USA in R. O. Brinkhurst collection). C, hair and pectinate chaetae in an anterior dorsal bundle in *Rhyacodrilus sodalis* from Lake Tahoe, USA (neoparatype). Scales: A and B, 100 μm ; C, 10 μm .

separation of these species is difficult because authentic characteristics discriminating them have hardly been established yet. However, it is most likely that they are different from the present species because they have much finer or no intermediate teeth in the dorsal pectinates, no ventral pectinates, and no gland cells around the male pores (Table 1).

This species also resembles the probably holarctic *R. punctatus* Hrabě, 1931 [8] and the North American *R. montana* (Brinkhurst, 1965) [1] in having usual pectinate chaetae in its ventral bundles. However, *R. punctatus* differs from this species in having lyra-shaped dorsal pectinate chaetae and a golden brown glandular epidermis, both of

which are not encountered in this species. Also, *R. montana* is different from this species by having very long dorsal hair chaetae in II.

R. hiemalis has been studied ecologically under the name *Rhyacodrilus* sp. by Yasuda and Okino [28] and Takada et al. [26] from Lake Suwa, and by Narita [12] from L. Biwa. I confirmed this by examining voucher specimens of these studies. In both lakes, this species breeds during the cold season, but migrates and aestivates in deeper (below 15 cm) sediments in summer to avoid the high temperature [12, 26]. Its life history trend is probably the same in the two other localities, L. Kitaura (type locality) and the adjacent L.

Kasumigaura, because the occurrence of mature individuals was restricted to winter and few worms of any stage were collected in summer using the basic type of Ekman-Birge sampler (15 cm high) (Fig. 6). There has been no record of oligochaetes, including any *Rhyacodrilus* species, which migrate seasonally into such deeper sediment (see [26]). In addition, although tubificid oligochaetes generally deposit free ellipsoidal cocoons in sediment, this species is obligated to attach cocoons to solid materials, usually molluscan shells, or sometimes pieces of wood ([12], present study). Its peculiar life history and breeding habit also characterize this species.

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