Redescription of Japanese *Bdellocephala annandalei* from Lake Biwa-ko with comparative redescription of the Far Eastern and Kamchatkan *Bdellocephala* species (Tricladida, Paludicola)

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ABSTRACT. *Bdellocephala annandalei* Ijima et Kaburaki, 1916, is an endemic planarian of Lake Biwa-ko in Central Japan. This lake-dwelling species inhabits the muddy bottom of the northern basin of the lake (20-103 m in depth). The species is characterized by its comparatively large size, uniformly light brown coloration, two small eyes, and a subterminal, ventral adhesive organ on the frontal end. A detailed taxonomic redescription of *B. annandalei* is given here and compared with the other three Far Eastern and Kamchatkan *Bdellocephala* species inhabiting epigean waters.

KEY WORDS: Platyhelminthes, Dendrocoelidae, Bdellocephala, Lake Biwa-ko, Japan, taxonomy.

INTRODUCTION

Lake Biwa-ko, located in the central part of Honshû, is the largest and oldest lake in Japan. Topographically, the lake consists of two parts, the northern basin (a wide and deep part; deepest point, 103.6 m) and the southern basin (a narrow and shallow part). The stratigraphic records of sediment indicate that the former has existed continuously for 0.43 m. yr. (MEYERS et al., 1993).

The occurrence of a large, flat, leech-like animal in the profundal zone of the lake has been recognized by fishermen of Lake Biwa-ko. Scientific samples of this large planarian were first collected from the profundal area of the lake by T. N. Annandale (1876-1924) and T. Kawamura (1883-1964) in the autumn of 1915. Then, the species was described as *Bdellocephala annandalei* by IJIMA & KABURAKI (1916). Although this original description was very simple, it contains woodcuts of a general view of the

body, an adhesive organ and a sagittal view of the copulatory apparatus. Later, Kaburaki (1922) gave a rather old-fashioned redescription of this species with three figures (an animal in color, and newly prepared figures of the adhesive organ and the copulatory apparatus).

The limnobiological survey made after the 1950s confirmed the presence of *B. annandalei* from various areas of the northern basin (KAWAKATSU, 1969; 80-81, pl. VIII, fig. 16; KAWAKATSU & NISHINO, 1993: 100, pl. III; 1994: 97-100; NISHINO & WATANABE, 2000). The latest distribution map of *B. annandalei* was shown in a paper by OKI et al. (1998: 316, fig. 1; see also KAWAKATSU & NISHINO, 1993: 100, pl. III; KAWAKATSU et al., 1996, 8: fig. 7). A complete list of literature for this lake-dwelling species will be found in KAWAKATSU & NISHINO (1993, 1994).

The basic purpose of this paper is to give a detailed redescription of this species from a modern taxonomic point of view. Chromosome numbers and the karyotype of *B. annandalei* have already been reported (OKI et al., 1998). The genus *Bdellocephala* de Man, 1875, is poorly defined (SLUYS et al., 1998). Based on the new data on the compar-

ative anatomy of the copulatory apparatus of the known *Bdellocephala* species, some taxonomic remarks are made.

MATERIAL AND METHODS

Kawakatsu has numerous preserved specimens of *B. annandalei* from various stations of the lake. For the present taxonomic study, the following samples in his collection were used; Specimen Lot Number registered in Kawakatsu's fixing notebook (KSL No.; simply shown as MK in the following sections) is given for each vial of samples.

KSL No. 381: Off Ômi-Hachiman City (depth, 40 m); fixed with 3% formalin solution (Oct. 23, 1962; coll. Dr. M. Nagoshi). / KSL Nos. 392 and 393: Off Oki-no-shima Island (depth, 30-45 m); fixed with Bouin's fluid (Sept.-Oct., 1963; coll. Mr. R. Chaya). / KSL No. 394: Off Onoe (depth, 40-60 m); fixed with Bouin's fluid (Sept.-Nov., 1963; coll. Mr. S. Matsuoka). / KSL No. 428: the same area as KSL Nos. 392 and 393; fixed with Bouin's fluid (Sept.-Oct., 1964; coll. Mr. R. Chaya). / KSL No. 1666 (2 sexual and 2 asexual specimens of *Bdellocephala* sp. according to Dr. Teshirogi's team): Off the Tsuzurao-zaki Cape (depth, 40-60 m); fixed with Bouin's fluid (Sept. 29, 1981; coll. Mr. M. Yagihashi).

Three large sexual specimens from the KSL No. 392 stained with borax-carmine were prepared as whole mounts. Many sets of serial sections (7-8 μ m) of the sexual specimens from the KSL Nos. 381, 392-394, 428, and 1666 were prepared. These sagittal, transverse and horizontal sections were stained with Delafield's hematoxylin and erythrosin or Mallory's triple stain.

Taxonomic comparison of lake-dwelling *B. annandalei* has been made with another epigean water species, *Bdellocephala brunnea* Ijima & Kaburaki, 1916. The following samples of the latter collected from the Lake Biwa water system were employed.

KSL Nos. 2287 (1 sexual and 1 asexual specimens) and 2288 (3 sexual specimens): Downstream of the Amagase Dam, Uji-gawa River (approximately 18 km downstream from the outlet of the lake), Uji City, in Kyôto Pref.; fixed with 70% ethanol (Oct. 31, 1997 and Jan.10, 1998; coll.

Nishino, in cooperation with Dr. H. Abe in the former and Mr. N. Kobayashi in the latter. Serial sections with Mallory-Carson hematoxylin and eosin staining were prepared by Sluys and are now housed in the Zoological Museum, University of Amsterdam: V. Pl. 946.1 (sagittal sections on 2 slides; MK 2287-1); V. Pl. 946.2 (sagittal sections on 8 slides; MK 2288-2); V. Pl. 947.1 (sagittal sections on 8 slides; MK 2288-1); V. Pl. 947.2 (sagittal sections on 14 slides; MK 2288-2).

For comparative purpose, serial sections of *Bdellocephala borealis* Kawakatsu, 1978 (Kawakatsu's collection) and *Bdellocephala grubiiformis* (Zabusova, 1929) (Timoshkin's collection; loc. Dalnee Lake, Kamchatka) were restudied by Kawakatsu and partly by Sluys.

RESULTS

Systematic

Suborder Tricladida Lang, 1884 Infraorder Paludicola Hallez, 1892 Family Dendrocoelidae Hallez, 1892 Genus *Bdellocephala* de Man, 1875

Description of *Bdellocephala annandalei* Ijima et Kaburaki, 1916

Photographs of *B. annandalei* in life are shown in KAWAKATSU & NISHINO (1993: 98, pl. I, fig. A; see also fig. B for the preserved condition) and KAWAKATSU et al. (1996: 7, fig. 6 D) (Fig. 1). Large, sexually mature specimens measure up to 35-40 mm or more in length and 10 to 12 mm in width. The body is of a low rotundate shape with a pair of bluntly protruded, elongated auricles on each side. The colorless sensory organ with elongated oblanceolate shape is visible on the outer side of the auricles. Two small eyes, each surrounded by a lanceolate, pigment-free ocular area, are present at middle level of the head. The space between them is nearly one half the width of the head at the level of eyes. Behind the auricles, the body first narrows slightly, then widens at the level of pharynx and copulatory apparatus. The posterior end of the body is obtuse.

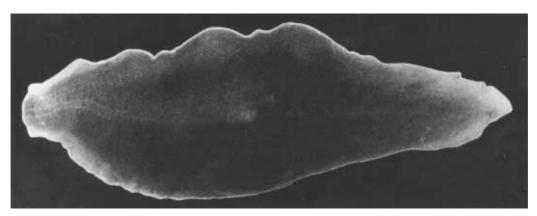


Fig. 1. – Bdellocephala annandalei. A dorsal view of a live specimen (ca. 50 mm long).

The ground color of the dorsal surface of the body is uniformly light brown to grayish tint. The body margin and the areas above the pharynx and copulatory apparatus are of a lighter hue. A narrow, indistinct, whitish, mid-dorsal double line can be seen on the prepharyngeal region of the body. The ventral surface is pale compared to that of the dorsal body.

B. annandalei has a frontal, subterminal, adhesive organ located on the ventral side of the body. It is a shallow, reniform organ with longitudinal folds. The surface of the organ is covered with glandular epithelium. Numerous, thickly swollen erythrophilic gland ducts filled with a granular secretion are found here; their cell bodies are scattered through the mesenchyme of this region. The muscular system of the organ is rather weakly developed. The marginal adhesive zone is well developed.

The subepithelial musculature of the dorsal body consists of the following layers: 1) a rather thick layer of circular fibres, with the more inside fibres being more loosely arranged, 2) a layer of diagonal fibres, and 3) a rather thick layer of loose, longitudinal (partly diagonal) fibres. On the ventral body, the subepithelial muscle zones are: 1) a rather thick layer of circular fibres, with the more inside fibres being more loosely arranged, 2) a thick layer of longitudinal muscle, and 3) a layer of diagonal fibres.

The pharynx is located at about the middle of the body and is one-fifth to one-sixth the body length. Its internal muscle zone consists of a very thick layer of intermingled circular and longitudinal fibres. The outer muscle zone of the pharynx consists of three layers: 1) thin, longitudinal fibres, 2) very thick, circular fibres and 3) rather thick, longitudinal fibres.

It was clear from the examination of whole mounts and histological sections of fully sexual specimens that the dorsal testes are small in size and numerous. Testes occur from behind the ovaries to nearly the posterior end of the body. In the prepharyngeal region, they are arranged on either side of the midline in eight to ten longitudinal zones, whereas in the pharyngeal and postpharyngeal regions there may be up to six zones. The spermiducal vesicles located on either side of the pharyngeal and postpharyngeal regions, from the anterior level of the mouth to the middle level of the penis bulb, are well developed in *B. annandalei*.

A pair of small ovaries occurs on the ventral side of the anterior region between the third and fourth intestinal diverticula. The two oviducts run posteriorly and unite to form a rather long common ovovitelline duct slightly anterior to the level of the genital pore. The yolk glands (or vitellaria) are distributed in the surrounding parenchyma.

The sagittal view of the copulatory apparatus of a well-extended specimen is shown in Fig. 2 (MK 392-a: redrawn from a pencil sketch of the organ from the same specimen in KAWAKATSU et al., 1996: 8, fig. 8).

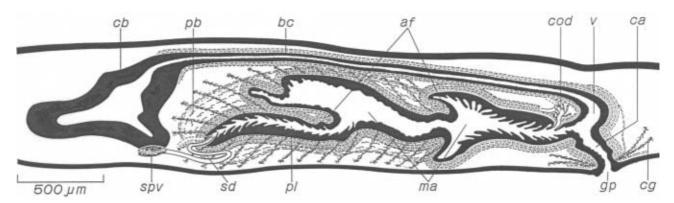


Fig. 2. – *Bdellocephala annandalei*. Sagittal view of the copulatory apparatus (MK 392-a). af, atrial fold; bc, bursal canal; ca, common genital antrum; cb, copulatory bursa; cg, cement gland; cod, common ovovitelline duct; gp, genital pore; ma, male genital antrum; pb, penis bulb; pl, penis lumen; sd, sperm duct (vas deferens); spv, spermiducal vesicle; v, vagina..

The male copulatory apparatus consists of two parts. An ovoid penis, of which the underside and the posterior half of the upperside, is embedded in the parenchyma; a wide, tubular, posterior portion has conspicuous folds. The former represents the penis bulb and is highly muscular. The tubular penis lumen is lined with a thick, highly glandular, nucleate epithelium with many plicae. Its surrounding muscular coat consists of three layers, i.e., a thin longitudinal, a thick circular layer intermingled with a few longitudinal fibres, and a rather thick, longitudinal

layer. The two vasa deferentia (sperm ducts) open separately into the penis lumen, which opens posteriorly into the anterior portion of the male genital antrum.

The shape of the male antrum varies between sectioned specimens. It is essentially a wide, tubular cavity that opens into the anterior section of the common genital antrum; sometimes, it shows a uroceolate or a calceolate cavity. The male antrum has several well-developed, dorsal and ventral folds. Sometimes, the antrum is almost separated into two cavities by a pair of well-developed

folds. The entire wall of the male antrum is covered with a very thick, glandular, nucleate epithelium (with many plicae in the posterior narrow portion) below which there are two muscle layers, one thick circular layer intermingled with longitudinal fibres, and the other longitudinal. The penis bulb and the wall of the anterior half of the male antrum are pierced by many erythrophilic gland ducts. The common ovovitelline duct opens dorsally near the posterior terminal portion of the male antrum.

In many slides of *B. annandalei*, a poorly developed, penis papilla-like projection is formed by the atrial folds located at the anterior portion of the male genital antrum. This structure may function as the penis papilla, found commonly in many other species and genera of triclad turbellarians. The penis lumen in this species functions as the seminal vesicle and ejaculatory duct.

The copulatory bursa is a middle- to large-sized organ of an ovoid, or pear shape. The bursal canal is a very long, slender duct that runs dorsally to the penis bulb and male antrum, and opens into the roof of the common antrum. The canal is lined with a tall, glandular, nucleate epithelium. The muscular coat surrounding the anterior and middle sections of the canal consists of an inner, thin layer of longitudinal fibres, a middle, thin layer of circular ones and an outer, thin layer of longitudinal muscle fibres. The posterior terminal section of the canal forms a moderately developed vagina lined by a thick, glandular epithelium and a moderately thick muscle coat (especially the circular muscle fibres). The short, tubular, common genital antrum communicates ventrally into the genital pore. Weakly erythrophilic cement glands open into the terminal part of the common antrum.

The cocoon of *B. annandalei* is spherical in shape (3-4 mm in diameter), having no stalk.

Bdellocephala sp. reported as a new species (YAGIHASHI et al., 1995) is undoubtedly a juvenile form or a small-sized specimen of *B. annandalei* (OKI et al., 1998: 316). The sagittal view of the copulatory apparatus of one of these small specimens is shown in a previous paper (KAWAKATSU et al., 1996: 9, fig. 9, MK1666-a).

Comparative redescription of the Far Eastern and Kamchatkan *Bdellocephala* species

Among the three known *Bdellocephala* species in Japan, *B. brunnea* is a species distributed from Kyôto Prefecture to Aomori Prefecture in Honshû (KAWAKATSU, 1969). The occurrence of this species in Okushiri Island in Southern Hokkaidô was recently reported by NISHITANI et al. (1995; see also NISHITANI, 1998). This species is usually found in rather cool waters, such as shallow springs, spring-fed streams and outlets of lakes.

B. brunnea has a dark to blackish coloration and measures between 10 and 20 mm in length and 3 to 5 mm in width. The head is truncate (or retuse when in an elongated condition) with a pair of blunt auricles; two eyes are

conspicuous. Morphologically and histologically, the adhesive organ in this species is more developed than in *B. annandalei*; both erythrophilic and cyanophilic glands can be found.

The animals examined from the Amagase Dam (KSL Nos. 2287-2288) have brownish tint in coloration, which is rare in this species. On the dorsal body, the subepidermal musculature consists of the following layers: 1) a thin, subepidermal layer of circular muscle, 2) a thin layer of longitudinal muscle, 3) a layer of diagonal fibres, and 4) a layer of longitudinal muscle fibres. On the ventral surface, the musculature is somewhat more complex: 1) a thin, subepidermal layer of circular muscle, 2) a thin layer of longitudinal muscle, 3) a layer of diagonal fibres, 4) a thick layer of longitudinal muscle, followed by 5) a thin layer of loosely arranged circular muscle fibres.

The outer pharyngeal musculature consists of three layers: 1) directly underneath the outer pharynx epithelium a thin layer of longitudinal muscle, 2) a thin layer of circular muscle, and 3) a distinct layer of longitudinal muscle. The zone of muscles adjacent to the inner pharynx epithelium consists of a thick layer of intermingled circular and longitudinal muscle fibres.

The sagittal view of the copulatory apparatus of this Amagase specimen is shown in Fig. 3. The anatomy of the copulatory apparatus of *B. brunnea* is very similar to that of *B. annandalei* (except for their dimensions). The subepithelial muscle zone of the genital antra and the muscle coat of the bursal canal (including the vaginal portion) are more weakly developed in *B. brunnea* than those of *B. annandalei*. According to Kawakatsu's study of the copulatory apparatus of *B. brunnea* from many locations in Japan, the degree of development of musculature in the copulatory apparatus varies to some extent in animals from different localities (unpublished data except for fig. 7 C and D in KAWAKATSU et al., 1978, reported erroneously as *B. borealis* from Okushiri Island in Hokkaidô). In the Amagase specimen, the vagina has a thin muscle coat.

Bdellocephala borealis Kawakatsu, 1978, is a middle-sized species known only from its type locality (an outlet of Hime-numa Pond) in Rishiri Island, Northern Hokkaidô (KAWAKATSU et al., 1978). The external appearance of this species is very similar to that of *B. brunnea*. However, the dorsal surface of *B. borealis* is uniformly grayish brown with numerous, small, indistinct, reddish brown pigment spots. The adhesive organ is well-developed in *B. borealis* (cf. KAWAKATSU et al., 1978: 84-85, figs. 3 A-D, 4).

The subepithelial muscle zone of the dorsal body consists of a thin, circular layer underlying the epithelium, next a rather thin layer of diagonal fibres, and the third, thick layer of loosely arranged, longitudinal fibres. The ventral subepithelial muscle zone consists of a thin, circular layer adjoining the ciliated epithelium, next a thin layer of diagonal fibres, the third, rather thick, longitudi-

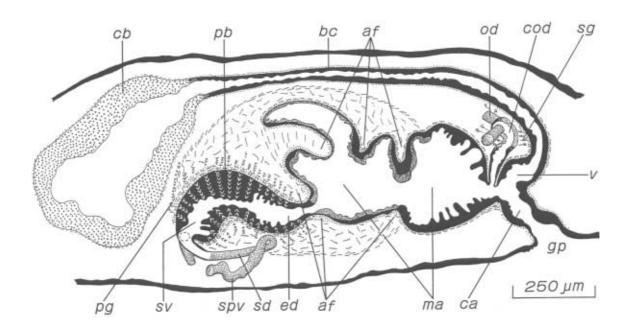


Fig. 3. – *Bdellocephala brunnea*. Sagittal view of the copulatory apparatus of a specimen from the Amgase Dam in the Lake Biwa water system (V. Pl.947.1; MK 2288-a). od, oviduct (ovovitelline duct); sg, shell gland; ed, ejaculatory duct; pg, penis gland; sv, spermiducal vesicle (bulbar cavity). For other abbreviations, see Fig. 2.

nal fibres; inside the third layer, the fourth, thick, diagonal fibres can be seen.

The outer pharyngeal muscle zone consists of five layers: a thin layer of diagonal fibres, next a thin layer of circular fibres, the third, thin layer of longitudinal fibres, the fourth, thick later of diagonal fibres, and the fifth, rather thick, longitudinal fibres.

In the copulatory apparatus of *B. borealis*, the musculature of the penis bulb and genital antra is well developed; the beginning of the penis lumen forms a narrow, napiform seminal vesicle; the muscle coat surrounding the vagina is well developed (cf. KAWAKATSU et al., 1978: 88, fig. 7 A and B, 91, fig. 8 C-E, 93, fig. 9 A-F).

Bdellocephala grubiiformis (Zabusova, 1929), is now considered a separate species, widely distributed only in Kamchatka, Primorskiy and Sakhalin (PORFIRJEVA et al., 1979; DYGANOVA & PORFIRJEVA, 1990: 81, fig. 47). Morphologically and anatomically, this species from the Russian Far East is similar to Japanese bdellocephalid species.

The subepithelial muscle zone of the dorsal body consists of a thin layer of circular fibres, next a thick layer of diagonal fibres, and the third, rather thick layer of loosely arranged, longitudinal fibres. The ventral subepithelial muscle zone consists of a thin, circular layer, next a thin layer of longitudinal fibres, and the third, rather thick layer of diagonal fibres.

The histology of the outer pharyngeal musculature of *B. grubiiformis* is very similar to that of *B. borealis*. The

fifth layer of longitudinal fibres is less developed in the former than in the latter.

In the copulatory apparatus of *B. grubiiformis*, a globose penis bulb with a calceolate penis lumen, a rather wide, male genital antrum with well-developed atrial folds, and a poorly developed vagina are conspicuous (Fig. 4).

Bdellocephala sp. from Shumshu (Simusyu) Island, the North Kurile Islands (MIYADI, 1937: 450) seems to be B. grubiiformis. The occurrence of Bdellocephala sp. in the NE China was reported by LIU (1993: 125, fig. 3, etc.). There is a fair possibility that this unidentified species is B. grubiiformis because the Chinese localities are located adjacent to Primorskiy (cf. KAWAKATSU, 1994: 53, fig. 3; 1996: 6, fig. 4).

Karyology

The chromosome numbers and the karyotypes of three Japanese *Bdellocephala* species are as follows:

B. brunnea: 2x = 28 and n = 14. Karyotype: 22 M + 6SM (Dahm, 1963; Nishitani et al., 1995; Nishitani, 1998). In the Okushiri population, animals with 42 chromosomes were also found (Nishitani et al., 1995); Nishitani (1998) considered it to be a triploidic form (i.e., 3x = 42 according to our karyological formula).

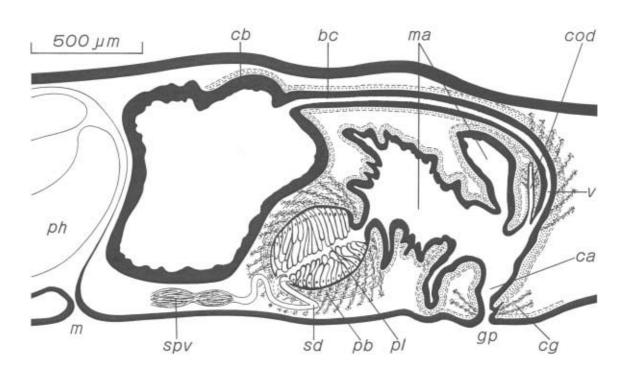


Fig. 4. – *Bdellocephala grubiiformis*. Sagittal view of the copulatory apparatus of a specimen from Dalnee Lake, Kamchatka (Timoshkin's collection). m, mouth; ph, pharynx. For other abbreviations, see Fig. 2.

B. borealis: 2x = 56 and n = 28. Karyotype: 38M + 18SM (NISHITANI et al., 1995; NISHITANI, 1998).

On the status of Dendrocoelopsis ichikawai

A short discussion about the molecular data of *Bdellocephala* species from Japan, Kamchatka and Lake Baikal in Russia was given in a previous paper (OKI et al., 1998). In a recent paper by KUZNEDELOV et al. (2000) based upon the 18S rRNA sequence data, a taxonomic revision of the genera, *Bdellocephala* de Man, 1875, and *Dendrocoelopsis* Kenk, 1930, was suggested. They argued that *Dendrocoelopsis* should be revised, and that the generic status of *Dendrocoelopsis ichikawai* Kawakatsu, 1977, should be reconsidered, since their results suggested that *D. ichikawai* belongs to the genus *Bdellocephala*.

We re-examined several sets of serial sections of *D. ichikawai* used in the original description (KAWAKATSU et al., 1977). However, we could not find any unique morphological, anatomical and histological characters thereby *D. ichikawai* should be transferred into the *Bdellocephala*. Notably, *D. ichikawai* shows a well-developed penial papilla, in contrast to the *Bdellocephala* species, and should remain in *Dendrocoelopsis*.

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