REDESCRIPTION OF *TROCHOCHAETA CARICA* (BIRULA, 1897) (POLYCHAETA, TROCHOCHAETIDAE) WITH NOTES ON REPRODUCTIVE BIOLOGY AND LARVAE

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Based on examination of the holotype, new collections from the type locality and other regions of the Kara and East Siberian Seas, an illustrated redescription of *Trochochaeta carica* is presented. Some morphological details, including the shape of the pygidium, eggs, sperm, and larva are described for the first time. Specimens were found in reproductive condition in the middle of August. Mature eggs measuring up to 500 × 564 and 405 × 650 µm in diameter and containing large quantities of yolk granules are spawned in maternal tubes. Spermatozoa have a round head, measuring 3.3 µm in diameter. The 21-segment larvae were still in the tubes of the adults. This larval stage is characterized by an outspread 'umbrella', a terminally notched prostomium without eyes, 11 pairs of well developed parapodia, two pairs of coarse setae in segment three, long provisional swimming setae and a four-lobed pygidium. The presence of long swimming setae in the larvae suggests a pelagic stage, which is important for dispersion of tubicolous species. The type of development is apparently entirely lecithotrophic. North Atlantic specimens, identified by PETTIBONE (1976) as *T. carica,* are more closely related to *T. pettiboneae* DEAN, 1987. We suggest that the distribution of *T. carica* is limited to Arctic Seas.

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INTRODUCTION

The monogeneric family Trochochaetidae contains seven valid species (PETTIBONE, 1976; DEAN, 1987). Data on egg structure and larval development are as yet known only for *Trochochaeta multisetosa* (OERSTED, 1843) (THORSON 1946, identified as Spionid larvae 'd'; HANNERZ 1956). *Trochochaeta carica* was briefly described by BIRULA (1897) from the Gulf of Ob in the Kara Sea, based on a single incomplete anterior fragment. Some additional figures of the same specimen were subsequently published by USHAKOV (1955). A small anterior fragment of *Trochochaeta* from the Gulf of St. Lawrence was described by FAUVEL (1932) as *T. carica*. ANNENKOVA (1952) reported *T. carica* from the Bering Strait, but without a description. PETTIBONE (1976) described some complete specimens from eastern Canada considering them to be *T. carica*.

The present study is based on the type and new material from the Kara and East Siberian Seas, obtained in 1986 and between 1990 and 1995 during various Russian, Russian-Norwegian and Russian-American expeditions. The material collected from the type locality of *T. carica* includes some well preserved, complete and mature specimens. Larvae of this species were found in the maternal tubes. This material allows us to supplement descriptions of *T. carica* with new morphological details. One specimen from the North Atlantic, referred by PETTIBONE (1976) to *T. carica* was re-examined.

MATERIAL AND METHODS

Three to five replicate samples per locality were collected using various types of grabs, with sampling areas of 0.1 and 0.2 m^2. The mesh diameter of the lowest sieve was 0.75 mm or 1 mm. The material was fixed in formalin, rinsed in freshwater and transferred to 75 % alcohol. All drawings of adults and larvae were of fixed material, using a stereomicroscope with mirror attachment. All material is deposited at the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIRAS).

Trochochaeta carica (Birula, 1897)
(Fig. 1-4)
Disoma carica Birula, 1897: 99-102, pl. 10, fig. 1a-d; – Ushakov 1955: 284, fig. 100, A-G.

Type material. Holotype: ZIRAS, N 2/25892, 27 segments, anterior fragment. Kara Sea, Gulf of Ob, 26.6 km NE of Cape Drovyanoy, 19 m, sandy mud, 11 Aug. 1896, coll. A.C. Botkin.

Other material examined. Kara Sea, Gulf of Ob, 72°30.34' N, 74°25.32' E, 17 m, silty clay, 15 Aug. 1993, coll. L.L. Jørgensen, R/V *Dalniye Zelentsy*, 34 adults and 9 larvae; 72°36.7' N, 73°19.8' E, 19 m, silty clay, 16 Sept. 1995, coll. A.A. Golikov, R/V *Ya. Smirnitsky*, one specimen; Gulf of Yenisey. 73°10.7' N, 80°00' E, 32 m, clay, 12 Sept.1995, coll. A.A. Golikov, R/V *Ya. Smirnitsky*, one specimen; 73°26.81' N, 80°29.59' E, 13 m, silt, 10 Aug.1994, coll. V.V. Khlebowich, R/V *Ya. Smirnitsky*, seven specimens; Estuary of Taymyr river. 76°12.7' N, 98°26.7' E, 14 m, clay, 9 Sept.1995, coll. A.A. Golikov, R/V *Ya. Smirnitsky*, one specimen.

East-Siberian Sea, Chaun Bay, 12, 4-15 m, clayey silt, silt, Aug. 1986, 1990, 1992, coll. B. Sirenko and S. Yagaev, five specimens; Estuary of Indigirka, 71°03' N; 152°40.9' E, 9 m, clay, 27 Aug. 1995, coll. A. Komendantov, R/V *Ya. Smirnitsky*, one specimen; Blagoveshchenskiy Strait, 74°26' N; 145°15.7' E, 16 m, silty clay, 30 Aug. 1995, coll. A.A. Golikov, R/V *Ya. Smirnitsky*, one specimen.

Additional material. [North Atlantic], Eastern Canada, New Brunswick, Saint John River Estuary, 23 m, summer 1973, coll. P. Steer, one specimen from the United States National museum N 51934, now deposited at ZIRAS.

Redescription. Body long slender, divided into short, flattened thoracic region and elongated, more slender abdominal region. Length of the largest complete specimen from the Gulf of Ob (type-locality) 48 mm, width of thorax 1.7 mm excluding setae, 88 segments. Prostomium shield-shaped, with nuchal ridge on posterior half, extending to first segment; eyes absent (Fig. 1A). Thoracic region consists of 13, or 12 segments (in two specimens) with well developed biramous parapodia. Notosetae smooth capillaries, neurosetae of different kinds. Anterior four segments with different types of modified parapodia (Fig. 1B; 2A-C).

First segment with elongate, anteriorly directed postsetal parapodial lobes, with short and long smooth capillary setae in both rami.

Second segment without notosetae. Postsetal parapodial lobes subconical, notopodial somewhat larger than neuropodial (Fig. 1B). Capillary neurosetae of two kinds: smooth and long curved bispinous setae with dotted stems (Fig. 1D, E). The spines on the convex side of the seta are stouter than those on the concave side.

Third segment with rounded notopodial postsetal lobes. Neuropodial lobes low, wide, slightly undulate, postsetal lobes bilobed (Fig. 2A, B). Neuropodia with five to six stout, curved, smooth acicular setae alternating with dotted capillary setae (Fig. 2A, 1F).

Fourth segment notopodial and neuropodial lobes similar, postsetal ones slightly undulate with smooth capillary setae (Fig. 2C).

Thereafter eight to nine thoracic segments (5 to 12-13) more similar in shape than first to fourth segments (Fig. 2D). The anterior notopodial postsetal lobes rounded to subconical, becoming digitiform on segment 12 or 13. Neuropodial lobes similar, slightly undulate, short, wide, sometimes with small upper lobes. Two last thoracic segments with subconical postsetal neuropodial lobes, longer than setal lobes. Neurosetae of two kinds: 1) straight, lanceolate acicular with long hair and sometimes with short spine on blunt tips, 6-9 setae in each neuropodium, and 2) curved capillaries, sometimes hairy (Fig. 1G; 2E).

Segment 14 (most specimens) or 13 (two specimens) with notopodia reduced to small lobes. Notosetae absent. Neuropodia with conical postsetal lobes (Fig. 1C). Neurosetae of four kinds: one or two simple short hairy setae, one or two smooth slightly limbate setae, some acicular hairy setae with terminal sheath (Fig. 2F), and some longer smooth simple capillaries.

Abdominal region beginning on segment 15 or 14, long, flattened, thin-walled, transparent. Notopodia and notosetae absent in anterior abdominal region, except for small papillae on two or three anterior segments. Notosetae reappear as two to five brown pointed acicular spines more posteriorly from segments 21-35 (Fig. 2G; Fig. 3A, B). Postsetal neuropodial lobes continue on each segment as thin, slightly undulate longitudinal flanges (Fig. 3E), becoming shorter towards the posterior and absent on the posterior 20-22 segments (Fig. 3A, B). Acicular setae of three kinds: 1) simple with more or less blunt tip; 2) simple, tapering gradually to capillary tip and 3) setae with terminal sheath, projecting as a fine thread (Fig. 1H). Segments decreasing in size towards posterior end (Fig. 3A, B). Short papillae, one pair per segment, present ventrally on either side of the median line in posterior abdominal region.

Pygidium short with four leaf-like lobes and sometimes (two specimens) with a short anal cirrus (Fig. 3A-C). Anus terminal.

Colour in alcohol, grey-brown pigmentation on dorsum of anterior four segments (Fig. 1A) and in thoracic parapodia, abdomen transparent.

Tubes cylindrical, U-shaped, consisting of fine particles cemented together, with coalescent branches. Hard, rather thick-walled and brittle (Fig. 3D). The tube may be long, but we have only fragments.

Ecology. *T. carica* has been found in the Kara and East Siberian Seas at depths of 9 to 32 m in fine sediments, at bottom temperatures from -0.4 to 5° C, and salinities from

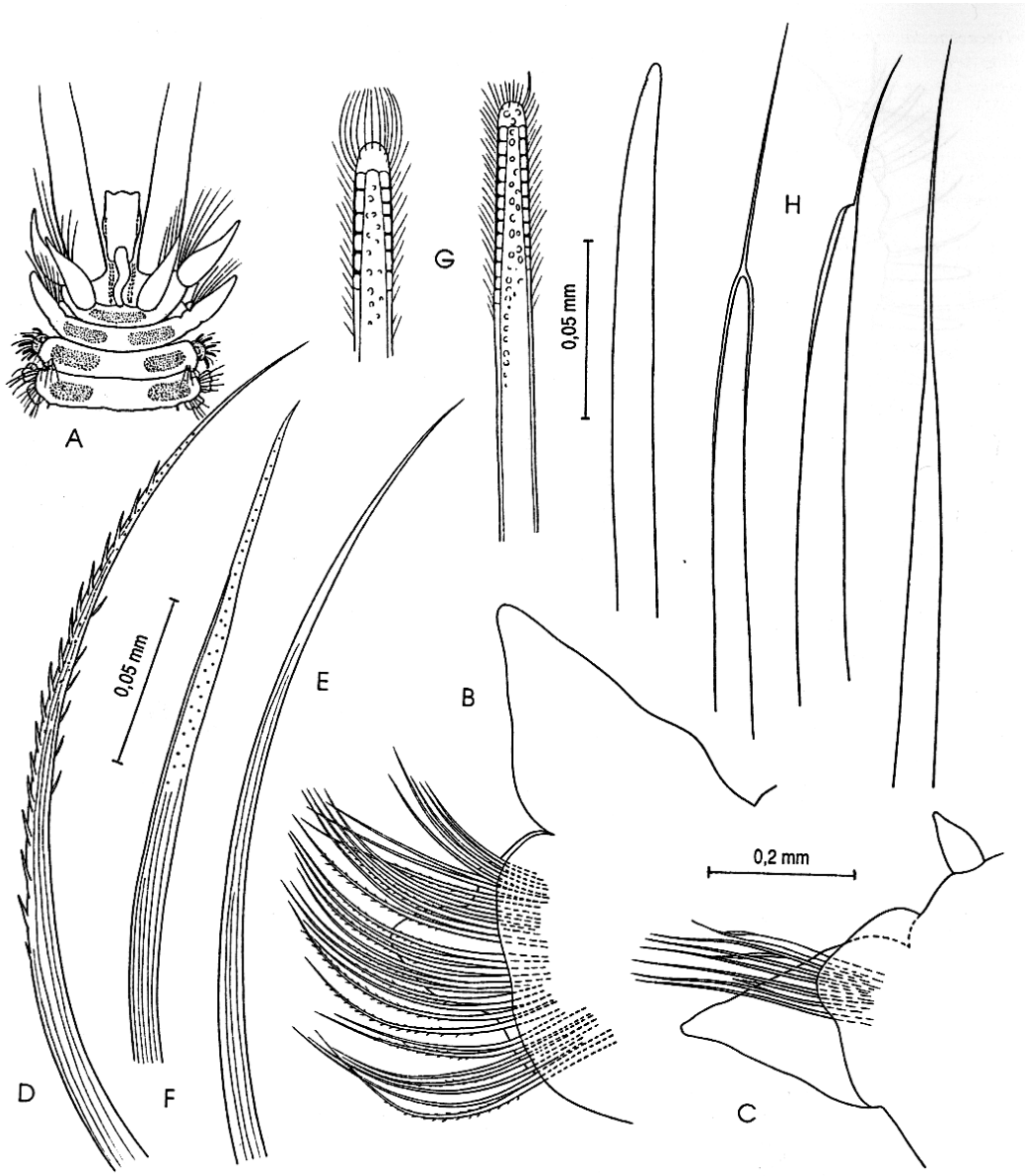

Fig. 1. *Trochochaeta carica* (Birula). A. Anterior end, dorsal view. B. Right parapodium 2, anterior view. C. Right parapodium 15, anterior view. D. Bispinous neuroseta from parapodium 2. E. Smooth capillary neuroseta from the same. F. Dotted capillary neuroseta from segment 3. G. Neurosetae from thoracic segments. H. Lower acicular neurosetae from abdominal segments. (Specimens from the Chaun Bay).

19 to 30 ‰. The species often occurs in estuarine areas of Siberian rivers.

Maximum population density and biomass (68 specimens, 1.1 g wet weight m^{-2}) were recorded in the Gulf of Ob in clay sediments at 17 m depth, with a bottom salinity of 29.2 ‰. The specimens were found in the upper 4-15 cm of sediment. The sediment surface was covered by a flocculant silt/clay layer, with underlying glutinous blue-

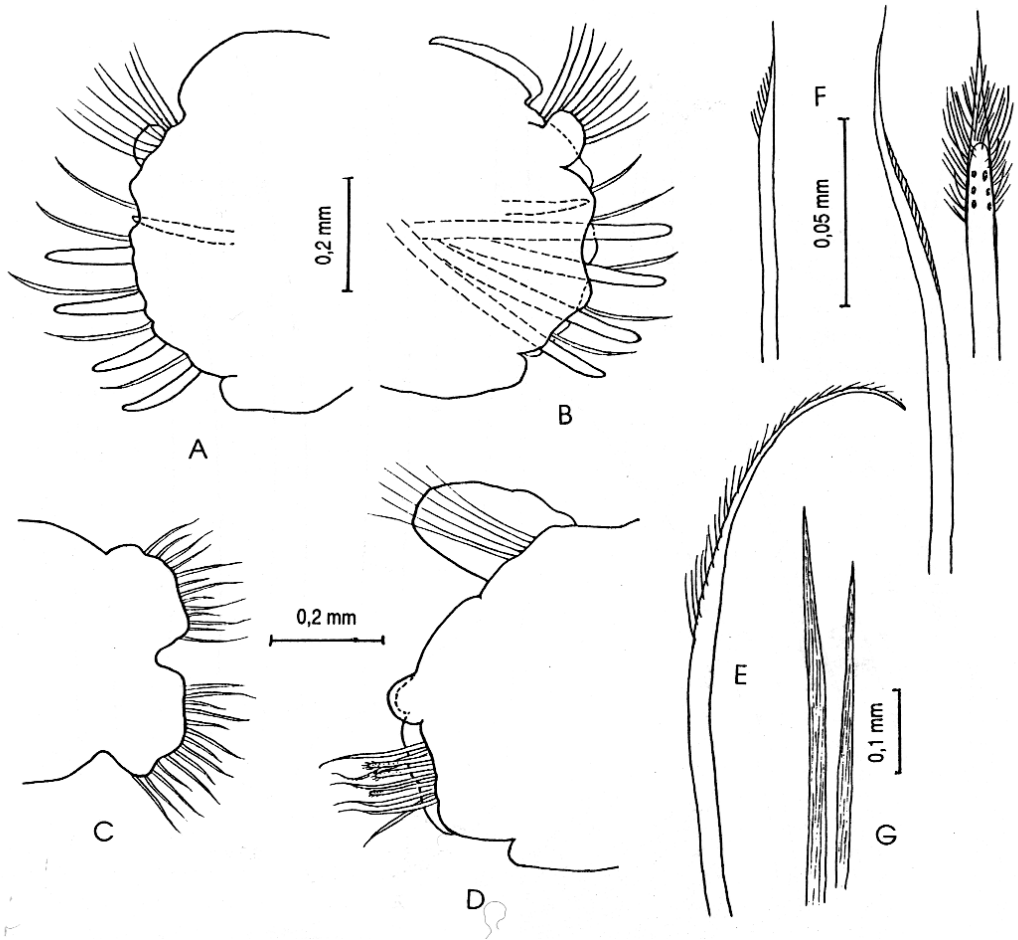

Fig. 2. *Trochochaeta carica* (Birula). A. Right parapodium 3, anterior view. B. The same, posterior view. C. Parapodium 4, posterior view. D. Right parapodium 7, anterior view. E. Neuroseta from the same. F. Three neurosetae from segment 14. G. Abdominal notosetae. (A-D, specimens from the Gulf of Ob; others from the Chaun Bay).

grey glacio-marine clay, or in some cases, sandy clay. The sediment contained approximately 17.7 % total organic carbon. The captured worms were usually found in the lower part of the U-shaped tubes. In the Gulf of Yenisey, a density of 23 specimens per m^2 was observed in silty sediments at 13 m depth and 19 ‰ bottom salinity.

Reproductive data. Eight sexually mature females and six males were collected on 15 Aug. 1993 and 10 Aug. 1994 in the Gulfs of Ob and Yenisey respectively (19 and 29.2 ‰ S, 0.05-2° C). The specimens contained sexual products in the abdominal region, beginning from segments 20-21. Females carried eggs in 20-30 segments, posterior 20-30 abdominal segments were without eggs. Up to 8-10 eggs per segment. Only 6-8 posterior segments of males were lacking sperm. Spermatozoa possess a large round head measuring 3.3 µm in diameter (Fig. 4G). The mature eggs from the body cavity were very large, ovoid, slightly flattened, without membrane vesicles and contained large quantities of yolk material (Fig. 4F). The diameter of these eggs was minimum 437 × 447 µm, maximum 500 × 564 µm and 405 × 650 µm. The nucleus is large, approximately 85 µm in diameter. In alcohol, the eggs are yellowish or pinkish in colour.

The type of development is apparently entirely lecithotrophic. The eggs develop in the maternal tubes up to at least the 20-21 segment larval stage. The larvae were obtained from tubes collected 15 Aug. 1993 (0.05° C, 29.2 ‰ S at the bottom).

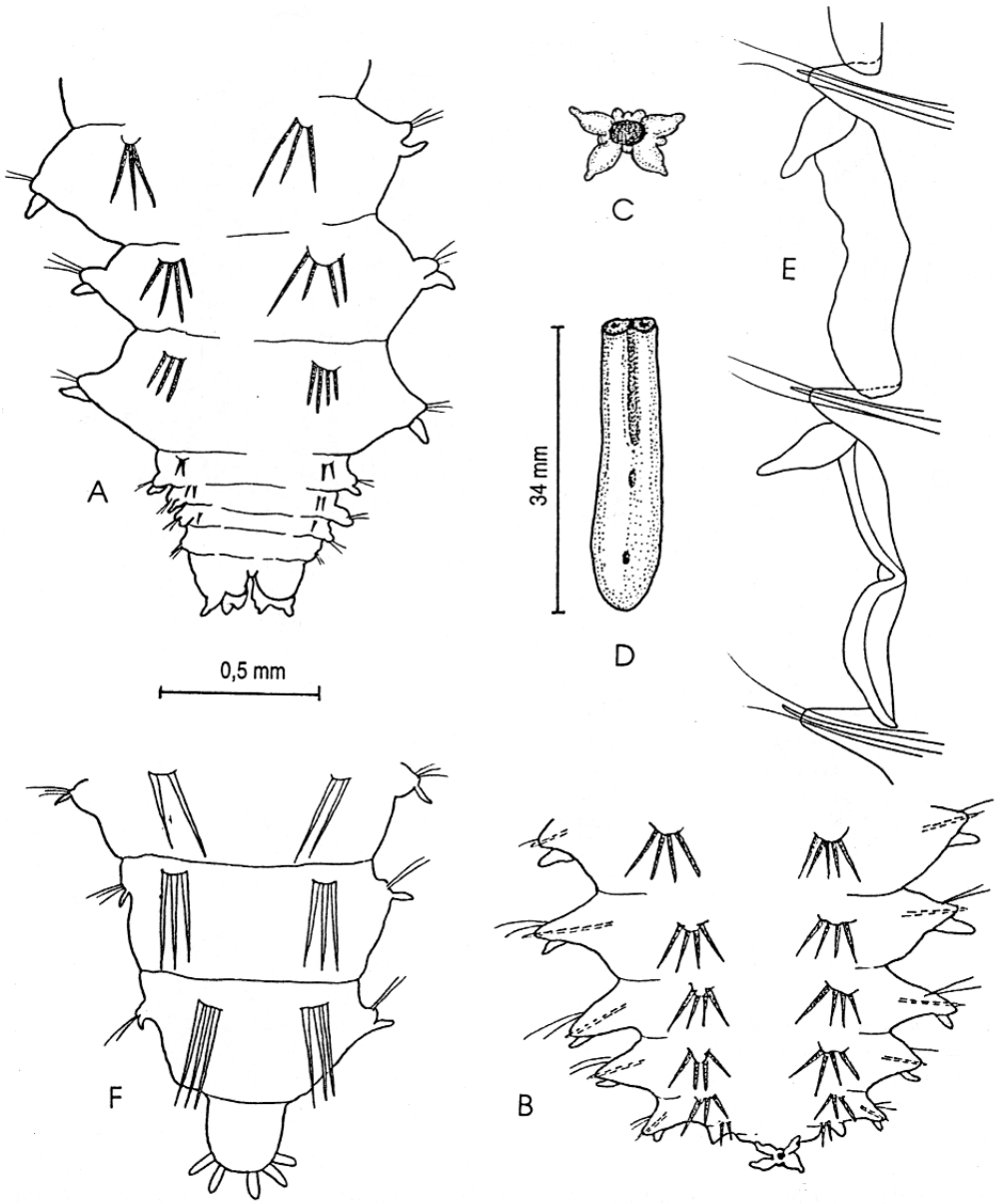

Fig. 3. *Trochochaeta carica* (Birula). A, B. Posterior ends of different specimens, dorsal view. C. Anus encircled by lobes. D. Fragment of tube, lower part. E. Abdominal neuropodia. (A-D, specimens from the Gulf of Ob; E, from the Chaun Bay). *Trochochaeta* sp. F. Posterior end, dorsal view. (Specimen from the Saint John River Estuary).

Description of 21-segment larva (Fig. 4A, B). Length of larvae 1.7-1.8 mm, thoracic width 0.5-0.56 mm excluding setae. Prostomium and peristome fused into an outspread 'umbrella'. Prostomium notched terminally, without eyes. Only one developed palp and no visible mouth. Eleven pairs well developed biramous parapodia. Provisional long bispinous bristles in 14 segments (Fig. 4A, B, E). Thin capillary slightly curved setae, approximately 2.5 μm width in anterior 12 segments. Second segment with one to two pairs slightly stouter and shorter neuropodial setae with curved tips (width 3.3 μm, Fig. 4C). Third segment with two pairs of large neurosetae, (about 10 μm width, Fig. 4D). Pygidium short, with four large lobes. Pharynx in the first three segments. Alimentary canal weakly differentiated. Cilia were not visible on the fixed larvae.

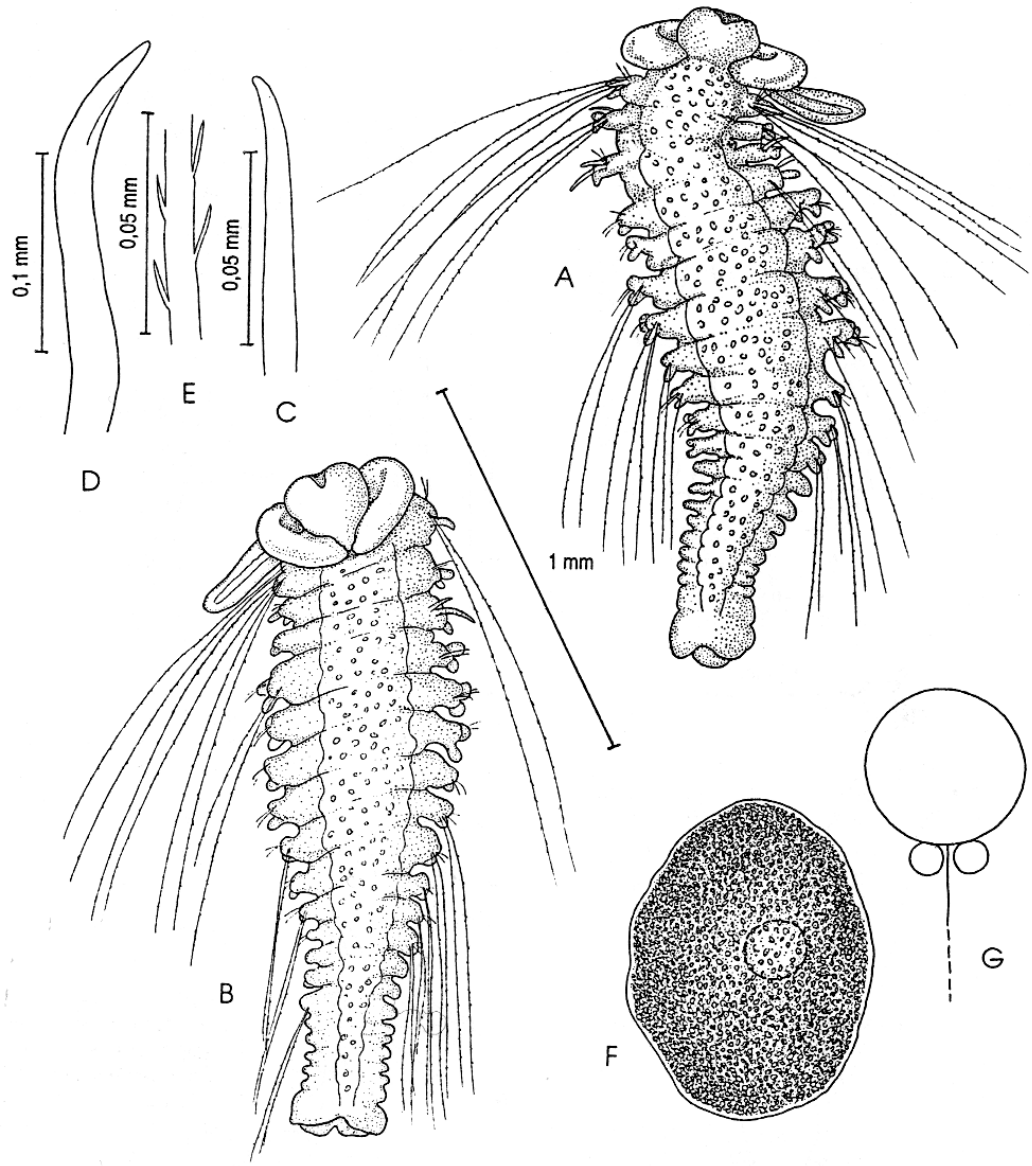

Fig. 4. *Trochochaeta carica* (Birula). A. Larva, dorsal view. B. The same, ventral view. C. Seta from segment 2. D. Seta from segment 3. E. Detail of provisional swimming seta. F. Egg. G. Sperm. (Specimens from the Gulf of Ob).

COMPARISON AND DISCUSSION

The North Atlantic specimens of Trochochaeta, identified by Pettibone (1976) as *T. carica*, differ from the holotype and other Arctic specimens in possessing 15 thoracic segments instead of 12-13, the pygidium is compact and cylindrical instead of short, and the anus is encircled by filiform anal cirri, not lobulated, as in *T. carica* (Fig. 3F; Pettibone 1976, fig. 1h). In addition, the abdominal neuropodial setal lobes are shorter than those of *T. carica*, and the tubes are soft, not hard. The North Atlantic specimens have more segments than those from the Arctic. For example, the 40 mm long specimen from Eastern Canada described by Pettibone (1976), has 130 segments, while one of the specimens from the Gulf of Ob, although 48 mm in length, has only 88 segments. It is also important that the 20-21-segment stage of *T. carica* already possesses a four-lobed pygidium. North Atlantic specimens appear to resemble more closely *T. pettiboneae* Dean, 1987, described from the Gulf of Maine.

The fragment from the Bering Strait identified as *T. carica* by Annenkova (1952) is indeterminable. Based on the above considerations, and also on the absence of the species in numerous benthic samples from the Far Eastern and Barents Seas, the distribution of *T. carica* is likely to be limited to high Arctic waters. Specimens of *T. carica* were found in reproductive condition in August, when relatively high water temperatures and salinities are observed in Arctic Seas.

Based on investigation of the larval development of *Trochochaeta multisetosa*, Hannerz (1956) and Pettibone (1976; 1982) considered the early development of Trochochaetidae as entirely pelagic, and characterized the larvae as predominantly planktotrophic. However, the present study shows that development of *T. carica* takes place predominantly within the maternal tube, and the larvae are entirely lecithotrophic. The size of yolky eggs of *T. carica* are much greater than the 200-250 µm, observed in *T. multisetosa*. In addition, the eggs of *T. multisetosa* differ from those of *T. carica* in their discoid form and by the presence of numerous membrane vesicles. The late larval stage of *T. carica* agrees with the pelagic larva of *T. multisetosa* in having an 'umbrella', long bispinous provisional setae, and coarse setae in the third segment. However, the former lacks prostomial eyes as distinct from the latter, and both larval forms also differ in the shape of the pygidium as well as the coarse setae of the third segment. In addition, we could not find the mouth in *T. carica* larvae, and the alimentary canal is weakly differentiated in the 21-segment stage, even compared with 11-segment larva of *T. multisetosa*. Moreover the 22-segment stage of *T. multisetosa* is already a juvenile benthic worm, lacking the outspread 'umbrella' and provisional bristles. On the other hand, the 21-segment larva of *T. carica* from the maternal tube is characterized by the 'umbrella' and long swimming provisional setae in the majority of segments.

It therefore follows that *T. carica* has a pelagic period in its larval development. This pelagic phase appears to be short, but important for the dispersion of this species, which as an adult adopts a sedentary, tubicolous mode of existence. The data speak in favour of the assumption of Mileikovsky (1971) about existence of lecithotrophic pelagic larval development of marine bottom invertebrates in the highest latitudes. It is interesting that the larva of *T. carica* has two pairs of short provisional neurosetae on the second segment, which disappear in the adult (Fig. 4C). These setae resemble the acicular spines in the same segments of adult *T. multisetosa, T. diverapoda* (Hoagland 1920) and *T. kirkegaardi* Pettibone, 1976.

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