

Caryophyllidean tapeworms (Platyhelminthes: Eucestoda) from freshwater fishes in Japan

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Abstract. The following caryophyllidean tapeworms were found in freshwater fishes from Japan (species reported from Japan for the first time marked with an asterisk): family Caryophyllaeidae: *Paracaryophyllaeus gotoi* (Motomura, 1927) from *Misgurnus anguillicaudatus* (Cantor); *Archigetes sieboldi* Leuckart, 1878 from *Pseudorasbora parva* (Temminck et Schlegel) and *Sarcocheilichthys variegatus microoculus* Mori (new hosts); family Lytocestidae: **Caryophyllaeides ergensi* Scholz, 1990 from *Tribolodon hakuensis* (Günther), *T. ezoe* Okada et Ikeda, *Hemibarbus barbus* (Temminck et Schlegel) and *Chaenogobius* sp. (new hosts); *Khawia japonensis* (Yamaguti, 1934) from *Cyprinus carpio* Linnaeus; *K. sinensis* Hsü, 1935 from *H. barbus* (new host) and *C. carpio*; **K. parva* (Zmeev, 1936) from *Carassius auratus langsdorffii* Valenciennes in Cuvier et Valenciennes and *Carassius* sp. (new hosts); and **Atractolytocestus sagittatus* (Kulakovskaya et Akhmerov, 1962) from *C. carpio*; family Capingentidae: **Breviscolex orientalis* Kulakovskaya, 1962 from *H. barbus* (new host); and Caryophyllidea gen. sp. (probably *Breviscolex orientalis*) from *C. carpio*. The validity of *C. ergensi*, originally described from *Leuciscus leuciscus baicalensis* from Mongolia, is confirmed on the basis of an evaluation of extensive material from Japan. *Atractolytocestus sagittatus* (syn. *Markevitschia sagittata*) is tentatively considered a valid species, differing from the only congener, *A. huronensis* Anthony, 1958, in its considerably greater number of testes.

The cestode fauna of freshwater fishes of Japan has been studied since the 1930s when Yamaguti (1934) reported a number of fish tapeworms, some of them new to science, including two caryophyllidean species, *Caryophyllaeus japonensis* (= *Khawia japonensis*) and *Glaridacris limnodrili* (= *Paraglaridacris limnodrili* according to Mackiewicz 1994). *Khawia japonensis* was described from the intestine of common carp, *Cyprinus carpio* (Cyprinidae) from Lake Biwa (Shiga Prefecture) and *P. limnodrili* from adults found in the intestine of *Pseudogobio esocinus* (Cyprinidae) and *Misgurnus anguillicaudatus* (as *M. fossilis*) (Cobitidae) from the suburbs of Kyoto and in the body cavity of the tubificid oligochaete *Limnodrilus* sp. from the Kamo River. Yamaguti (1952) found *Paraglaridacris limnodrili* in *Pseudogobio esocinus* from Lake Suwa (Nagano Prefecture). Yamaguti (1934) also reported *Caryophyllaeus gotoi* Motomura, 1927 (= *Paracaryophyllaeus gotoi*), a species originally described from Korea. Nakajima and Egusa (1978) recorded *Khawia sinensis* Hsü, 1935 from common carp cultured in central Japan. Shimazu (1981) recorded “a monozootic cestode” from *Tribolodon ezoe* in Hokkaido. Nagasawa et al. (1989) and Awakura (1994) dealt with this cestode as “Caryophyllidea gen. sp.” Shimazu (1997) listed in

this review of tapeworms of freshwater fishes in Japan *K. japonensis* and *C. gotoi*.

In addition to the above-mentioned species found in fishes, Motomura (1929) obtained adults of *Archigetes sieboldi* Leuckart, 1878 (under the name *A. appendiculatus* Ratzel, 1897) from the body cavity of tubificid oligochaetes, *Limnodrilus gotoi*, *L. willeyi* and *Tubifex hattai*, from Sendai (Miyagi Prefecture) and Tokyo.

During studies on the helminth parasites of freshwater fishes in Japan carried out by three of the present authors (T. Shimazu, K. Nagasawa and T. Scholz), a number of tapeworms of the order Caryophyllidea were collected. As some of them were not reported previously from Japan, the species found are listed in the present paper with data on their morphology, spectrum of fish hosts and distribution in Japan.

MATERIALS AND METHODS

The specimens studied were found in the intestine of the following fish species: order Cypriniformes: *Carassius auratus langsdorffii* Valenciennes in Cuvier et Valenciennes, *Carassius* sp., *Cyprinus carpio* Linnaeus, *Hemibarbus barbus* (Temminck et Schlegel), *Pseudorasbora parva* (Temminck et Schlegel), *Sarcocheilichthys variegatus microoculus* Mori, *Tribolodon hakuensis* (Günther) and *T. ezoe* Okada et Ikeda

(all Cyprinidae); *Misgurnus anguillicaudatus* (Cantor) (Cobitidae); Perciformes: *Gymnogobius* sp. (Gobiidae). Data on localities and dates of sampling are provided in a survey of species below.

The cestodes were fixed using different methods: flattened and fixed with alcohol-formalin-acetic acid (AFA) or 70% ethanol, or fixed with hot fixative (AFA, Bouin's fixative or 5% neutral formaldehyde solution); they were then stained with Heidenhain's iron haematoxylin, alum carmine or borax carmine. Sections (thickness 15 µm) were made using standard procedures and stained with haematoxylin-eosin. Measurements are in micrometres unless otherwise stated; descriptions are based on gravid specimens only. Morphological terms proposed by Mackiewicz (1994) were used in descriptions of scoleces. Species first reported from Japan and new fish hosts are marked with an asterisk. Vouchers are deposited in The Natural History Museum, London, UK (BMNH), the helminthological collection of the Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech Republic (IPCAS), and Meguro Parasitological Museum, Tokyo (MPM).

SURVEY OF SPECIES

Family Caryophyllaeidae Leuckart, 1878

Paracaryophyllaeus gotoi (Motomura, 1927) Fig. 1
Syns. *Caryophyllaeus gotoi* Motomura, 1927; *Paracaryophyllaeus dubininae* Kulakovskaya, 1961

Description (n = 2; testis number also counted in 10 additional specimens unsuitable for measuring because of their deformation): Body 9.2–10.6 mm long; maximum width (392–520) at level of ovary. Scolex 544–620 wide, club-shaped, with bluntly ended anterior extremity, longitudinally furrowed on dorsal and ventral sides (Fig. 1 A, H). Testes few (23–36; n = 12), large (99–141 × 86–118; n = 26) compared to vitelline follicles, elongate oval to almost spherical, beginning far (3.94–5.79 mm) posterior to anterior extremity and at long distance (2.48–3.52 mm) from anteriormost vitelline follicles, not reaching to cirrus-sac posteriorly. Cirrus-sac oval, 344–368 × 250–280; male genital pore opening into small, shallow common genital atrium, anterior to uterovaginal opening. Ovary H-shaped, 312–464 wide, with lateral arms 440–880 long which taper posteriorly and wide ovarian bridge situated pre-equatorially to lateral arms. Vagina slightly curved distally; proximally slightly widened to form seminal receptacle anterodorsal to ovarian bridge; vagina opens into common genital pore. Vitelline follicles numerous, starting far posterior to anterior extremity (1.46–2.27 mm), not reaching cirrus-sac posteriorly; postovarian group between posterior margin of ovary and posterior end of body, not reaching to posterior extremity. Uterus with numerous glands, forming loops between posterior arms of ovary, then ascending beside ovary and cirrus-sac to form a few loops anterior to cirrus-sac, and opens

into common genital atrium. Eggs operculate, 49–57 × 31–35 (n = 20).

Hosts: *Misgurnus anguillicaudatus* (Cobitidae) (common name “dojō”); ? *Gymnogobius* sp. (Gobiidae).

Localities: Lake Kizaki at Oomachi, Nagano Prefecture, May 1981; Lake Saruruto at Shibeche, Hokkaido, July 1984; Barato River at Ishikari, Hokkaido, August 1984; Oono River at Oono, Hokkaido, August 1994; Kôshoku, Nagano Prefecture, April 1985; a stream at Midori, Iiyama, Nagano Prefecture, May 1989 and December 1994; Nôgu River at Oomachi, Nagano Prefecture, July 1989; Hiroi River at Kotobuki, Iiyama, Nagano Prefecture, November 1999 (*M. anguillicaudatus*); Oono River at Oono, Hokkaido, August 1984 (*Gymnogobius* sp.) (all collected by T. Shimazu).

Specimens deposited: BMNH 2001.1.26.2–3, IPCAS C-218, MPM 19776–19783.

Comments: This species was originally described from *Misgurnus anguillicaudatus* from Korea by Motomura (1927) and first reported from Japan by Yamaguti (1934). The most typical features of this species are the low number of testes, the presence of uterine loops anterior to the cirrus-sac and the shape of the anterior end (scolex) which is longitudinally furrowed dorsally and ventrally (Yamaguti 1934). Although cestodes from several localities were available in this study, measurements of only two specimens from Iiyama are presented as other worms were deformed due to their fixation under pressure; in the latter worms, only the number of testes was counted. The specimens studied by the present authors correspond well with those described by Motomura (1927) and Yamaguti (1934).

A caryophyllidean cestode found in the intestine of the perciform fish *Gymnogobius* sp. in the Oono River corresponds to *P. gotoi* in its morphology such as the shape of the scolex, the low number of the testes and the uterus reaching anteriorly to the cirrus-sac. However, this specimen is distorted so its specific identification is only tentative.

In 1961, Kulakovskaya described a new genus, *Paracaryophyllaeus*, with the species *P. dubininae* as its type-species from the intestine of the same fish host (*M. anguillicaudatus*) from the Ukraine. *Paracaryophyllaeus dubininae* was then reported from other cobitid fishes, *Cobitis taenia* and *C. caucasica*, from the former USSR, including the Amur River basin, and from Hungary and Bulgaria (Ergens et al. 1975, Kakacheva-Avramova 1983, Protasova et al. 1990). Dubinina (1971) synonymised *P. dubininae* with *Caryophyllaeus gotoi*, the latter species being transferred to *Paracaryophyllaeus*, and thus becoming the type-species as *P. gotoi*. Although Protasova et al. (1990, p. 139) considered this synonymy as incorrect because of its contradiction (not specified by these authors) to the rules of the International Code of Zoological Nomenclature, it was accepted by Dubinina (1987) and Mackiewicz (1994) and it is followed in the present paper.

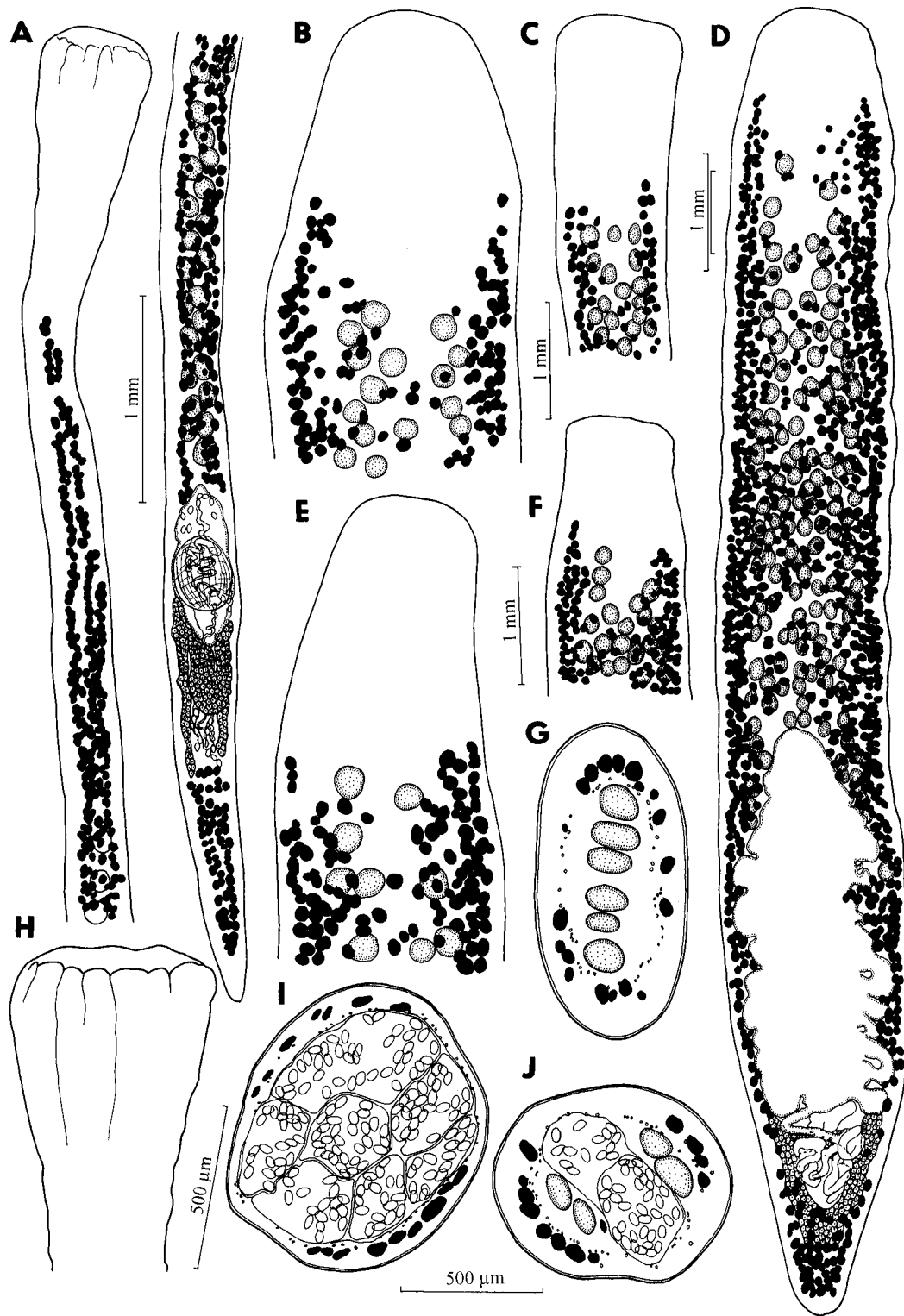


Fig. 1. *Paracaryophyllaeus gotoi* (Motomura, 1927) from *Misgurnus anguillicaudatus* (A, H); *Caryophyllaeides ergensi* Scholz, 1990 (B-G, I, J). A, D – entire worm; B, C, E, F, H – anterior end; G, I, J – cross-sections.

**Archigetes sieboldi* Leuckart, 1878

Fig. 2

Description (n = 11; all specimens flattened): Body 2.96–4.85 mm long (n = 9); maximum width 0.95–1.52 mm (n = 11). Scolex, bothrioloculodiscate (Fig. 2 D, F), indistinctly separated from neck region; width of apical disc 173–296 (n = 9). Testes few (42–67; n = 3), 88–174 × 61–97 (n = 21) in least flattened specimen, elongate oval to almost spherical, always posterior (43–192; n = 10) to anteriormost vitelline follicles, not reaching to cirrus-sac posteriorly. External seminal vesicle tear-shaped, thick-walled, anterior to cirrus-sac (Fig. 2 E), 81–147 × 41–131 (n = 6); cirrus-sac spherical to pyriform, 147–224 × 102–160 (n = 8); male genital pore joins with uterovaginal opening; gonopore single, posterior to uterovaginal canal. Ovary dumbbell- or H-shaped, 700–1,120 wide (n = 8), with short (280–660; n = 8) lateral arms. Vagina slightly curved; opens into uterovaginal canal. Vitelline follicles numerous, starting 552–832 (n = 10) posterior to anterior extremity, reaching to cirrus-sac posteriorly; postovarian group between posterior margin of ovary and posterior end of body. Uterus forming loops starting posterior to ovary, then ascending anterior to external seminal vesicle and cirrus-sac, and joins uterovaginal canal. Eggs operculate, 50–58 × 31–39 (mean $53.4 \pm 1.6 \times 34.0 \pm 1.7$; n = 32; coefficient of variability 3% and 5%, respectively).

Hosts: **Pseudorasbora parva*, **Sarcocheilichthys variegatus microoculus* (Cyprinidae).

Localities: Lake Suwa at Suwa, Nagano Prefecture, May 1992 (*P. parva*); Lake Kizaki at Oomachi, Nagano Prefecture, May 1981 (*S. v. microoculus*) (all collected by T. Shimazu).

Specimens deposited: IPCAS C-45, MPM 18802.

Comments: All specimens studied were strongly flattened, which made it impossible to provide measurements comparable with published data. Poor quality of preparations also did not allow to count testes in more than three worms; moreover, these counts may have been underestimated because the testes were difficult to distinguish from numerous, dark-stained vitelline follicles. The morphology of the scolex, which is bothrioloculodiscate (see Mackiewicz 1994, fig. 5.4), and the distribution of vitelline follicles, which are always anterior to the first testes and lacking alongside the ovary, indicate that the specimens belong to the species *Archigetes sieboldi* (see Kennedy 1965, Protasova et al. 1990, Mackiewicz 1994).

This tapeworm can mature either as a progenetic plerocercoid in the body cavity of tubificid oligochaetes, or in the intestine of freshwater fish (Kennedy 1965, Mackiewicz 1994). According to Kennedy (1965), *A. sieboldi* have been found in Europe, the former USSR, USA, Brazil and South Africa. Motomura (1929) found *A. sieboldi* in tubificids from Miyagi Prefecture and Tokyo but the present data represent its first record from

a fish in Japan and both fish species are new definitive hosts.

Family *Lytocestidae* Hunter, 1927

**Caryophyllaeides ergensi* Scholz, 1990

Fig. 1

Description (n = 24, all specimens from *T. hakuensis*): Body of gravid worms 7.1–27.2 mm (n = 24); maximum width (0.97–2.69 mm; n = 14) at level of scolex. Scolex cuneiform. Testes numerous, oval, 141–330 × 144–250 (n = 14), starting slightly posterior (0.13–0.80 mm; n = 9) to anteriormost vitelline follicles (in one specimen 0.26 mm anterior to vitellaria), 1.14–2.44 mm (n = 10) posterior to anterior extremity. Posterior-most testes surround anterior part of uterine loops, terminating far anterior to ovary. Cirrus-sac elongate to oval, 584–960 × 304–528 (n = 6), in most specimens overlapped by uterine loops; male pore opening into shallow common genital atrium. Ovary inverted A-shaped, near posterior extremity. Vagina forming curved seminal receptacle, opens into common genital pore. Vitelline follicles cortical (Fig. 1 G, I, J), numerous, starting anterior to first testes along lateral margin (Fig. 1 B, C), at 0.93–2.17 (n = 10) from anterior extremity; follicles discontinuous along ovary with several follicles present along ovarian arms (1–8 follicles, usually 3–6, present in region anterior to ovarian bridge). Uterus forming numerous loops, starting in postovarian region and reaching anteriorly to mid-third or anterior half of body, to 36–54% of total body length (mean 46 ± 5 ; n = 24; coefficient of variability 11%) (36–53% in specimens from Okitsu River (n = 11), 42–45% from Lake Ogawara (n = 2), 45–54% from Hiroi River (n = 6) and 42–53% from Lake Suwa (n = 5)). Eggs numerous, operculate, variable in shape, 48–70 × 30–44 (mean $57.2 \pm 5.9 \times 36.2 \pm 3.2$; n = 39; coefficient of variability 10% and 9%, respectively).

Hosts: **Tribolodon hakuensis* (common name “ugui”), **T. ezoe*, **Hemibarbus barbus* (all Cyprinidae); **Gymnogobius* sp. (Gobiidae).

Localities: Onishibetsu River at Sarufutsu; Lake Abashiri at Abashiri; Lake Tôro at Shibeche; Shokambetsu River at Mashike, all July 1984; Chitose River at Ebetsu; Oono River at Oono; Mogusa River at Matsumae; Barato River at Ishikari, all August 1984, all localities in Hokkaido; Lake Suwa at Suwa, May 1992; Hiroi River at Kotobuki, Iiyama, both Nagano Prefecture, November 1996; Lake Ogawara at Kamikita, Aomori Prefecture, September 1997 (collected by T. Shimazu); Okitsu River, Shizuoka Prefecture, June, July and September 1994 (collected by K. Nagasawa) (all *T. hakuensis*); Lake Tôro at Shibeche, Hokkaido, September 1981 (*T. ezoe*); Chikuma River at Togura, Nagano Prefecture, August 1987 (*H. barbus*); Shubumbetsu River at Mashike, Hokkaido, July 1984; Oono River at Oono, Hokkaido, August 1984 (*Gymnogobius* sp.) (all collected by T. Shimazu).

Specimens deposited: BMNH 2001.1.29.1–6, 2001.5.30.3–7, IPCAS C-217, MPM 19784–19795.

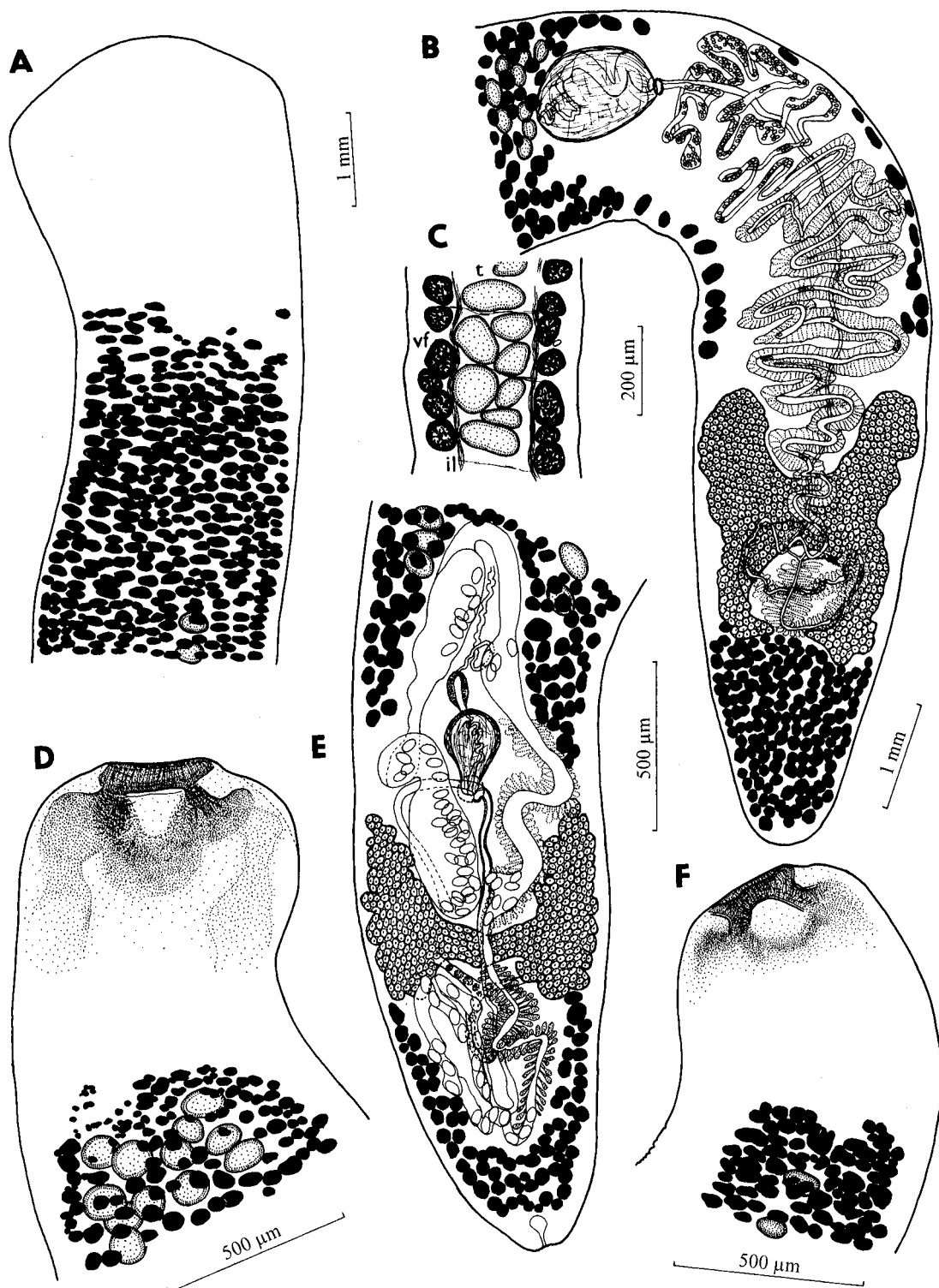


Fig. 2. *Khawia parva* (Zmeev, 1936) from *Carassius* sp. (A-C); *Archigetes sieboldi* Leuckart, 1878 from *Pseudorasbora parva* (D-F). A, D, F – scolex; B, E – posterior end, dorsal view; C – sagittal section, note cortical vitelline follicles. Abbreviations: il – internal longitudinal musculature; t – testes; vf – vitelline follicles.

Comments: All specimens studied correspond to those of *Caryophyllaeides ergensi*, originally described from *Leuciscus leuciscus baicalensis* from Mongolia (Scholz 1990). This species was differentiated from *C. fennica* (Schneider, 1902), previously the only species of *Caryophyllaeides* Nybelin, 1922, by the extent of the uterus (occupying the posterior half to two-thirds of the body length in *C. ergensi* versus the posterior fifth to third of the body length in *C. fennica*), the anterior position of the first testes in the former taxon (versus markedly more posterior in the latter), and the presence of the vitelline follicles along the ovarian lobes in *C. ergensi* (absent in *C. fennica*) (Schneider 1902, Scholz 1990).

The present material differs from that from Mongolia in the somewhat shorter extent of its uterine loops (reaching to 36-54% of body length versus 48-68% in specimens from Mongolia) and the presence of fewer vitelline follicles along the ovary. However, the specimens from Japan differ markedly from those of *C. fennica* in the morphology of the anterior end (scolex) and position of the anteriormost testes and vitelline follicles. In the specimens from Japan, the vitelline follicles are scarce in the median field where numerous testes are present (Fig. 1 B, C, F), thus forming a U-shaped band. They are also always present, although in some specimens not numerous, along the posterior loops of the uterus, and their configuration is markedly different from that typical of *C. fennica* (see Scholz 1989).

All fish species represent new definitive hosts of *C. ergensi*, which is first reported from Japan. However, most specimens, including all from hosts other than *T. hakuensis*, were deformed due to their flattening. Therefore, the description is only based on selected specimens from *T. hakuensis*.

In the present study, an extraordinarily high variability in the size of intrauterine eggs was observed. As eggs may become collapsed due to dehydration during their staining and mounting in Canada balsam, it is suggested that egg size be considered as species-specific character with caution unless freshly laid eggs are available for measurements. For example, a considerable difference between intrauterine eggs from permanent preparations and those laid in water was observed in *Khawia sinensis* by Scholz (1989, 1991a).

Scholz (1990) did not make cross-sections of *C. ergensi*, as all specimens available at that time were stained and mounted as permanent preparations. The present study made it possible to confirm the cortical position of the vitelline follicles which defines the family Lytocestidae. On the basis of the evaluation of specimens from Japan and their comparison with the types of *C. ergensi* (IPCAS C-217) and vouchers of *C. fennica*, the validity of *C. ergensi* is confirmed and its host spectrum and geographical distribution are ex-

tended to encompass three cyprinids and one gobiid fish (? accidental host) as new definitive hosts and Japan as a new area of the parasite's distribution.

Khawia japonensis (Yamaguti, 1934) Fig. 3
Syn. *Caryophyllaeus japonensis* Yamaguti, 1934

Description (n = 1): Body 26.3 mm long; maximum width (2.00 mm) at ovarian region. Scolex cuneifimbriate (crenate), 1.22 mm long and 1.91 mm wide, markedly delimited from body (Fig. 3 C). Testes oval, 147-224 × 99-166 (n = 13), medullary, starting 2.24 mm posterior to first vitelline follicles, not reaching to cirrus-sac. Cirrus-sac oval, 832 × 536; male genital pore anterior to uterovaginal pore, opening into common genital atrium. Ovary H-shaped, 1.92 mm wide, with long (3.31 mm) lateral arms, slightly arched inwards posteriorly. Vagina with wide seminal receptacle dorsal to ovarian isthmus (Fig. 3 E); vaginal canal opens into common genital atrium. Vitelline follicles numerous, starting 1.50 mm posterior to anterior extremity, surrounding cirrus-sac and with several follicles reaching alongside uterine loops almost to ovary; postovarian group formed by follicles starting posterior to ovarian bridge. Uterus forming numerous loops between posterior lobes of ovary and posterior half of cirrus-sac (Fig. 3 F). Eggs numerous, operculate, 45-50 × 26-31 (n = 11).

Host: *Cyprinus carpio* Linnaeus (Cyprinidae) (common name "koi").

Locality: Lake Suwa, Nagano Prefecture, May 1975 (collected by T. Shimazu); Lake Biwa at Moriyama, Shiga Prefecture, May 2001 (collected by T. Scholz).

Specimen deposited: IPCAS C-348.

Comments: The specimen fits into the original description of *Khawia japonensis*, described as *Caryophyllaeus japonensis* by Yamaguti (1934) from common carp, *Cyprinus carpio*, in most morphological features such as the shape of the scolex with crenate anterior margin, the anterior position of the vitelline follicles which reach almost to the scolex and their presence along the uterine loops. The tapeworm from Lake Suwa differs slightly in the absence of the vitelline follicles along the ovarian lobes and the presence of the first vitelline follicles anterior to the testes. However, there is apparently some variation in these characters, as obvious from discrepancies in the species diagnosis of *K. japonensis* provided by Yamaguti (1934), Kulakovskaya (1961) and Dubinina (1987). Protasova et al. (1990) documented, on the basis of evaluation of freshly collected material, that the testes may start anteriorly or posteriorly to the first vitelline follicles (see fig. 23a, b in Protasova et al. 1990) and the vitelline follicles may be absent along the ovarian arms or, in other specimens, few follicles may be present (Protasova et al. 1990, p. 168 and fig. 23v, g).

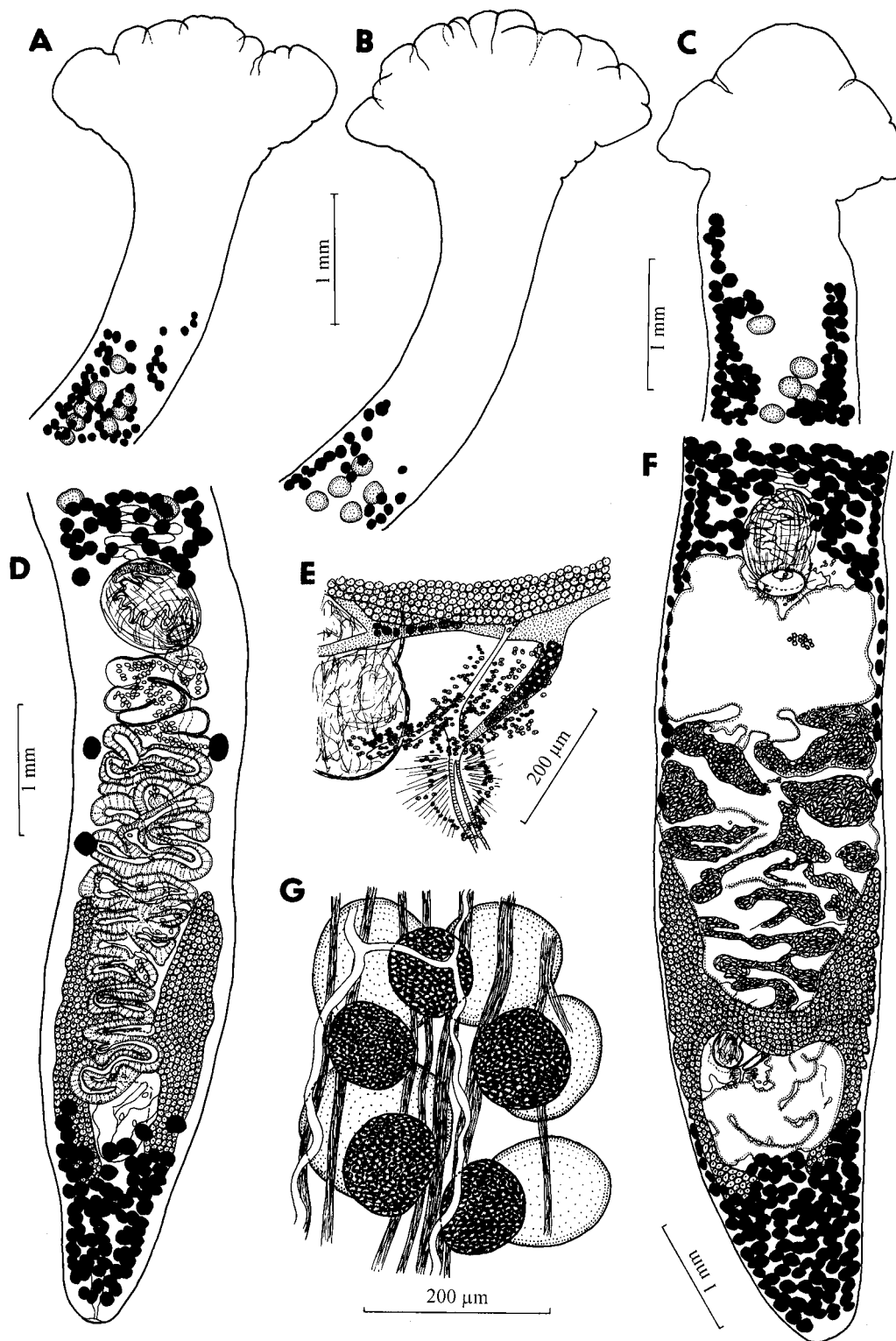


Fig. 3. *Khawia sinensis* Hsü, 1935 from *Hemibarbus barbus* (A, B, D, G); *Khawia japonensis* (Yamaguti, 1934) from *Cyprinus carpio* (C, E, F). A-C – anterior end; D, F – posterior part of body (D – dorsal view); E – postovarian complex; G – internal longitudinal muscle fibres with vitelline follicles and testes.

Previously, *K. japonensis* has been reported from Japan and the Amur River basin in the Far East of Russia (Protasova et al. 1990). Its development in experimentally infected hosts, tubificid oligochaetes, was studied by Demshin (1978).

***Khawia sinensis* Hsü, 1935**

Fig. 3

Description (n = 3, one specimen incomplete): Body 27-35 mm long; maximum width (1.16-1.18 mm) in posterior region. Scolex cuneifimbriate (Fig. 3 A, B), with deep incisions on anterior margin, 2.19-2.37 mm wide. Testes numerous, oval to almost spherical, 128-192 × 99-154 (n = 19), medullary; anteriormost testes 4.80-5.10 mm posterior to anterior extremity and 2.67-2.74 mm posterior to anteriormost vitelline follicles; posteriorly, testes reach almost to cirrus-sac. Cirrus-sac oval, 610-730 × 528-536; male genital pore anterior to uterovaginal pore, opening into common genital atrium. Ovary posterior, H-shaped, 974-1,015 wide, with long (1,810-2,274), wide lateral arms, and short, wide ovarian bridge (Fig. 3 D). Vagina widened to form seminal receptacle dorsal to ovarian bridge, opens into common genital atrium. Vitelline follicles numerous, cortical (Fig. 3 G), situated between neck region and cirrus-sac; first follicles 2.19-2.23 mm posterior to anterior extremity; postovarian follicles not reaching to ovarian bridge anteriorly; follicles essentially lacking beside uterine loops (only 3 follicles present) and absent along ovarian lobes anterior to ovarian bridge. Uterus forming numerous loops between ovary and posterior margin of cirrus-sac, surrounded by numerous glands except at distal extremity. Eggs numerous, operculate, 39-49 × 26-32 (n = 21).

Host: *Cyprinus carpio*, **Hemibarbus barbus* (Cyprinidae) (common name “nigoi”).

Localities: Lake Biwa at Moriyama, Shiga Prefecture, May 1992 and 2001 (*C. carpio*); Hiroi River at Kotobuki, Iiyama, Nagano Prefecture, October 1996 (all *H. barbus*; collected by T. Shimazu and T. Scholz – *C. carpio*).

Specimens deposited: BMNH 2001.1.26.4-5, IPCAS C-46.

Comments: The specimens found possess morphological features that indicate that they belong to *Khawia sinensis*, a species originally described by Hsü (1935) from common carp in China. Since then, the tapeworm has been disseminated with the introduction of the host to continental Asia and Europe, including the British Isles (Dubinina 1987, Chubb and Yeomans 1995).

Nakajima and Egusa (1978) reported *Khawia sinensis* from common carp cultured in central Japan. These authors identified their specimens as *K. sinensis* and differentiated them only on the basis of the size of eggs that are smaller (45-50 × 22-34 in their specimens) than those of *K. japonensis* (48-57 × 36-42). However, the latter species also differs from *K. sinensis* in other morphological characters (see above).

The fish *Hemibarbus barbus* represents a new definitive host of *K. sinensis* that was previously reported only from common carp, *Cyprinus carpio*, and grass carp, *Ctenopharyngodon idella* (see Dubinina 1987, Protasova et al. 1990). The life cycle of *K. sinensis* has been studied by various authors in the former USSR and central Europe (Kulakovskaya 1963, Demshin and Dvoryadkin 1980, Scholz et al. 1990, Scholz 1991a, b).

***Khawia parva* (Zmееv, 1936)**

Fig. 2

Syn. *Caryophyllaeus parvus* Zmееv, 1936

Description (n = 2, both specimens flattened): Body 33.5-34.5 mm long; maximum width 2.23-2.60 mm. Scolex cuneiform (Fig. 2 A), 1.66-2.96 mm wide. Testes numerous, oval to almost spherical, 131-307 × 112-243 (n = 22), medullary; anteriormost testes 1.71-3.37 mm posterior to anteriormost vitelline follicles; posteriorly, testes reach to cirrus-sac. Cirrus-sac oval, 750-1,160 × 629-853; male genital pore anterior to uterovaginal pore, opening into common genital atrium. Ovary posterior, H-shaped, 1.87-2.05 mm wide, with long (2.68-2.82) lateral arms arched inwards posteriorly, and wide ovarian bridge. Vagina widened to form seminal receptacle dorsal to ovarian bridge (Fig. 2 B), opens into common genital atrium. Vitelline follicles numerous, cortical (Fig. 2 C), situated between neck region and cirrus-sac, with several follicles alongside uterus, not reaching to ovary; first follicles 2.80-4.06 mm posterior to anterior extremity; postovarian follicles reaching only to posterior arms of ovary; follicles lacking along ovarian lobes. Uterus forming numerous loops between ovary and posterior margin of cirrus-sac, surrounded by numerous glands except at distal extremity. Eggs numerous, operculate, 54-63 × 32-38 (n = 21).

Hosts: **Carassius auratus langsdorfii* Valenciennes in Cuvier et Valenciennes, **Carassius* sp. (probably *C. a. langsdorfii*) (Cyprinidae).

Localities: Lake Kizaki at Oomachi, Nagano Prefecture, June 1983 (*C. auratus langsdorfii*); Lake Tôro at Shibechea, Hokkaido, October 1981, Lake Saruruntô (Saruruto) at Shibechea, Hokkaido, July 1984 (*Carassius* sp.) (collected by T. Shimazu).

Specimens deposited: BMNH 2001.5.30.1-2, IPCAS C-339, MPM 19796-19797.

Comments: The specimens correspond in their morphology and measurements to those of *Khawia parva*, with the exception of the size of eggs, which are somewhat larger than reported by Protasova et al. (1990). However, this difference is not considered to be sufficient for differentiation of the present material from *K. parva* as measurements of eggs may vary considerably (see Comments on *Caryophyllaeides ergensi* – p. 280).

Khawia parva was described as *Caryophyllaeus parvus* from the intestine of *Carassius carassius* in the Amur River by Zmeev (1936) and then transferred to *Khawia* Hsü, 1935 by Kulakovskaya (1961) on the basis of the cortical position of the vitelline follicles and other morphological characters. This cestode is a specific parasite of *Carassius* spp. (*C. carassius*, *C. auratus*) and its life cycle was studied by Demshin (1984), who demonstrated that tubificid oligochaetes of the genus *Limnodrilus* serve as intermediate hosts. The present findings represent a new geographical record of *K. parva*, which was previously recorded only from Russian Far East (Protasova et al. 1990).

Atractolytocestus sagittatus (Kulakovskaya et Akhmerov, 1965) Fig. 4

Syn. *Markevitschia sagittata* Kulakovskaya et Akhmerov, 1965

Description (n = 12): Body 10.6–13.3 mm long (n = 9); maximum width (1.34–2.23; n = 12) at middle of body or ovarian region. Scolex variable in shape, mostly bulboacuminate (Fig. 4 A, E), 1.24–2.38 wide (n = 6). Testes numerous (precise number not counted but considerably exceeding 100–200), oval to spherical, 118–298 × 77–179 (n = 13). Anteriormost testes reaching to scolex, very close to anterior extremity (0.73–1.36 mm; n = 10), always anterior to first vitelline follicles, surrounding cirrus-sac posteriorly and reaching alongside uterine loops to ovary (Fig. 4 H). Cirrus-sac oval to transversely oval, 528–690 × 480–810 (n = 10); male genital pore anterior to female pore, opening into common genital atrium. Ovary H-shaped, 0.96–1.58 mm wide (n = 12), with short (690–1,048; n = 12), wide lateral arms. Vagina forming seminal receptacle dorsal to ovarian bridge (Fig. 4 I), opens into shallow common genital atrium. Vitelline follicles numerous, extending 60–325 (n = 10) posterior to anteriormost testes, almost lacking in median field just posterior to scolex (Fig. 4 B, F); follicles uninterrupted and numerous along ovarian arms, connected to postovarian group. Uterus looped, occupying space between posterior arms of ovary and cirrus-sac, surrounded by numerous vitelline follicles and, in distal part, by testes. Eggs operculate, 53–57 × 31–34 (n = 15).

Host: *Cyprinus carpio* (Cyprinidae) (common name “koi”).

Localities: Lake Suwa, Nagano Prefecture, May 1975; Lake Takkobu at Kushiro-cho, Hokkaido, July 1983 (collected by T. Shimazu); Lake Biwa at Moriyama, Shiga Prefecture, May 2001 (collected by T. Scholz).

Specimens deposited: IPCAS C-340, MPM 19798.

Comments: The specimens from Japan appear to be conspecific with *Atractolytocestus sagittatus* described by Kulakovskaya and Akhmerov (1965) as *Markevitschia sagittata* from the intestine of *Cyprinus carpio* from the Amur River basin in Russia. The shape of the scolex and the distribution of the testes, which

reach posteriorly to the ovary, and vitelline follicles, which are uninterrupted and numerous along the ovarian arms, are the most distinctive features that differentiate this species from other caryophyllideans occurring in the Palaearctic region.

Jones and Mackiewicz (1969) noted a close morphological similarity between this species and *A. huronensis* Anthony, 1958, the type and only species of *Atractolytocestus*, described from the intestine of *C. carpio* from North America. The authors also mentioned the dissimilarity of *A. huronensis* with any North American caryophyllidean, suggesting that it may have been imported to North America with its host. Later, Mackiewicz (1994) synonymised *Markevitschia* Kulakovskaya et Akhmerov, 1965 with *Atractolytocestus* Anthony, 1958, but *M. sagittata* was not formally synonymised with *A. huronensis*. Notwithstanding the smaller size of the body, both taxa differ most markedly in the number of the testes: 6–20 in *A. huronensis* versus c. 80 in *M. sagittata*, according to Jones and Mackiewicz (1969), who studied one voucher specimen of the latter species, and 75–200 according to Protasova et al. (1990).

In this study, the precise number of the testes could not be counted because they are too numerous, lie in at least two overlapping layers and are surrounded by numerous vitelline follicles. However, it is obvious that the number of testes considerably exceeds 100–200, in some specimens reaching to several hundreds. Even considering only the region anterior to the first vitelline follicles, as many as 20–60 testes can be counted (Fig. 4 A, B). The testes are numerous and reach posteriorly up to the ovarian arms, which is a feature unique among other Palaearctic caryophyllideans (see Mackiewicz 1994 and Protasova et al. 1990). On the basis of the above-mentioned characteristics, *A. sagittatus* is tentatively considered to be a valid species distinct from *A. huronensis* in the number and configuration of the testes.

Cyprinus carpio is the only known definitive host of *A. sagittatus*. This cestode is now first reported outside the former USSR. Tubificid oligochaetes, *Limnodrilus udekemianus* and *L. hoffmeisteri*, have been shown to serve as experimental intermediate hosts (Demshin and Dvoryadkin 1981).

Family C a p i n g e n t i d a e Hunter, 1930

****Breviscolex orientalis*** Kulakovskaya, 1962 Fig. 4

Description (n = 4, unless otherwise stated): Body 6.0–12.6 mm long, almost of same width throughout; maximum width 0.76–1.22 mm. Scolex cuneiform (Fig. 4 C, G), 710–893 wide, only slightly wider than neck region. Testes medullary, oval to nearly spherical, 90–182 × 83–176 (n = 13), starting close (432–750) to anterior extremity; anteriormost testes may start anteriorly (8–80) or posteriorly (56–176) to anteriormost

vitelline follicles; posteriorly, testes reach to posterior margin of cirrus-sac. Cirrus-sac spherical to transversely oval, 240-464 × 224-432; male genital pore opens through common genital pore. Ovary H-shaped, 544-808 wide, with short (512-914), wide arms and short ovarian bridge. Vagina with seminal receptacle dorsal to ovarian bridge, opens through common genital pore. Vitelline follicles largely cortical, with some follicles paramuscular (partly in medulla – Fig. 4 J), relatively large, starting close (424-720) to anterior extremity and passing laterally to cirrus-sac, uterine loops and ovarian arms to unite with postovarian group; alongside ovary follicles may be interrupted (Fig. 4 D). Uterus forms loops between region posterior to ovarian arms and cirrus-sac, not overlapping it. Eggs operculate, relatively large, 66-74 × 40-44 (n = 9).

Host: **Hemibarbus barbus* (Cyprinidae) (common name “nigoi”)

Localities: Chikuma River at Togura, Nagano Prefecture, August 1987; Lake Biwa at Moriyama, Shiga Prefecture, May 1992; Hiroi River at Kotobuki, Iiyama, Nagano Prefecture, October 1996 (collected by T. Shimazu).

Specimens deposited: BMNH 2001.1.30.1-5, IPCAS C-219, MPM 18801 and 19799-19800.

Comments: This species was described from *Hemibarbus maculatus* and *Chilogobio czerskyi* from the Amur basin (Bolon Lake, Zeya River) in Russia (Kulakovskaya 1962). The specimens reported here are larger than those originally described (body size 7-8 mm). Scholz and Ergens (1990) found tapeworms tentatively identified as *B. orientalis* in the cobitid fish *Barbatula barbatula toni* in Mongolia and they also reported larger specimens (14.8 mm) than those described by Kulakovskaya (1962).

Attempts to obtain the type specimens of *B. orientalis* were unsuccessful because neither the types nor vouchers from the type-host (*Hemibarbus maculatus*) could be located in the helminthological collection of the Zoological Institute of the Russian Academy of Sciences in St. Petersburg (A. Galkin – personal communication). Therefore, identification was based on literary data and comparison with specimens from Mongolia.

One of the diagnostic features of *B. orientalis* is the presence of the vitelline follicles alongside the ovarian arms (Kulakovskaya 1962, Dubinina 1987, Protasova et al. 1990), which was confirmed in the present material. However, there is variability in the number of follicles, which can be relatively few in some specimens (Fig. 4 D).

On the basis of the paramuscular position of the vitelline follicles, *B. orientalis* was placed into the family Capingentidae (see Kulakovskaya 1962), being the only member of this family in the Palaearctic region

(Mackiewicz 1972, 1981, 1994, Dubinina 1987). Cross-sections of the worms from Japan have also confirmed the paramuscular position of the follicles as observed by Kulakovskaya (1962). It should, however, be noted that the fibres of the longitudinal musculature are situated mostly in the median (inner) region of the vitelline field or entirely medullary to it (Fig. 4 J), thus approaching the topography present in the Lytocestidae possessing cortically situated vitelline follicles (compare Fig. 1 G, J in this paper).

This is the first record of *B. orientalis*, previously reported only from Russia (Dubinina 1987, Protasova et al. 1990) and possibly Mongolia (Scholz and Ergens 1990), from Japan.

Caryophyllidea gen. sp. (? *Breviscolex orientalis* Kulakovskaya, 1962) Fig. 5

Description (n = 4; all specimens distorted due to flattening): Body 9.5-25.0 mm long (n = 3), with maximum width (2.42-3.44 mm; n = 4) in anterior third. Scolex widely rounded, with prominent corners, separated from body by slight constriction (Fig. 5 A, B), 1.56-2.54 mm wide (n = 3). Testes spherical to elongate, 122-384 × 74-277 (n = 11), commencing close (0.45-1.22 mm; n = 3) to anterior extremity and anteriorly (0.22-0.26 mm) to first vitelline follicles or at same level; testes extend back to cirrus-sac, with several testes surrounding it to reach uterine region, absent alongside proximal part of uterine loops anterior to ovary. Cirrus-sac transversely oval to spherical, 552-976 × 800-1,256 (n = 4), opens into common genital atrium. Ovary H-shaped, 1.89-2.25 wide, with short (0.74-1.79; n = 4), wide arms. Vagina widened proximally to form seminal receptacle. Vitelline follicles numerous, present along cirrus-sac and uterine loops; individual follicles, often not forming continuous field, present beside ovarian arms (Fig. 5 D). Uterus strongly coiled, with proximal loops reaching posterior to ovary; anteriorly, loops reaching to anterior half of cirrus-sac. Eggs numerous, operculate, relatively large, 68-78 × 41-48 (n = 21).

Host: *Cyprinus carpio* (Cyprinidae) (common name “koi”).

Locality: Lake Biwa at Moriyama, Shiga Prefecture, May 1992 (collected by T. Shimazu).

Specimens deposited: IPCAS C-341, MPM 18803.

Comments: The specimens studied were fixed under pressure, which apparently caused deformation of their body, especially the scolex (Fig. 5 C). In their morphology, they differ from *Atractolytocestus sagittatus* (see above), found in the same host, in possessing a much larger body, the scolex of different shape (almost cuneiform versus bulboacuminate), the testes not reaching to the ovary and much larger eggs.

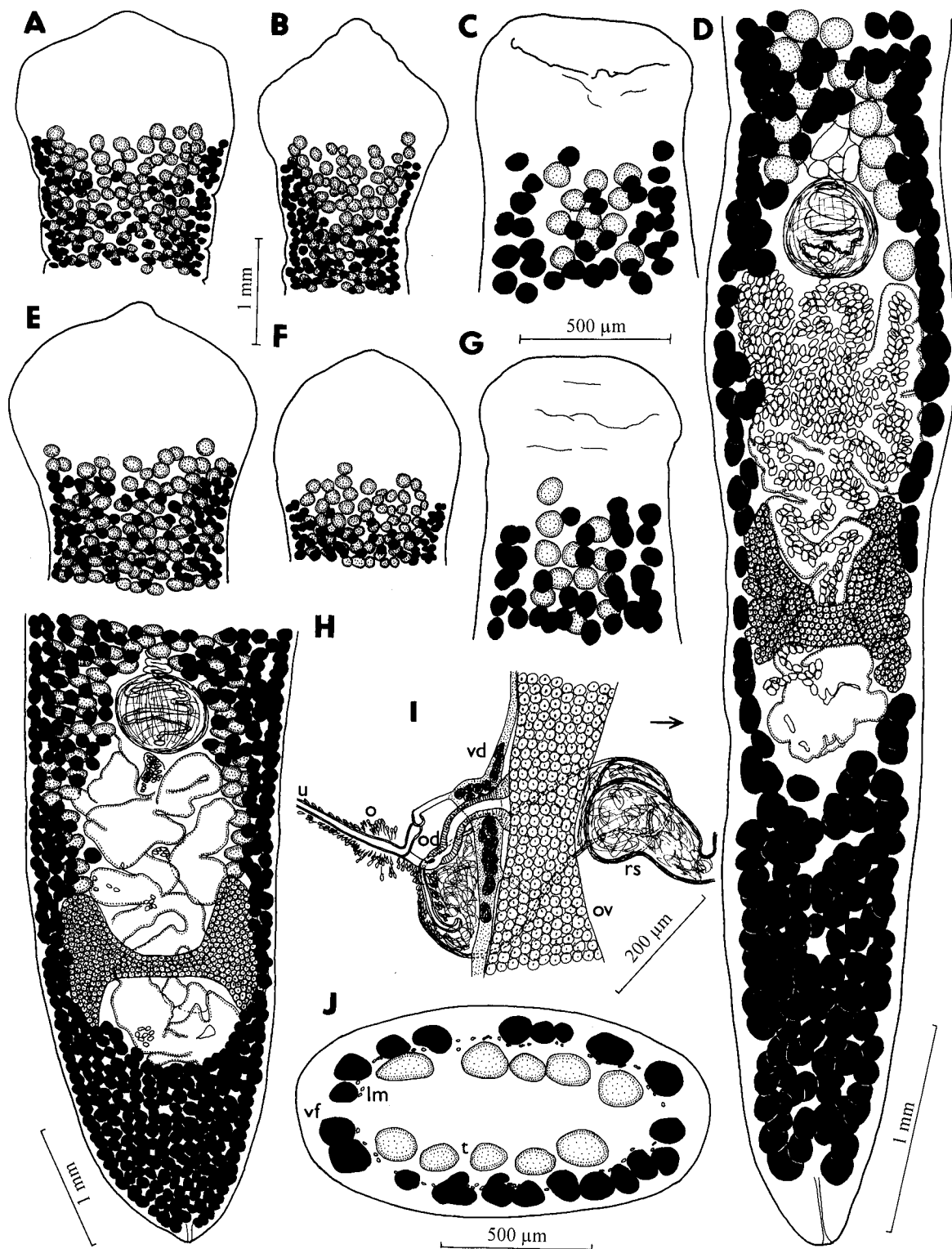


Fig. 4. *Atractolytocestus sagittatus* (Kulakovskaya et Akhmerov, 1965) from *Cyprinus carpio* (A, B, E, F, H, I); *Breviscolex orientalis* Kulakovskaya, 1962 from *Hemibarbus barbus* (C, D, G, J). A-C, E-G – anterior end; D, H – posterior part of body; I – postovarian complex (ventral view; turned 90°; anterior direction indicated by arrow); J – cross-section. Abbreviations: lm – longitudinal muscles; o – ootype; od – oviduct; ov – ovary; rs – seminal receptacle; t – testes; u – uterus; vd – vitelline duct; vf – vitelline follicles.

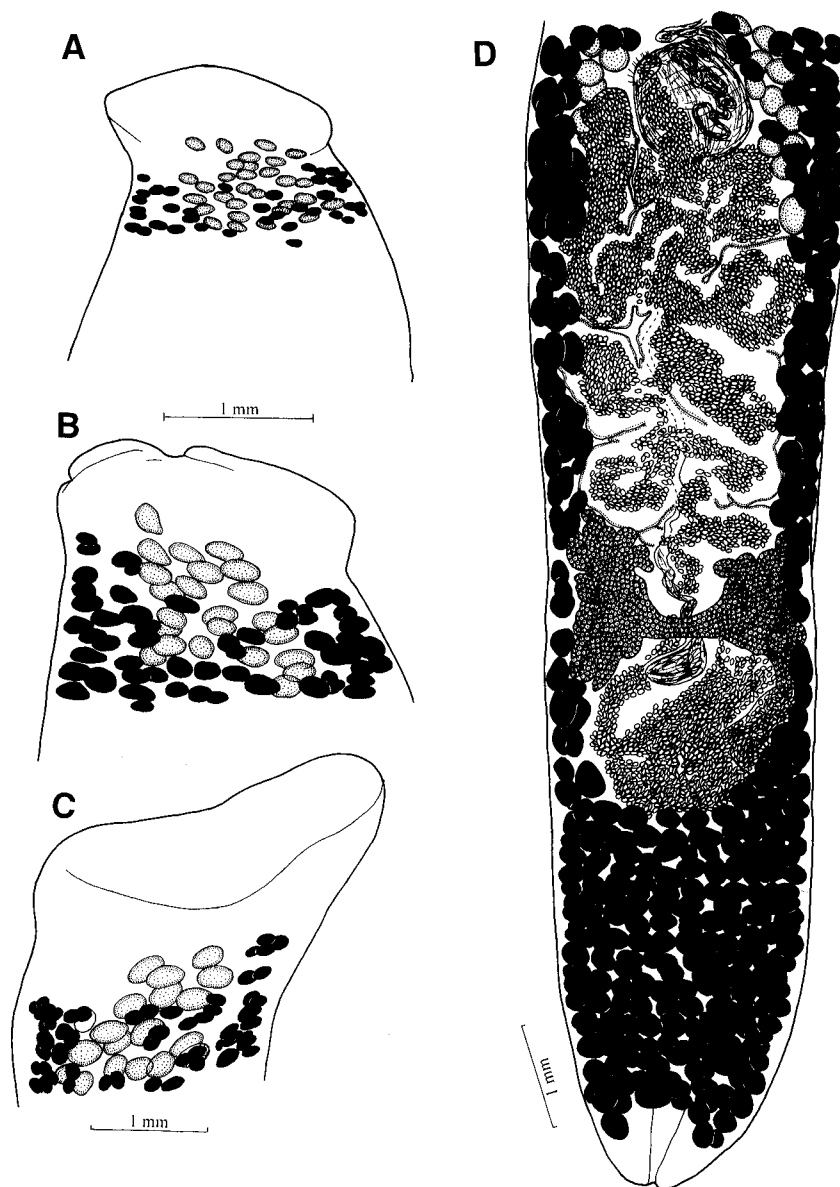


Fig. 5. Caryophyllidea gen. sp. (? *Breviscolex orientalis* Kulakovskaya, 1962) from *Cyprinus carpio*. A-C – anterior end; D – posterior part of body (only anteriormost vitelline follicles and testes illustrated in A).

The tapeworms from *C. carpio* in Lake Biwa closely resemble *Breviscolex orientalis* in almost all morphological characteristics, such as the presence of individual vitelline follicles alongside the ovary, a similar shape of the scolex, the presence of uterine loops in the postovarian region, and the size of eggs. The specimens from common carp, which were strongly flattened, differ only in the size of the body which is considerably larger (see pp. 283-284).

Breviscolex orientalis belongs to the family Capingentidae because of the paramuscular position of

the vitelline follicles, and it has been found only in species of *Hemibarbus* and *Chilogobio*, never in carp (Kulakovskaya 1962, Schmidt 1986, Protasova et al. 1990). The precise position of the internal longitudinal musculature in relation to the vitelline follicles could not be assessed in the tapeworms from *C. carpio* from Lake Biwa as all were flattened and mounted. Therefore, they are identified only tentatively as *B. orientalis* until new, adequately processed material is available.

DISCUSSION

A total of nine cestode species of the order Caryophyllidea have been dealt with in the present study, five of them (*Archigetes sieboldi*, *Caryophyllaeides ergensi*, *Khawia parva*, *Atractolytocestus sagittatus*, and *Breviscolex orientalis*) being reported from Japanese fishes for the first time. Together with the previous data, the caryophyllidean fauna in Japanese freshwater fishes now includes 10 taxa that belong to three of four recognised families of the order (Mackiewicz 1994); family Capingentidae in the form of *B. orientalis* is recorded from Japan for the first time. In addition to new geographical records, new definitive hosts of *A. sieboldi*, *C. ergensi*, *Khawia sinensis*, *K. parva* and *B. orientalis* are reported.

This study also enabled us to confirm the validity of *C. ergensi*, a species recently described from Mongolia and not reported since its original description (Scholz 1990). New material from other definitive hosts made it

possible to supplement the species diagnosis and to confirm species-specific characters that distinguish this taxon from its only congener, *C. fennica*, a frequent parasite of cyprinid fishes in the Palaearctic region (Scholz 1990, Protasova et al. 1990).

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REFERENCES

- AWAKURA T. 1994: Cestodes of freshwater fishes of Hokkaido. Sci. Rep. Hokkaido Fish Hatchery 48: 79-82.
- CHUBB J.C., YEOMANS W.E. 1995: *Khawia sinensis* Hsü, 1935 (Cestoda: Caryophyllidea), a tapeworm new to the British Isles: a threat to carp fisheries? Fish. Manage. Ecol. 2: 263-277.
- DEMSHIN N.I. 1978: Biology of *Khawia japonensis* (Caryophyllidea, Cestoda) – a parasite of the Amur carp. Parazitologiya 12: 493-496. (In Russian.)
- DEMSHIN N.I. 1984: [Biology of *Caryophyllaeus fimbriceps* Annenkova-Chlopina, 1919 and *Khawia parva* (Zmejev, 1936) (Caryophyllidea, Cestoda) – parasites of cyprinid fish.] Parazity zhivotnykh i rastenii, AN SSSR, pp. 63-70. (In Russian.)
- DEMSHIN N.I., DVORYADKIN V.A. 1980: [Biology of *Khawia sinensis* Hsü, 1935 (Caryophyllidea, Cestoda) – a parasite of Amur carp.] Gidrobiol. Zh. 16: 77-82. (In Russian.)
- DEMSHIN N.I., DVORYADKIN V.A. 1981: The development of *Markevitschia sagittata* (Cestoidea: Caryophyllidae), a parasite of Amur wild carp, in the external medium and in the intermediate host. Parazitologiya 15: 113-117. (In Russian.)
- DUBININA M.N. 1971: [Fish tapeworms from the Amur basin.] Parazitol. Sb. 25: 77-119. (In Russian.)
- DUBININA M.N. 1987: [Class tapeworms – Cestoda Rudolphi, 1808.] In O.N. Bauer (Ed.), Key to the Parasites of Freshwater Fishes of the USSR. Vol. 3. Nauka, Leningrad, pp. 5-76. (In Russian.)
- ERGENS R., GUSSEV V.A., IZYUMOVA N.A., MOLNÁR K. 1975: Parasite fauna of fishes of the Tisa River basin. Rozprawy ČSAV, Academia, Prague, 85, No. 2, 117 pp.
- HSÜ H.F. 1935: Contribution à l'étude de cestodes de Chine. Rev. Suisse Zool. 42: 477-570.
- JONES A.W., MACKIEWICZ J.S. 1969: Naturally occurring triploidy and parthenogenesis in *Atractolytocestus huronensis* Anthony (Cestoidea: Caryophyllidea) from *Cyprinus carpio* L. in North America. J. Parasitol. 55: 1105-1118.
- KAKACHEVA-AVRAMOVA D. 1983: Helminths of Freshwater Fishes in Bulgaria. Publ. House of the Bulgarian Academy of Sciences, Sofia, 262 pp. (In Bulgarian.)
- KENNEDY C.R. 1965: Taxonomic studies on *Archigetes* Leuckart, 1878 (Cestoda: Caryophyllaeidae). Parasitology 55: 439-451.
- KULAKOVSKAYA O.P. 1961: [On the fauna of the Caryophyllaeidae (Cestoda, Pseudophyllidea) of the USSR.] Parazitol. Sb. 20: 339-354. (In Russian.)
- KULAKOVSKAYA O.P. 1962: [A new genus and species of caryophyllidean cestodes *Breviscolex orientalis* (Caryophyllaeidae, Cestodes) from fishes of the Amur basin.] Dokl. Akad. Nauk SSSR 143: 1001-1004. (In Russian.)
- KULAKOVSKAYA O.P. 1963: [On the biology and distribution of the tapeworm *Khawia* [sic] *sinensis* Hsü, 1935.] Problemy Parazitologii 2: 200-205. (In Russian.)
- KULAKOVSKAYA O.P., AKHMEROV A.C. 1965: [New caryophyllidean *Markevitschia sagittata* n. gen. n. sp. (Cestoda, Lytocestidae) from carp of the River Amur.] Parazity i parazitozny cheloveka i zhivotnykh. Naukova Dumka, Kiev, pp. 264-271. (In Russian.)
- MACKIEWICZ J.S. 1972: Caryophyllidea (Cestoidea): a review. Exp. Parasitol. 31: 417-512.
- MACKIEWICZ J.S. 1981: Caryophyllidea (Cestoidea): evolution and classification. Adv. Parasitol. 19: 139-206.
- MACKIEWICZ J.S. 1994: Order Caryophyllidea Beneden in Carus, 1863. In: L.F. Khalil, A. Jones and R.A. Bray (Eds.), Keys to the Cestode Parasites of Vertebrates. CAB International, Wallingford, Oxon, pp. 21-43.
- MOTOMURA J. 1927: On *Caryophyllaeus gotoi* n. sp. a new monozoic cestode from Korea. Sci. Rep. Tohoku Imp. Univ. 4: 51-53.

- MOTOMURA I. 1929: On the early development of the monozoic cestode *Archigetes appendiculatus*, including the oogenesis and fertilisation. Annot. Zool. Jpn. 12: 109-129.
- NAGASAWA K., AWAKURA T., URAWA S. 1989: A checklist and bibliography of parasites of freshwater fishes of Hokkaido. Sci. Rep. Hokkaido Fish Hatchery 44: 1-49.
- NAKAJIMA K., EGUSA S. 1978: Notes on *Khawia sinensis* Hsü found in cultured carp. Fish Pathol. 12: 261-263. (In Japanese, with English abstract.)
- PROTASOVA E.N., KUPERMAN B.I., ROITMAN V.A., PODDUBNAYA L.G. 1990: [Caryophyllideans of the Fauna of the USSR.] Nauka, Moscow, 238 pp. (In Russian.)
- SCHMIDT G.D. 1986: CRC Handbook of Tapeworm Identification. CRC Press, Boca Raton, Florida, 675 pp.
- SCHNEIDER G. 1902: *Caryophyllaeus fennicus* n. sp. Arch. Naturgesch. 1: 65-71.
- SCHOLZ T. 1989: Amphilinida and Cestoda, parasites of fish in Czechoslovakia. Acta Sci. Nat. Brno 23, No. 4, 56 pp.
- SCHOLZ T. 1990: *Caryophyllaeides ergensi* sp. n. (Cestoda: Caryophyllidea) from *Leuciscus leuciscus baicalensis* from Mongolia. Folia Parasitol. 37: 231-235.
- SCHOLZ T. 1991a: Early development of *Khawia sinensis* Hsü, 1935 (Cestoda: Caryophyllidea), a carp parasite. Folia Parasitol. 38: 133-142.
- SCHOLZ T. 1991b: Development of *Khawia sinensis* Hsü, 1935 (Cestoda: Caryophyllidea) in the fish host. Folia Parasitol. 38: 225-234.
- SCHOLZ T., ERGENS R. 1990: Cestodes of fish from Mongolia. Acta Soc. Zool. Bohemoslov. 54: 287-304.
- SCHOLZ T., ŠPETA V., ZAJÍČEK J. 1990: Life history of the tapeworm *Khawia sinensis* Hsü, 1935, a carp parasite, in the pond Dražský Skaličňay near Blatná, Czechoslovakia. Acta Vet. Brno 59: 51-63.
- SHIMAZU T. 1981: Some digenetic trematodes of freshwater fishes from eastern Hokkaido, Japan. J. Nagano-ken Jun. Coll. 36: 13-26.
- SHIMAZU T. 1997: Cestodes of freshwater earthworms and freshwater fishes in Japan: a review. J. Nagano Pref. Coll. 52: 9-17. (In Japanese, with English summary.)
- YAMAGUTI S. 1934: Studies on the helminth fauna of Japan. Part 4. Cestodes of fishes. Jpn. J. Zool. 6: 1-112.
- YAMAGUTI S. 1952: Studies on the helminth fauna of Japan. Part 49. Cestodes of fishes, II. Acta Med. Okayama 8: 1-76.
- ZMEEV G.Ya. 1936: [Flukes and tapeworms of fish of the Amur River.] Parazitol. Sb. 6: 423-435. (In Russian.)

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