Research Article

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A synoptic review of *Caryophyllaeus* Gmelin, 1790 (Cestoda: Caryophyllidae), parasites of cyprinid fishes

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Abstract: Tapeworms of the genus *Caryophyllaeus* Gmelin, 1790 (Caryophyllidae: Caryophyllaeidae), common parasites of cyprinid fishes, are reviewed and taxonomic status of 42 nominal taxa that have been placed in the genus during its long history is clarified. The following seven species occurring in the Palaearctic Region are recognised as valid: *C. laticeps* (Pallas, 1781), *C. auriculatus* (Kulakovskaya, 1961), *C. balticus* (Szidat, 1941) comb. n. (syn. *Khawia baltica* Szidat, 1941), *C. brachycollis* Janiszewska, 1953, *C. fimbriceps* Annenkova-Chlopina, 1919, *C. syrdarjensis* Skrjabin, 1913, and newly described *Caryophyllaeus chondrostomi* sp. n. (= *C. laticeps* morphotype 4 of Bazsalovicsová et al., 2014) from common nase, *Chondrostoma nasus* (Linnaeus), found in Austria and Slovakia. The new species differs by the paramuscular or cortical position of preovarian vitelline follicles, a large, robust body (up to 64 mm long), conspicuously long vas deferens, flabellate scolex with small wrinkles on the anterior margin, and anteriormost testes located in a relatively short distance from the anterior extremity. *Caryophyllaeus kashmirenses* Mehra, 1930 and *Caryophyllaeus prussicus* (Szidat, 1937) comb. n. are considered to be *species inquirendae*, *C. truncatus* von Siebold in Baird, 1853 and *C. tuba* von Siebold in Baird, 1853 are *nomina nuda*. Data on the morphology, host spectra, distribution and known life-cycles of valid species are provided. Phylogenetic interrelations of four species of the genus including its type species and newly described *C. chondrostomi* were assessed based on an analysis of sequences of *lsrDNA* and *cox1*. A key to identification of all valid species of *Caryophyllaeus* is also provided.

Keywords: tapeworms, freshwater fish, Cyprinidae, systematics, identification key, phylogenetic relationships, Palaearctic Region

This article contains supporting information (Table S1) online at <http://folia.paru.cas.cz/suppl/2017-64-027.pdf>

Tapeworms of the genus *Caryophyllaeus* Gmelin, 1790 (Cestoda: Caryophyllidae) are among the most common intestinal parasites of cyprinid fishes in the Palaearctic Region, especially in Europe and the former USSR (Protasova et al. 1990), with the first species described (under the name *Taenia laticeps*) by Pallas (1781). Since that time, as many as 42 nominal taxa have been placed in the genus (see Table 1), which was erected by Gmelin (1790) to accommodate *Caryophyllaeus piscium* Gmelin, 1790 (syn. of *T. laticeps*).

Recent morphological and molecular evaluation of an extensive set of tapeworms of *Caryophyllaeus* from cyprinid fishes has revealed morphological polymorphism in two species, *C. laticeps* (Pallas, 1781) and *C. brachycollis* Janiszewska, 1953, and their wide (euryxenous) host specificity (Bazsalovicsová et al. 2014). In *C. laticeps*, five morphotypes, mostly specific to their cyprinid hosts, including common carp (*Cyprinus carpio* Linnaeus), common nase (*Chondrostoma nasus* [Linnaeus]), Macedonian vimba (*Vimba melanops* [Heckel]), and white-eyed bream (*Ballerus sapa* [Pallas]), were recognised. In *C. brachy-*

collis, two morphotypes typical of the barbels (Barbinae) and chub (*Squalius cephalus* [Linnaeus]), and freshwater breams (Leuciscinae), respectively, were distinguished based on their morphology and DNA sequences (see Barčák et al. 2014, Bazsalovicsová et al. 2014, Hanzelová et al. 2015).

In the present paper, all species placed in the genus since its erection by Gmelin (1790) are surveyed on the basis of a critical review of available literature and morphological evaluation of an extensive set of specimens deposited in helminthological collections and newly found tapeworms collected by the present authors and their collaborators. The generic diagnosis of *Caryophyllaeus* is emended and an annotated list is provided together with an identification key of all species recognised as valid.

MATERIALS AND METHODS

The present revision is based on (i) a critical review of literary data including papers published in the 18th and 19th Centuries; (ii) taxonomic study of numerous specimens deposited in museum collections in Europe and former Soviet Union; and (iii) mor-

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phological and genetic evaluation of newly collected tapeworms (see Barčák et al. 2014, Bazsalovicsová et al. 2014, Hanzelová et al. 2015). The methodology of the morphological study, i.e. fixation and processing of newly collected specimens, including evaluation using light and scanning electron (SEM) microscopy, has been described in previous papers by the present authors (Oros et al. 2010, Scholz et al. 2011, Barčák et al. 2014, Hanzelová et al. 2015). Extensive molecular data on *Caryophyllaeus brachycollis* and *C. laticeps* were provided by Bazsalovicsová et al. (2014). In morphological descriptions, measurements are in millimetres (mm) unless otherwise indicated; terminology of microtriches follows Chervy (2009). The scientific and common names of fish hosts are from FishBase (Froese and Pauly 2016).

The specimens studied were deposited in the following helminthological collections: The Natural History Museum, London, UK (BMNH); the former Helminthological Laboratory of the Russian Academy of Sciences, Moscow, Russia (GELAN); Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic (IPCAS); Institute of Parasitology, SAS, Košice, Slovakia (IPSAS); Natural History Museum, Geneva, Switzerland (MHNG-PLAT); Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM); Schmalhausen Institute of Zoology of the Ukrainian Academy of Sciences, Kiev, Ukraine (ZIK); and Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZIRAS).

Molecular analysis was performed on the newly collected tapeworms from *Cyprinus carpio* obtained by park staff from a pond in the Parco Regionale del Delta del Po (Ferrara Province), Italy. After rinsing in saline solution and preservation in 99% ethanol, middle body parts were used for DNA isolation using DNeasy® Blood & Tissue Kit (QIAGEN, Hilden, Germany). For PCR amplification, LSU5 and 1500R primers (Littlewood et al. 2000, Olson et al. 2003) were used for partial large subunit nuclear ribosomal RNA (D1–D3 domains of *lsrDNA*, 1,578 bp), while CFCYT2 and CRCYT2 primers (Bazsalovicsová et al. 2011) were used for partial mitochondrial gene cytochrome c oxidase subunit I (*cox1*, 657 bp). PCR products were enzymatically purified with exonuclease I and alkaline phosphatase (Werle et al. 1994) and directly sequenced at GATC Biotech (Cologne, Germany). PCR products were sequenced using both amplification primers, while internal primers 900F and 400R (Olson et al. 2003) were additionally used in the case of *lsrDNA*.

Phylogenetic analysis was performed on a concatenated dataset of the tapeworms newly found in Italy and sequences available in GenBank™ (Table S1). Contiguous gene sequences were assembled and aligned using Geneious ver. 9.1.6 (<http://www.geneious.com>; Kearse et al. 2012); individual gene alignments were built with E-INS-i algorithm of MAFFT (Katoh and Standley 2013). Phylogenetic relationships were estimated under maximum likelihood criterion in RAxML 7.2.8 program (Stamatakis 2006) implemented in Geneious employing GTR + I + G model, which was determined with PartitionFinder ver 1.1.1. (Lanfear et al. 2012). Bootstrap nodal support values (1,000 replicates) were also estimated in RAxML.

RESULTS

Species composition of the genus

The following seven species of *Caryophyllaeus*, rather than the 42 nominal taxa from the Palaearctic, Nearctic, Afrotropical (Ethiopian) and Indomalayan (Oriental) zoogeographical regions, placed in the genus during more than 200 years since its erection by Gmelin (1790), are recognised as valid (Table 1; species are listed alphabetically except for the type species, which appears first): *Caryophyllaeus laticeps* (type species); *C. auriculatus* (Kulakovskaya, 1961); *C. balticus* (Szidat, 1941) comb. n. (syn. *Khawia baltica* Szidat, 1941); *C. brachycollis*; *C. fimbriceps* Annenkova-Chlopina, 1919; *C. syrdarjensis* Skrjabin, 1913; and a new species, *C. chondrostomi*, from *Chondrostoma nasus* described below. An annotated list of valid species of *Caryophyllaeus* with data on their fish hosts, geographical distribution and life-cycles (if known) is provided below together with an amended diagnosis of the genus that reflects, among others, new inclusion of *C. balticus* which possesses cortical vitelline follicles, thus having been previously placed in the genus *Khawia* Hsü, 1935 of the family Lytocestidae Hunter, 1927. *Caryophyllaeus kashmirenses* Mehra, 1930 and *Caryophyllaeus prussicus* (Szidat, 1937) comb. n. are considered to be *species inquirendae*.

Amended diagnosis of *Caryophyllaeus* Gmelin, 1790

Syns.: *Chariophyllus* Bloch, 1782; *Caryophyllinus* Schrank, 1788

Diagnosis. Caryophyllidea, Caryophyllaeidae, with characters of family except for vitelline follicles being both medullary and/or cortical. Scolex dorsoventrally flattened, lacking apical structures and lateral loculi (afossate), variable in shape. Testes numerous, reaching posteriorly to cirrus-sac. Internal seminal vesicle may be present; external seminal vesicle absent. Ovary follicular, H-shaped. Seminal receptacle present. Vagina joins with uterus to form common uterovaginal duct. Vitelline follicles usually medullary, rarely both medullary and cortical, or exclusively cortical, extensive, separated into preovarian and postovarian groups of follicles; follicles may be present alongside preovarian loops of uterus, exceptionally few follicles lateral to ovarian arms. Uterus never extends anterior to cirrus-sac; uterine region usually short in relation to body length. Uterine glands present. Male and female genital pores separated, opening close to each other on ventral side of body. Parasites of cyprinid fishes (Cypriniformes: Cyprinidae) in the Palaearctic Region (Europe, northern Africa, Palaearctic Asia).

Type species: *Caryophyllaeus piscium* Gmelin, 1790 (syn. *Caryophyllaeus laticeps* [Pallas, 1781] Lühe, 1910).

Remarks. The genus was erected by Gmelin (1790) to accommodate *Caryophyllaeus piscium*. Numerous authors

Table 1. List of species placed in *Caryophyllaeus* Gmelin, 1790 and their current taxonomic status. Species of the genus recognised herein as valid in bold.

Species name	Current taxonomic status or valid name	Region*	Remarks
<i>acutus</i> Bovien, 1926	Syn. of <i>Lucknowia microcephala</i> (Bovien, 1926) Ash, Scholz, Oros et Kar, 2011	IND	<i>Lucknowia microcephala</i> redescribed by Ash et al. (2011a)
<i>appendiculatus</i> Ratzel, 1868	Syn. of <i>C. mutabilis</i> (= <i>C. laticeps</i>) according to Šrámek (1901; p. 114)	PAL	Described from larvae (metacestodes) without eggs, i.e. not progenetic; they may belong to any species occurring in Europe
<i>armeniacus</i> Cholodkovsky, 1915	<i>Khawia armeniaca</i> (Cholodkovsky, 1915) Shulman, 1958	PAL, ETH (?)	Redescribed by Scholz et al. (2011a)
<i>auriculatus</i> (Kulakovskaya, 1961) Scholz, Oros, Choudhury, Brabec et Waeschenbach, 2015	Valid species	PAL	Originally described in <i>Monobothrium</i> Diesing, 1863 by Kulakovskaya (1961)
<i>balticus</i> (Szidat, 1941) comb. n.	Valid species	PAL	Originally described in <i>Khawia</i> Hsü, 1935 by Szidat (1941)
<i>brachycollis</i> Janiszewska, 1953	Valid species	PAL	Redescribed by Barčák et al. (2014)
<i>caspicus</i> Annenkova-Chlopina, 1919	Syn. of <i>Caryophyllaeus laticeps</i>	PAL	Listed as a synonym in Protasova et al. (1990)
<i>catostomi</i> (Cooper, 1920) Woodland, 1923	<i>Glaridacris catostomi</i> Cooper, 1920	NEA	Originally described in <i>Glaridacris</i> Cooper, 1920 but Woodland (1923) synonymised this genus with <i>Caryophyllaeus</i>
<i>chalmersius</i> Woodland, 1924	<i>Monobothrioides chalmersius</i> (Woodland, 1924) Hunter, 1930	ETH	Originally described in <i>Caryophyllaeus</i> , then placed to <i>Lytocestus</i> Cohn, 1908 by Fuhrmann and Baer (1925)
<i>communis</i> Schrank, 1788	Syn. of <i>Caryophyllaeus laticeps</i>	PAL	Described as <i>Caryophyllinus communis</i> Schrank, 1788, with reference to Bloch (1782) and Goeze (1782) – see remark to <i>C. piscium</i> ; syn. of <i>C. mutabilis</i> (= <i>C. laticeps</i>) according to Šrámek (1901)
<i>cyprinorum</i> Zeder, 1803	Syn. of <i>Caryophyllaeus laticeps</i>	PAL	Listed as a synonym of <i>C. mutabilis</i> (= <i>C. laticeps</i>) by van Beneden (1858) and Šrámek (1901)
<i>fennicus</i> Schneider, 1902	<i>Caryophyllaeides fennica</i> (Schneider, 1902) Nybelin, 1922	PAL	Type species of <i>Caryophyllaeides</i> Nybelin, 1922
<i>filiformis</i> Woodland, 1923	<i>Lytocestus filiformis</i> (Woodland, 1923)	ETH	To be transferred to another genus
<i>fimbriceps</i> Annenkova-Chlopina, 1919	Valid species	PAL	Possibly disappeared from European waters (see Remarks)
<i>fuhrmanni</i> Szidat, 1937	Syn. of <i>Caryophyllaeus laticeps</i>	PAL	Treated as doubtful species (Janiszewska 1954) and synonymised by Mackiewicz (1962)
<i>gotoi</i> Motomura, 1927	<i>Paracaryophyllaeus gotoi</i> (Motomura, 1927)	PAL	Probably a complex of species (Scholz et al. 2014)
<i>hexacotyle</i> (Linton, 1897) Woodland, 1923	Syn. of <i>Isoglaridacris hexacotyle</i> (Linton, 1897) Mackiewicz, 1968	NEA	Originally described in <i>Monobothrium</i> but Woodland (1923) synonymised this genus with <i>Caryophyllaeus</i> ; Hunter (1927) placed the species in <i>Glaridacris</i>
<i>indicus</i> Moghe, 1925	<i>Lytocestus indicus</i> (Moghe, 1925) Woodland, 1926	IND	Redescribed by Ash et al. (2011a)
<i>japonensis</i> Yamaguti, 1934	<i>Khawia japonensis</i> (Yamaguti, 1934) Hsü, 1935	PAL	Redescribed by Scholz et al. (2011a)
<i>javanicus</i> Bovien, 1926	Syn. of <i>Lytocestus indicus</i>	IND	<i>Lytocestus indicus</i> redescribed by Ash et al. (2011a)
<i>kasmirenses</i> Mehra, 1930	<i>Species inquirenda</i>	IND	Described by Mehra (1930) from <i>Schizothorax microgogon</i> Heckel, Srinagar, Kashmir in abstract only
<i>laruei</i> Lamont, 1921	<i>Glaridacris laruei</i> (Lamont, 1921) Hunter, 1927	NEA	Transferred to <i>Glaridacris</i> as <i>G. laruei</i> comb. n. by Hunter (1927)
<i>laticeps</i> (Pallas, 1781) Lühe, 1910	Valid species	PAL	Described as <i>Taenia laticeps</i> by Pallas (1781); type species; redescribed by Hanzelová et al. (2015)
<i>microcephalus</i> Bovien, 1926	<i>Lucknowia microcephala</i> (Bovien, 1926) Ash, Scholz, Oros et Kar, 2011	IND	Redescribed by Ash et al. (2011a)
<i>minutus</i> Chen, 1973	Syn. of <i>Atractolytocestus huronensis</i> Anthony, 1958		Erroneous generic placement, corrected in the present study
<i>mutabilis</i> Rudolphi, 1802	Syn. of <i>Caryophyllaeus laticeps</i>	PAL	Long time considered valid, e.g. by Baird (1853) who listed <i>T. laticeps</i> as its senior synonym; Lühe (1910) first listed <i>C. laticeps</i> with <i>C. mutabilis</i> as its synonym, but in the legend to his fig. 4 wrote “ <i>C. mutabilis</i> ”
<i>niloticus</i> Kulmatycki, 1928	Syn. of <i>Wenyonia virilis</i> Woodland, 1923	ETH	Kulmatycki (1928) finished his description of <i>C. niloticus</i> in May 1920, but its publication was delayed until 1928 due to author's eye disease; the author himself admitted in a footnote on the first page of his paper that his species is identical with <i>Wenyonia virilis</i>
<i>oxycephalus</i> Bovien, 1926	Syn. of <i>Lytocestus indicus</i>	IND	<i>Lytocestus indicus</i> redescribed by Ash et al. (2011a)
<i>parvus</i> Zmeev, 1936	<i>Khawia parva</i> (Zmeev, 1936) Kulakovskaya, 1961	PAL	Listed as a synonym of <i>C. fennica</i> by Dubinina (1962); redescribed by Scholz et al. (2011a)
<i>piscium</i> Gmelin, 1790	Syn. of <i>Caryophyllaeus laticeps</i>	PAL	Gmelin (1790) referred to conspecific worms reported by Bloch (1782) and Goeze (1782); the former author (p. 34) did not give them specific name, placing them in <i>Chariophyllus</i> Bloch, 1782, whereas the latter author (pp. 180, 181) called his worms from cyprinids as <i>Fasciola fimbriata</i> (p. 180) but later (p. 181) considered them identical with <i>Taenia laticeps</i> of Pallas (1781)
<i>prussicus</i> (Szidat, 1937)	<i>Species inquirenda</i>	PAL	Possibly a synonym of <i>C. laticeps</i>

Continued.

Table 1. Continued.

Species name	Current taxonomic status or valid name	Region*	Remarks
<i>punctulatus</i> Molin, 1858	Syn. <i>Monobothrium punctulatum</i> Diesing, 1863; <i>species insertae sedis</i> ; described from the European eel, <i>Conger conger</i> (Linnaeus), i.e. from a marine fish	PAL	Not a caryophyllidean cestode (see Woodland 1923 and Scholz et al. 2015)
<i>serialis</i> Bovien, 1926	<i>Bovienia serialis</i> (Bovien, 1926) Fuhrmann, 1931	IND	Redescribed by Ash et al. (2011a)
<i>skrjabini</i> Popoff, 1924	Syn. of <i>Caryophyllaeides fennica</i>	PAL	Kulakovskaya (1961) first synonymised this species with <i>C. fennica</i>
<i>stentoreus</i> Schrank, 1788	Syn. of <i>Caryophyllaeus laticeps</i>	PAL	Described as <i>Caryophyllinus stentoreus</i> Schrank, 1788; description (Schrank 1788, p. 6) contains only brief description: “Der Körper walzenähnlich, trompetenförmig” (tubular, trumpet-shaped)
<i>syrdarjensis</i> Skrjabin, 1913	Valid species	PAL	Described from <i>Schizothorax intermedius</i> McClelland
<i>tenuicollis</i> Bovien, 1926	<i>Pseudocaryophyllaeus tenuicollis</i> (Bovien, 1926) Ash, Scholz, Oros et Kar, 2011	IND	Redescribed by Ash et al. (2011a)
<i>terebrans</i> (Linton, 1893) Woodland, 1923	<i>Glaridacris terebrans</i> (Linton, 1893) Mackiewicz, 1974	NEA	Originally described in <i>Monobothrium</i> but Woodland (1923) synonymised this genus with <i>Caryophyllaeus</i>
<i>trisinatus</i> Molin, 1861	<i>Species insertae sedis</i> ; larvae described from the European hake, <i>Merluccius merluccius</i> , i.e. from a marine fish	PAL	Not a caryophyllidean; probably larvae (metacestodes) of a species of ‘Tetraphyllidea’, i.e. cestodes maturing in elasmobranchs
<i>truncatus</i> von Siebold in Baird, 1853	<i>Nomen nudum</i>	PAL	No description of worms found in <i>Chondrostoma nasus</i> Linnaeus was provided by von Siebold in Baird (1853)
<i>tuba</i> von Siebold in Baird, 1853	<i>Nomen nudum</i>	PAL	Nybelin (1922 – p. 111) considered this species from <i>Salmo trutta fario</i> Linnaeus as a synonym of <i>Cyathocephalus truncatus</i> (Pallas, 1781), but it was not described by von Siebold in Baird (1853) and thus it is <i>nomen nudum</i>
<i>tuba</i> Monticelli, 1892	<i>Monobothrium wagneri</i> Nybelin, 1922	PAL	Homonym of <i>Caryophyllaeus tuba</i> von Siebold in Baird, 1853; a new name, <i>Monobothrium wagneri</i> , was proposed by Nybelin (1922 – p. 118)

*Zoogeographical regions: ETH – Ethiopian; IND – Indomalayan; NEA – Nearctic; PAL – Palaearctic.

(Joyeux and Baer 1936, Wardle and McLeod 1952, Janiszewska 1954, Yamaguti 1959, Dubinina 1962, Schmidt 1986) reported Müller (1787) as an authority of the genus, whereas Stiles and Hassal (1912), Nybelin (1922) and Mackiewicz (1972, 1994) credited the authority to Gmelin (1790). As Müller (1787) on p. 79 lists only “Nelkenwurm” (the common name for *Caryophyllaeus*), but not the Latin name, the authority of the genus is attributed to Gmelin (1790). Species that are currently placed in *Caryophyllaeus* were originally accommodated in the following genera: *Fasciola* Linnaeus, 1758; *Taenia* Linnaeus, 1758; *Chario-phyllus* Bloch, 1782; *Caryophyllinus* Schrank, 1788; *Phylline* Abildgaard, 1793; and *Khawia* (see Hanzelová et al. 2015 for references).

An annotated list of valid species of *Caryophyllaeus* Gmelin, 1790

Caryophyllaeus laticeps (Pallas, 1781) – type species

Figs. 1, 2, 8A,B

Syns.: *Taenia laticeps* Pallas, 1781; *Fasciola fimbriata* Goeze, 1782; *Caryophyllinus communis* Schrank, 1788; *Caryophyllinus stentoreus* Schrank, 1788; *Caryophyllaeus piscium* Gmelin, 1790; *Caryophyllaeus mutabilis* Rudolphi, 1802; *Caryophyllaeus appendiculatus* Ratzel, 1868; *Caryophyllaeus cyprinorum* Zeder, 1803; *Caryophyllaeus caspicus* Annenkova-Chlopina, 1919; *Caryophyllaeus fuhrmanni* Szidat, 1937; *Khawia coregoni* Kritscher, 1990

Material examined. See Bazsalovicsová et al. (2014), Hanzelová et al. (2015) and Xi et al. (2016); in addition, 20 hot-formalin fixed specimens from *Carassius carassius*

(Linnaeus), Filo d’Argenta, Ferrara Province, Italy, collected on 20 May 2002 by B.S. Dezfuli (IPCAS C-2/11), nine specimens from *Cyprinus carpio*, Parco Regionale del Delta del Po near Campotto, Italy, collected on 3 May 2016 by D.B. (IPSAS IT209/16-1, IT211/16-1–IT211/16-4, IT212/16-1–IT212/16-4) and five specimens from *Ballerus sapa*, River Danube near Iža, Slovakia, collected on 23 April 2013 by V.H. (IPSAS SK12/13-1, SK12/13-2, SK12/13-4, SK12/13-5, SK12/13-7) were studied.

Diagnosis (compiled from Hanzelová et al. 2015, who described five morphotypes; see also Table 2). Body elongated, slender to robust, with maximum width at cirrus-sac region, narrowing towards posterior end. Scolex variable in shape, always wider, usually conspicuously, than neck and remaining body. Testes oval to almost spherical, intermingled with vitelline follicles. Anteriormost testes far from anterior extremity. Posteriorly, testes reach to anterior margin of cirrus-sac. Vas deferens well-developed, long, in distal (posterior) part not surrounded by vitelline follicles. Cirrus-sac small to moderately large, subspherical, not far from posterior end of body. Internal sperm duct enlarged to form conspicuous internal seminal vesicle (Figs. 1B, 2E,F). Ovary with symmetrical lateral lobes (anterior lobes more or less of same length as posterior lobes or anterior lobes only slightly shorter). Vagina slightly sinuous, especially in its proximal part. Seminal receptacle pyriform. Vitelline follicles medullary, exceptionally paramuscular. Preovarian vitelline follicles irregularly-shaped, numerous, distributed lateral and median, surrounding testes, absent alongside ovary. Postovarian follicles usually numerous. Uterus forms several loops between ovary and posterior part of cirrus-sac.

Fig. 1. *Caryophyllaeus laticeps* (Pallas, 1781) from *Abramis brama* (Linnaeus), Slovakia. **A** – anterior part of the body (note long distance of anteriormost testes from anterior margin of scolex); **B** – posterior part of body, ventral view (note vas deferens not surrounded by vitelline follicles nor testes in medial line and well-developed internal seminal vesicle). **Abbreviations:** amt – anteriormost testis; amvf – anteriormost vitelline follicle; cs – cirrus-sac; ieg – intrauterine eggs; isv – internal seminal vesicle; mgp – male genital pore; ov – ovary; pvf – postovarian vitelline follicles; sr – seminal receptacle; te – testes; ug – uterine glands; ut – uterus; uvp – uterovaginal pore; va – vagina; vd – vas deferens; vf – vitelline follicles.

Type host: Freshwater bream, *Abramis brama* (Linnaeus) (Cyprinidae: Leuciscinae).

Additional hosts: Cyprinid fishes of the subfamilies Alburninae (4 species), Barbinae (9), Cyprininae (4), Gobioninae (1), Leuciscinae (19) and Tincinae (1); however, some records require verification (see Hanzelová et al. 2015).

Type locality: Not specified by Pallas (1781).

Type specimens: Since no type specimens were deposited, Hanzelová et al. (2015) designated the specimen from *Abramis brama*, Cheboksary Water Reservoir on the River Volga, Russia as the neotype of *C. laticeps* (IPCAS C-2/1).

Sequence data. Partial *cox1* sequences (JQ034066–JQ034068, JQ034070, JQ034071, JQ034077; Brabec et al. 2012; KF051092–KF051099, KF051102–KF051104, KF051107, KF051108, KF051114, KF051115, KF051117, KF051118, KF051126, KF051127, KF051131, KF051132; Bazsalovicsová et al. 2014), complete *nad3* sequences (JQ034003–JQ034005, JQ034007, JQ034008, JQ034014; Brabec et al. 2012), partial mitochondrial genome (JQ268540; Waeschenbach et al. 2012; KT781573–KT781580; Xi et al. 2016), *cox1* pseudogene (JQ034065, JQ034069, JQ034072–JQ034076; Brabec et al. 2012), *nad3* pseudogene (JQ034002, JQ034006, JQ034009–JQ034013; Brabec et al. 2012), partial *lsrDNA* sequences (AF286911; Olson et al. 2001; AY157180; Lockyer et al. 2003; JQ034121–JQ034123; Brabec et al. 2012; KF051141–KF051153, KF051159–KF051163, KF051169, KF051173, KF051176, KF051177; Bazsalovicsová et al. 2014), partial *ssrDNA* sequences (Z98308–10; Mariaux 1998; AJ287488; Littlewood and Olson 2001; JQ034138–JQ034140; Brabec et al. 2012), complete ITS2 sequences (KF700250–KF700252; Králová-Hromadová et al. 2013), microsatellite C53 sequences (KM267645–KM267650; Králová-Hromadová et al. 2015).

Life cycle. *Limnodrilus claparedeanus* Ratzel, *Psammoryctides barbatus* (Grube) and *Tubifex tubifex* (Müller) (Naididae: Tubificinae) have been reported as natural or experimental intermediate hosts of *C. laticeps* (see Mrázek 1901, Sekutowicz 1934, Kennedy 1969, Davydov and Poddubnaya 1988, Protasova et al. 1990, Poddubnaya 1995). However, some metacestode stages found in naturally infected hosts may have been misidentified, such as some of the young stages in the intestine photographed by Sekutowicz (1934), which resemble Morphotype 2 of *C. brachycollis*. Milbrink (1975), referring to a paper by Timm (1972), reported four species of *Potamothrix* Vejvodský et Mrázek, namely *P. bedoti* (Piquet), *P. hammoniensis* (Michaelsen), *P. heuscheri* (Bretscher) and *P. vejvodskyi* (Hrábě), as intermediate hosts of *C. laticeps*.

Distribution. Europe (Albania, Austria, Belarus, Bulgaria, Czech Republic, Estonia, Finland, France, Germany, Hungary, Ireland, Italy, Latvia, Liechtenstein, Lithuania, Macedonia, Montenegro, Norway, Poland, Romania, Russia, Serbia, Slovakia, Spain, Sweden, Switzerland, UK including Northern Ireland and Ukraine), Palearctic Asia (Azerbaijan, China, Georgia, Iran, Iraq, Japan, Kazakhstan, Russia, Turkey and Uzbekistan), and northern Africa (Egypt and Morocco) (Gibson 2013a; for distribution of individual morphotypes – see Hanzelová et al. 2015).

Remarks. *Caryophyllaeus laticeps* is a polymorphic species with several morphotypes that differ from each other in the shape and size of the body and scolex, the extent of the vitelline follicles and other morphological characteristics (Hanzelová et al. 2015); individual morphotypes also differ from each other genetically (Bazsalovicsová et al. 2014). This species can be distinguished from *C. brachycollis* and *C. fimbriceps*, which may occur in the same fish hosts, by the following morphological characteristics: (i) a subspherical, thin-walled cirrus-sac near the posteri-

Table 2. Measurements (in millimetres unless otherwise stated) of species of the genus *Caryophyllaeus* Gmelin, 1790.

Species	<i>C. laticeps</i> (Pallas, 1781)	<i>C. laticeps</i>	<i>C. chondrostomi</i> sp. n.	<i>C. auriculatus</i> (Kulakovskaya, 1961)	<i>C. baliticus</i> (Sizdat, 1941)	<i>C. brachycollis</i> Janiszewska, 1953	<i>C. fimbriiceps</i> Annenkova-Chlopina, 1919	<i>C. syrdarjensis</i> Skrjabin, 1913
Host	cyprinids	<i>Carassius carassius</i> (Linnaeus), <i>Cyprinus carpio</i> Linnaeus	<i>Chondrostoma nasus</i> (Linnaeus)	<i>Leuciscus danilewskii</i> (Kessler)	<i>Tinca tinca</i> Linnaeus	eyprinids	<i>Cyprinus carpio</i>	<i>Schizothorax curvifrons</i> Heckel
Locality	Palaeartic region*	Italy (new material)	Austria	Ukraine	Czech Republic	France, Russia, Slovakia	Czech Republic	Kyrgyzstan, Kazakhstan
Sample size	n = 63	n = 23	n = 15	n = 5	n = 10	n = 32	n = 15	-
Body length (A)	9–41	12–23.5	26–64	18.5–26	23–55	11–32	9.5–15	6.3–16
width	0.6–1.7	0.5–1.2	1.2–2.8	1.2–1.4	0.9–2.6	0.5–1.2	0.9–1.5	1.0–1.5
Scolex length	1.0–2.3	0.7–1.6	1.5–2.2	0.6–1.5	1.6–3.5	0.9–1.8	1.0–1.6	-
width	1.0–2.9	0.8–1.8	2.1–4.4	1.3–1.8	1.9–3.9	1.2–2.8	0.9–1.9	-
Neck width (µm)	380–1,236	572–923	707–1,617	843–1,415	480–1,760	406–937	500–1,118	-
ratio to scolex width (%)	22–74	41–96	26–38	51–91	25–45	24–69	43–58	-
Testis size (µm)	90–317 × 61–252	53–82 × 44–79	123–311 × 106–295	110–171 × 76–118	70–320 × 50–260	75–203 × 68–196	101–192 × 84–119	50–153
number	180–1,030	-	505–866	-	550–750	141–499	-	-
distance from first VF	0.3–6.2	0.8	0.3–2.7	0.1–0.9	3.8–7.7	0.1–4.3	0.4–1.4	-
distance from the AE (B)	2.2–10.8	2.1	1.4–4.9	0.6–1.7	6.9–11.8	0.8–8.3	1.9–2.9	1.5
B : A (%)	17–34	-	4–14	3–7	23–33	6–26	16–24	-
Length of TF	6.1–27.0	-	19.8–51.4	15.3–21.6	12.3–16.7	7.3–20.2	6.8–9.7	-
Cirrus-sac size (µm)	307–1,302 × 322–998	592–971 × 330–896	1,178–2,811 × 807–1,804	584–788 × 448–542	610–850 × 390–530	537–1,227 × 311–651	644–1,112 × 486–738	850
extent to body width (%)	42–87	49–84	51–85	33–43	43–73	40–74	43–74	-
Vas deferens length	0.3–3.8	1.5–4.0	4.0–11.2	1.3–2.0	-	-	0.3–0.5	-
extent to TF (%)	6–24	-	17–24	7–8	-	-	3–6	-
Ovary total width	0.4–1.5	0.4–1.0	0.8–2.5	0.9–1.2	1.1–1.9	0.4–1.1	0.7–1.4	-
length of ovarian arms	0.5–1.7	0.7–1.4	1.0–2.8	0.6–1.1	3.3–3.8	0.8–1.7	0.9–1.4	-
width of ovarian arms (µm)	103–499	101–284	203–740	119–345	260–310	113–537	113–224	-
distance from posterior end (C)	0.8–3.1	1.4–2.5	1.9–5.0	1.3–1.9	1.1–1.7	1.3–3.0	1.1–1.9	-
C : A (%)	4–14	10–15	7–11	5–8	4–7	7–14	9–13	-
Vitelline follicles size (µm)	62–229 × 39–214	64–190 × 46–160	85–182 × 58–154	83–155 × 50–88	40–270 × 20–190	47–200 × 43–140	85–175 × 64–135	85 × 40–50
distance from AE	0.9–6.9	1.2–2.5	1.0–2.1	0.5–0.9	3.0–4.9	0.8–4.0	1.1–2.0	1.4
Uterus extent	0.6–3.2	1.3–2.5	2.5–6.6	1.2–1.8	2.9–6.4	1.3–3.5	1.1–2.2	-
extent to length of TF (%)	7–25	-	11–17	7–8	24–30	9–19	19–23	-
Seminal receptacle size (µm)	184–956 × 115–477	128–385 × 66–270	231–630 × 93–390	158–194 × 121–144	135–276 × 68–106	303–489 × 229–370	285–429 × 181–329	-
Egg size (whole mounts; µm)	57–74 × 39–52	54–71 × 37–52	51–54 × 34–37	86–95 × 57–70	59–73 × 39–46	59–75 × 40–45	51–62 × 39–45	63 × 48
Egg size (freely laid; µm)	62–67 × 40–47	-	-	-	66–70 × 39–43	-	-	-
Genital pores	separated	separated	separated	separated	separated	separated	separated	genital atrium
Posterior vitelline follicles	large, usually >30	numerous	numerous	small, 16–28	numerous	numerous	numerous	small, few**
Internal seminal vesicle	usually present	usually present	present	absent	absent	absent	absent	present, small

AE – anterior extremity; TF – testicular field; VF – vitelline follicle; * see Hanzelová et al. 2015 and Xi et al. 2016; ** 38 in number according to fig. 4 in Skrjabin (1913).

Fig. 2. Morphologically similar specimens of *Caryophyllaeus laticeps* (Pallas, 1781) from *Carassius carassius* (Linnaeus) (A, B, E) and from *Cyprinus carpio* Linnaeus (C, D, F) found in the neighbouring localities near Argenta, Italy. A, C – anterior part of the body; B, D – posterior part of the body, both ventral views; E, F – cirrus-sac with a large internal seminal vesicle.

or end, containing a well-developed internal seminal vesicle (vs a large, thick-walled, strongly muscular cirrus-sac without a distinct internal seminal vesicle in *C. brachycollis* and *C. fimbriceps* – see fig. 2M,L in Scholz 1989 and figs. 2 and 3A,B in Barčák et al. 2014); (ii) the absence of the vitelline follicles alongside the median line of the body at the level of the distal course of the vas deferens (follicles present, i.e. circum-medullary, overlaying vas deferens in *C. brachycollis* and *C. fimbriceps*); (iii) a more posterior position of the ovary (more anterior in *C. brachycollis* – fig. 2 in Barčák et al. 2014); and (iv) possession of the scolex of different shape (*C. fimbriceps* possesses a cuneicrispate scolex – see fig. 2D,E in Scholz 1989 and fig. 1H,I,J in Oros et al. 2010).

Comparison of tapeworms found in *Carassius carassius* and *Cyprinus carpio* from Italy (Figs. 2, 8B) with those of *C. laticeps* studied by Hanzelová et al. (2015) revealed their conspecificity, which was also confirmed by molecular data (*IsrDNA* and *cox1* sequences of tapeworms from *C. carpio*; Fig. 9). In addition, these tapeworms are in some characteristics similar to *Caryophyllaeus prussicus* comb. n. (syn. *Bothrioscolex prussicus* Szidat, 1937) (see figs. 4, 5 in Szidat 1937 and Figs. 2, 8B in the present paper). Szi-

dat's (1937) worm resembles these tapeworms from Italy in the testes difficult to observe (a unique characteristic among all caryophyllideans), the shape and size of the body, a cuneicrispate scolex wider than the body, and extensive vitelline follicles that reach anteriorly to some distance posterior to the scolex and that only partially surround the region of the vas deferens on the ventral side.

However, *C. prussicus*, which was described based on a single specimen, allegedly differs from the specimens recently found in Italy in its possession of a smaller cirrus-sac, as could be assumed from fig. 5 in Szidat (1937) (vs a somewhat larger cirrus-sac in Italian specimens) and by having a more posterior extent of the preovarian vitelline follicles (reaching up to the ovary in *C. prussicus* vs reaching only posterior to the cirrus-sac in the specimens from Italy). The species is considered as *species inquirenda* (see below).

Among all caryophyllidean cestodes, *C. laticeps* infects the widest range of fish hosts (38 species of cyprinids), with most hosts from the subfamily Leuciscinae (19 species), especially breams (species of *Abramis* Cuvier and *Ballerus* Heckel). Such a wide range of fish hosts (i.e. euryxenous host specificity) is rather unusual among these cestodes, as

most of them are stenoxenous or oioxenous (Mackiewicz 1972, Scholz and Kuchta 2017, Scholz and Oros 2017). However, some of the records require confirmation, e.g. those reported by Rahemo and Mohammad (2004) from tench, *Tinca tinca* (Linnaeus) and *Carassobarbus luteus* (Heckel).

Caryophyllaeus laticeps has a large distribution that includes Europe and most of Palaearctic Asia, even though reports from countries outside of the former USSR are rather scarce (Xi et al. 2016) and need of verification. Significantly, almost nothing is known about the distribution of the individual morphotypes recognised by Hanzelová et al. (2015) outside of Europe. Records of *C. laticeps* from North America, e.g. that of Rehder (1959) from common carp in Iowa, represent in fact *Khawia iowensis* Calentine et Ulmer, 1961 (= syn. of *K. japonensis* [Yamaguti, 1934]) (Mackiewicz 1974, Scholz et al. 2011).

Caryophyllaeus laticeps is by far the most intensively studied species of the genus and one of the most studied fish cestode at all (see Discussion). Ultrastructure of several organ systems and structures such as the tegument, nervous system, vitelline follicles, sperm, and frontal and uterine glands has been studied since the late 1960's (Béguin 1966, Mackiewicz 1968, Bazitov 1979, Richards and Arme 1982a,b, Davydov and Poddubnaya 1988, Davydov et al. 1994, Poddubnaya 1995, 1996, Bruňanská and Kostič 2012, Bruňanská et al. 2013, Biserova et al. 2014). Extensive data on seasonal patterns in the occurrence and maturation of *C. laticeps* in different cyprinids from Europe and the former USSR were reviewed by Chubb (1982); more recent data were provided by Evlanov and Kolokolnikova (1991) and Evlanov et al. (1992).

Caryophyllaeus auriculatus (Kulakovskaya, 1961)

Figs. 3, 8C

Syn.: *Monobothrium auriculatum* Kulakovskaya, 1961

Material examined. Six flattened, partly decomposed specimens from *Leuciscus danilewskii* (Kessler) No. 298-1, Siverskyi Donets, Ukraine, collected on 22 May 1952 (ZIK – not numbered, ZIRAS 1415); two specimens from *L. danilewskii* No. 433-2, Siverskyi Donets, Ukraine, collected on 16 July 1952, designated as *Caryophyllaeus laticeps*, but with a strikeout species name.

Diagnosis (based on five specimens from *L. danilewskii*; see Table 2 for measurements). Body slender to moderately robust, elongated, with maximum width at ovarian region, then steeply narrowing towards posterior extremity. Scolex cuneiform with lateral ('auricular') projections, neck very short or absent. Anteriormost testes close or in short distance from anterior extremity and from anteriormost vitelline follicles. Testes posteriorly reach anterior margin of cirrus-sac. Vas deferens medially not surrounded by vitelline follicles, cirrus-sac oval, internal seminal vesicle not observed. Ovary at distance from posterior margin of body, vagina ventral to uterus. Seminal receptacle anterodorsal to ovarian isthmus, Mehli's gland posterior to ovarian isthmus. Preovarian vitelline follicles reach to posterior margin of cirrus-sac, anteriormost follicles at short distance from anterior extremity; postovarian vitelline follicles small

Fig. 3. *Caryophyllaeus auriculatus* (Kulakovskaya, 1961) from *Leuciscus danilewskii* (Kessler), Ukraine. **A** – anterior part of the body (probably syntype; note very short distance of anteriormost vitelline follicles from the narrow scolex); **B** – posterior part of the body, ventral view (note low number of postovarian vitelline follicles and presence of seminal receptacle). *Abbreviations:* sr – seminal receptacle.

and few (16–28). Uterus forms several loops between cirrus-sac and postovarian vitelline follicles.

Type and only known host: Danilewskii's dace, *Leuciscus danilewskii* (Kessler) (Cyprinidae: Leuciscinae).

Type locality: River Siverskyi Donets (or Seversky Donets in Russian), usually simply called the Donets (sometimes incorrectly called the Northern Donets owing to the confusion of the Russian *severnii* with *siverskyi*), the largest tributary of the River Don, Ukraine.

Type specimens: Not designated, but specimens collected on 22 May 1952 and mounted on slides designated No. 298-1

apparently belong to a type series.

Sequence data. Not available.

Life cycle. Not known.

Distribution. Europe (Ukraine – see Kulakovskaya 1961, Protasova et al. 1990).

Remarks. Kulakovskaya (1961) described this species as *Monobothrium auriculatum* from specimens found by N.N. Shevchenko in Danilewski's dace from northeastern Ukraine. The original description was brief and illustrations quite schematic (see fig. 3.1 in Kulakovskaya 1961). Kulakovskaya (1961) placed the species in *Monobothrium* Diesing, 1863 based on the following morphological characteristics: (i) alleged absence of a seminal receptacle (which is in fact present; see Fig. 3B); (ii) a relatively small cirrus-sac (but resembling that of *C. laticeps*); (iii) shape of the ovary (actually different from the ovary of *M. wagneri* Nybelin, 1922, which is butterfly-shaped, with markedly shorter and wider lateral lobes, whereas *C. auriculatus* possesses an H-shaped ovary with longer and narrower lateral lobes – see fig. 1A in Scholz 1987); (iv) thick tegument; and (v) large eggs (the two last features are not considered to be suitable for circumscription of genera). Scholz et al. (2015) transferred *M. auriculatum*, which has never been reported since its original description, to *Caryophyllaeus* because of its morphology, which markedly differs from that of the type and currently only known species of *Monobothrium*, *M. wagneri*.

Caryophyllaeus auriculatus somewhat resembles *C. laticeps* in its morphology, especially in the shape of the body, scolex and cirrus-sac, and in the appearance of the vas deferens, which forms a long area of tightly coiled loops anterior to the cirrus-sac that is not surrounded by vitelline follicles medially, i.e. on the ventral and dorsal side (see fig. 2 in Hanzelová et al. 2015 and Fig. 1B in the present paper). Both species differ from each other in the number and size of the postovarian vitelline follicles (PVF) (much fewer, i.e. 16–28, and smaller in *C. auriculatus* vs usually numerous, i.e. more than 30, but always forming a conspicuous field of PVF due to their larger size in *C. laticeps*), the absence of vitelline follicles alongside the preovarian uterine loops in *C. auriculatus* (present in *C. laticeps*) and an internal seminal vesicle (usually present in the latter species), and shape of the scolex, which has more prominent anterolateral corners in *C. auriculatus*.

***Caryophyllaeus balticus* (Szidat, 1941) comb. n.**

Figs. 4, 8D

Syn.: *Khawia baltica* Szidat, 1941 (new synonym)

Material examined. Forty-seven specimens from *Tinca tinca* in the Czech Republic (IPCAS C-42) and two specimens from Switzerland (MHNG – not registered) (see Scholz et al. 2011 for details).

Diagnosis (compiled from Scholz et al. 2011; see Table 2 for measurements). Body slender, maximum width at level of cirrus-sac. Scolex flabellate, markedly wider than neck, with wrinkles along front edge; neck long. Anterior-most testes located at very long distance from anterior extremity and far posterior to anteriormost vitelline fol-

Fig. 4. *Caryophyllaeus balticus* (Szidat, 1941) comb. n. (syn. *Khawia baltica*) from *Tinca tinca* (Linnaeus), Czech Republic. **A** – anterior part of the body (note long neck and flabellate scolex); **B** – posterior part of the body, dorsal view (note small cirrus-sac and vitelline follicles present alongside ovary). Abbreviations: cs – cirrus-sac; vf – vitelline follicle. Modified from Scholz et al. (2011a).

licles. Posteriorly, testes reach to anterior margin of cirrus-sac, rarely to its posterior half. Cirrus-sac small, oval, thin-walled, difficult to observe. Ovary bilobed, with long and slender ovarian arms. Vagina slightly sinuous, forming elongated seminal receptacle in its proximal part. Vitelline follicles cortical, usually spherical. Anteriormost vitelline follicles far posterior to anterior extremity, reaching posteriorly alongside cirrus-sac to uterine loops; a few follicles present alongside ovary. Postovarian follicles extensive (several hundreds). Uterine region long, loops of uterus reaching anteriorly to level of posterior margin of cirrus-sac.

Type and only known host: Tench, *Tinca tinca* Linnaeus (Cyprinidae: Tincinae); records from other fishes are considered to be unreliable (Scholz et al. 2011).

Type locality: Rossitten, Courland Spit (Kuhrische Nehrung), East Prussia (now the Russian enclave of Kaliningrad).

Type specimens: Do not exist (probably destroyed during the Second World War (Calentine and Ulmer 1961). Neotype (paragenophore IPCAS C-42) from *Tinca tinca* (host coll. No. 2841a), a fishpond near Jindřichův Hradec (49°8'39"N; 15°0'11"E), South Bohemia, Czech Republic, 22. 4. 2010, collected by Roman Kuchta and Céline Levron.

Sequence data. Partial *cox1* sequence (JN004233), complete *nad3* sequence (JN004244), complete *ssrDNA* sequence (JN004255), partial *lsrDNA* (JN004266; all Scholz et al. 2011), and complete ITS2 (JQ647870; Králová-Hromadová et al. 2012).

Life cycle. Scholz (1993) demonstrated experimentally that the oligochaete *Tubifex tubifex* serves as intermediate host; plerocercoids were formed after one month at a temperature of 20–22 °C (Scholz 1993).

Distribution. Europe (Czech Republic, Lithuania, Poland, Russia – Kaliningrad District, Switzerland, Ukraine), Asia (Georgia) (Scholz et al. 2011, Gibson 2013b).

Remarks. The species was originally described as *Khawia baltica* by Szidat (1941) and redescribed by Scholz et al. (2011), who assessed interrelations of all seven species of the lytocestid genus *Khawia* based on *ssrDNA*, *lsrDNA*, *nad3* and *cox1* sequences. All analyses invariably showed a distant position of *K. baltica* relative to the other species of *Khawia* (see figs. 9 and 10 in Scholz et al. 2011). Furthermore, a more comprehensive multigene analyses revealed *K. baltica* as a sister taxon to the lineage comprised of *C. laticeps* and *C. brachycollis* (see Xi et al. 2013, Scholz et al. 2015), thus making *Khawia* polyphyletic.

As a member of the family Lytocestidae, *K. baltica* possesses cortical vitelline follicles, whereas all species of *Caryophyllaeus* are mainly medullary (the new species from *Chondrostoma nasus* described below has vitelline follicles mainly paramuscular, with some follicles present also in the cortex). There is also another difference between *K. baltica* and species of *Caryophyllaeus* in the relative length of the uterine region (much longer in the former species). In contrast, *K. baltica* resembles some species of *Caryophyllaeus*, especially Morphotype 1 of *C. laticeps*, in its possession of a flabellate scolex with numerous, shallow longitudinal grooves (see figs. 1 and 4 in Hanzelová et al. 2015), and a long neck, vitelline follicles present alongside the whole preovarian uterine region, and a less robust ovary with long and slender lateral lobes (Scholz et al. 2011, Hanzelová et al. 2015).

Khawia baltica thus occupies in its morphology an intermediate position between species of *Khawia* (all with the cortical position of the vitelline follicles) and *Caryophyllaeus* (all but one species with medullary vitelline follicles), but molecular data unequivocally support a close relationship of this taxon with species of the latter genus (Fig. 9). Moreover, all recent phylogenetic studies have demonstrated that the position of the vitelline follicles and testes in relation to the inner longitudinal musculature is a homoplastic character that does not reflect the interrelationships of the caryophyllidean cestodes and their evolutionary history (Oros et al. 2008, Brabec et al. 2012, Scholz et al. 2015). Consequently, *K. baltica* is transferred to *Caryophyllaeus* as a new combination and the generic diag-

Fig. 5. *Caryophyllaeus brachycollis* Janiszewska, 1953 from *Barbus carpathicus* Kotlík, Tsigenopoulos, Ráb et Berrebi, Slovakia (A) and from *Abramis brama* (Linnaeus), Slovakia (B, C). **A, C** – anterior parts of body of morphotypes described by Barčák et al. (2014). **B** – posterior part of body, ventral view (note muscular, elongated cirrus-sac). Abbreviation: cs – cirrus-sac.

nosis of *Caryophyllaeus* is emended to reflect the cortical position of the vitelline follicles in this species.

Caryophyllaeus brachycollis Janiszewska, 1953

Figs. 5, 8G,H

Syn.: *Caryophyllaeus laticeps* (Pallas, 1781) *pro parte*

Material examined. See Barčák et al. (2014) and Bazsalovicsová et al. (2014); additionally, one specimen of Morphotype 1 from *Alburnus neretvae* Buj, Sanda et Perea (host No. ALNE 2), Mušnica stream near Avtovac, Bosnia and Herzegovina, 6 July 2015 (IPCAS C-51/11); one specimen of Morphotype 1 from *Squalius squalus* (Bonaparte) (host No. SQSQ 16), Drežnica, Croatia, 10 October 2016 (IPCAS C-51/10); one specimen of Morphotype 2 from *Pseudochondrostoma polylepis* (Steindachner) (host No. PSPO 25), Alcoa, Fervença, Portugal, 25 June 2016 (IPCAS C-51/12), collected by Andrea Vetešníková Šimková (all fishes represent new host records).

Diagnosis (compiled from Barčák et al. 2014 who described two morphotypes called herein M1 (Figs. 5A, 8G) and M2 (Figs. 5C, 8H; see Table 2 for measurements). Body robust (M1) or slender (M2), elongated, with maximum width at level of cirrus-sac, then narrowing towards posterior extremity. Scolex spatulate, with tapered anterior edge (M1) or flabellate with curved anterior margin (M2), slightly (M1) or markedly (M2) wider than neck. Testes oval to subspherical, intermingled with vitelline follicles; anteriormost testes close (M1) or at long distance from scolex (M2); posteriorly testes reach anterior margin of cirrus-sac. Vas deferens surrounded by vitelline follicles. Cirrus-sac large, thick-walled, elongated to ovoid, containing long, muscular cirrus. Internal seminal vesicle absent. Ovary follicular. Vagina sinuous in its proximal part, almost straight distally. Seminal receptacle oval to subspherical, anterodorsal to ovarian isthmus. Preovarian vitelline follicles lateral and median, surrounding testes and distal (posterior) part of vas deferens; postovarian vitelline follicles numerous (several dozens). Uterine region moderately long.

Type host: Not indicated by Janiszewska (1953), who found cestodes in four species of cyprinids (Cyprinidae) from two subfamilies, *Barbus barbus* (Linnaeus), *B. petenyi* Heckel (both Barbinae), *Squalius cephalus* and *Leuciscus idus* (Linnaeus) (both Leuciscinae).

Additional hosts: Cyprinid fishes of the subfamilies Alburninae (2 species), Barbinae (8), Cyprininae (1) and Leuciscinae (15).

Type locality: Not specified explicitly, but tapeworms were found in rivers in Poland (the Rivers Odra and Vistula and their tributaries Barycz, Raba and Ropa).

Type specimens: Barčák et al. (2014) designated the specimen found in *Barbus barbus* from the Argens River near Marseille, France (IPCAS C-3/5) as the neotype of *C. brachycollis* because type specimens were not preserved by Janiszewska (1953).

Sequence data. Partial *cox1* sequences (JQ034064; Brabec et al. 2012; KF051100, KF051105, KF051106, KF051109–KF051113, KF051121–KF051124, KF051133–KF051136; Bazsalovicsová et al. 2014), complete *nad3* sequences (JQ034001; Brabec et al. 2012), partial *lsrDNA* sequences (JQ034120; Brabec et al. 2012; KF051137–KF051140, KF051154–KF051158, KF051166–KF051168, KF051170, KF051174, KF051175, KF051181; Bazsalovicsová et al. 2014), partial *ssrDNA* sequences (JQ034137; Brabec et al. 2012), and complete ITS2 sequences (KF700248, KF700249; Králová-Hromadová et al. 2013). New partial *lsrDNA* sequences of specimens from *Alburnus neretvae* in Bosnia and Herzegovina (KY617021), *Squalius squalus* in Croatia (KY617019) and *Pseudochondrostoma polylepis* in Portugal (KY617020).

Life cycle. Janiszewska (1953, 1954) reported a metacystode (plerocercoid according to the terminology proposed by Chervy 2002) allegedly belonging to *C. brachycollis*, from *Limnodrilus udekemianus* Claparède and *L. hoffmeisteri* Claparède (Naididae: Tubificinae) both in Poland. Kulakovskaya (1962) successfully infected *L. hoffmeisteri* and *Tubifex tubifex* with oncospheres of

C. brachycollis and found plerocercoids infective for fish after 3–4 months of development in the intermediate hosts; metacystodes may survive up to 2 years (Protasova et al. 1990).

Distribution (new geographical records marked with an asterisk). Europe (Austria, *Bosnia and Herzegovina, Bulgaria, *Croatia, Czech Republic, Finland, France, Greece, Hungary, Italy, Montenegro, Poland, Portugal, Russia, Serbia, Slovakia and Ukraine) and Palaearctic Asia (China, Iraq and Russia) (see Gibson 2013c and Barčák et al. 2014 for references and verified records).

Remarks. Barčák et al. (2014) redescribed this species and characterised two morphotypes that differ conspicuously from one another mainly in the shape of the scolex and the anterior extent of the vitelline follicles and testes. This cestode occurs in a wide spectrum of cyprinid fishes, but it is most frequent and abundant in barbels (Barbinae) and chub, *Squalius cephalus* (Morphotype 1) and breams (*A. brama*, *Ballerus* spp.; Morphotype 2). All records from Asia should be verified, especially those from Iraq and China.

Caryophyllaeus fimbriceps Annenkova-Chlopina, 1919

Figs. 6A,B; 8F

Material examined. Fourteen and 27 strongly flattened and deformed specimens from *Cyprinus carpio* in the Czech Republic and Slovakia, respectively; two specimens from ‘sazan’ (wild form of *C. carpio*) in Zelenga Lake (ZIRAS No. 1360) and in the River Volga (ZIRAS No. 1371), Russia; eight specimens from *Tinca tinca*, Czech Republic (Scholz 1989).

Diagnosis (based on five specimens from *C. carpio*, Czech Republic; see Table 2 for measurements). Body elongated, moderately robust, with maximum width at level of cirrus-sac, then narrowing towards posterior end. Scolex cuneicrispate, i.e. flabellate with short conspicuous indentations on anterior margin, neck short. Anteriormost testes far from anterior extremity and in moderate distance from anteriormost vitelline follicles, testes posteriorly reach anterior margin of cirrus-sac. Area filled with vas deferens very short, difficult to observe. Cirrus-sac spherical to oval; internal seminal vesicle absent. Preovarian vitelline follicles medullary, anteriormost vitelline follicles not far from anterior extremity, posteriorly reach up to anterior margin of ovarian arms, i.e. absent alongside ovary; postovarian vitelline follicles numerous (several dozens). Ovary close to posterior margin of body; vagina slightly sinuous; seminal receptacle dorsal to ovarian isthmus. Uterus forms several loops between cirrus-sac and postovarian vitelline follicles.

Type host: Common carp, *Cyprinus carpio* Linnaeus (Cyprinidae: Cyprininae).

Additional hosts: In addition to common carp, the following cyprinid fishes have been reported by Dubinina (1987) and Protasova et al. (1990) (but all these fish hosts should be verified): *Abramis brama*, *Alburnus alburnus* (Linnaeus), *Ballerus sapa*, *Carassius carassius*, *Chondrostoma polylepis* (syn. *Pseudochondrostoma polylepis* [Steindachner]), *Leuciscus idus*, *L. leuciscus* (Linnaeus), *Rutilus rutilus* (Linnaeus),

Fig. 6. *Caryophyllaeus fimbriceps* Annenkova-Chlopina, 1919 from wild population of common carp ('sazan'), *Cyprinus carpio* Linnaeus, Russia (A, B). *Caryophyllaeus syrdarjensis* from *Schizothorax intermedius* McClelland (= *S. curvifrons* Heckel). Redrawn from Skrjabin (1913) (C, D). A, C – anterior part of body. B – posterior part of body, ventral view. D – posterior part of body, probably ventral view (Skrjabin 1913 did not provide this information).

Squalius cephalus, *Vimba vimba* (Linnaeus) and *Tinca tinca*. Especially doubtful are records from *Coregonus wartmanni* (Bloch) (Salmonidae) and *Huso huso* (Linnaeus) (Acipenseridae).

Type locality: Not explicitly specified (specimens described were found in carp from Caucasus and the Caspian Sea – see table in Annenkova-Chlopina 1919).

Type specimens: Not known to exist, almost certainly never deposited.

Sequence data. Not available.

Life cycle. Several naids (Tubificinae), namely *Psammoryctes albicola* (Michaelsen), *Psammoryctides barbatus*, *Limnodrilus claparedeanus*, *L. udekemianus*, *Tubifex ignotus* (Štolc) and *T. tubifex*, serve as intermediate hosts (Demshin 1984, Protasova et al. 1990).

Distribution. Europe (Austria, Belorussia, Bulgaria, Czech Republic, Great Britain, Greece, Hungary, Italy, Latvia, Lithuania, Poland, Romania, Russia – Karelia and the River Volga basin, Serbia, Slovakia, Spain and Ukraine), Asia (rivers and fish cultures in the basins of the Azov, Black and Caspian Seas and Lake Aral, Azerbaijan, Georgia, Iran, Kazakhstan, Kyrgyzstan, Tajikistan; introduced with carp to western Siberia) (Dubinina 1962, 1987, Gibson et al. 2005, Gibson 2013d).

Remarks. This cestode was described by Annenkova-Chlopina (1919) from 'sazan', which is the name used

for wild common carp. Dogiel and Bykhovsky (1939) distinguished *C. fimbriceps* from *C. laticeps* by the shape of the scolex, which possesses deep notches on the anterior edge in the former species, and a smaller size of the body, with gravid, i.e. egg-bearing, specimens only 3.5 mm long (mostly longer than 6 mm in *C. laticeps*). Common carp is apparently the principal definitive host, whereas records from other fish need verification.

In the 1950's and 1960's, *C. fimbriceps* was listed among pathogenic parasites of cultured carp as it caused slower growth or even mortality of heavily infected fry and yearlings (Kulakovskaya and Svirepo 1967, Bauer et al. 1973). Mitterpák and Huňady (1984) reported an epizootic outbreak of infection with *C. fimbriceps*, which resulted in considerable losses among young carps (1 and 2-years old) in eastern Slovakia. However, only very few, unverified records of *C. fimbriceps* have been published since then, e.g. from Serbia (Dikanović et al. 2013) and Iran (Sattari et al. 2007). Reports of cestodes allegedly belonging to *C. fimbriceps* from freshwater bream, *Abramis brama*, in Poland, Romania and Russia in the 1980's (Georgescu and Naziru 1984, Vasilevskaya 1984, Reda 1988) and Caspian roach, *Rutilus caspicus* (Yakovlev), in Iran (Khara et al. 2011) need verification, because the authors did not provide morphological descriptions nor line-drawings and no vouchers are available.

Long-term effort of the present authors to find *C. fimbriceps* failed, which well corresponds to a considerable decrease of reliable reports of this cestode since the 1970's. The absence of recent records indicates possible extinction of this cestode in Europe. Disappearance of this previously common parasite of carp may be related to introduction of invasive cestodes parasitising the same fish host, such as the caryophyllideans *Khawia sinensis* Hsü, 1935 and *Atractolytocestus huronensis* Anthony, 1958, and the bothriocephalidean *Schyzocotyle acheilognathi* (Yamaguti, 1934) (syn. *Bothriocephalus acheilognathi* Yamaguti, 1934) (Musselius et al. 1964, Körting 1975, Kennedy 1994, Oros et al. 2004, 2009, Scholz et al. 2012). Molecular data on *C. fimbriceps* are thus not available and morphological and molecular study of the species based on new material is pending.

***Caryophyllaeus syrdarjensis* Skrjabin, 1913** Fig. 6C,D

Material examined. None.

Diagnosis (based on Skrjabin 1913; see Table 2 for measurements). Body robust, more flattened anteriorly, becoming widely oval in cross section posteriorly, with maximum width at level of cirrus-sac, then narrowing towards widely rounded posterior end. Scolex cuneiform, without any obvious grooves on anterior edge, only slightly wider than neck region. Testes almost spherical, intermingled with vitelline follicles. Anteriormost testes close to anterior extremity and always posterior to anteriormost vitelline follicles. Posteriorly, follicles reach to mid-length of cirrus-sac. Vas deferens strongly coiled, occupies large region anterior to cirrus-sac, surrounded by vitelline follicles and testes in posterior (distal) part. Cirrus-sac relatively small, strongly muscular, subspherical (elongated in sagittal section), close to posterior end of body. Internal seminal vesicle small. Ovary with short and narrow lateral lobes, very close to posterior extremity. Vagina described to be identical as in *C. laticeps*, apparently joining uterus to form short common uterovaginal duct. Seminal receptacle not reported. Preovarian vitelline follicles transversely elongated, much smaller than testes; anteriormost vitelline follicles begin at short distance posterior to anterior extremity; posteriorly, follicles reach level of posterior part of cirrus-sac, rarely reaching to ovarian lobes. Postovarian follicles form relatively small group. Uterus forms several strongly coiled loops between ovary and posterior part of cirrus-sac. Genital pores open in genital atrium, i.e. not opening separately outside.

Type and only known host: Sattar snowtrout, *Schizothorax intermedius* McClelland (= *Schizothorax curvifrons* Heckel) (Cyprinidae: Barbinae); record of *C. syrdarjensis* from *Barbus barbus* (Cyprinidae: Barbinae) in Ukraine in an unpublished summary of DSc. thesis by Kulakovskaya (1969) is apparently erroneous.

Type locality: River Talas, Syr Darya basin, "Russisch-Turkestan" (in fact part of Kyrgyzstan or Kazakhstan).

Type specimens: Not known to exist, almost certainly never preserved; Skrjabin (1913) did not indicate their deposition and they were not found in the two principal helmintholog-

ical collections of the former Soviet Union, i.e. ZIRAS in St. Petersburg and collection of the former Helminthological Laboratory of the Russian Academy of Sciences (GELAN) in Moscow (T.S. – unpubl. data).

Sequence data. Not available.

Life cycle. Not known.

Distribution. The River Talas basin in former Russian-Turkestan district (contemporary area of Kazakhstan and Kyrgyzstan); since record of *C. syrdarjensis* from Ukraine (see above) is considered erroneous, the species has never been found since its original description.

Remarks. Skrjabin (1913) described this species from 15 specimens found in *Schizothorax intermedius* (= *S. curvifrons*) from the River Talas basin; prevalence of infection was 10% (2 fish infected of 20 examined). Morphological description of *C. syrdarjensis* was relatively detailed, but only few measurements were provided. In a simple identification key, the new species was differentiated from *C. laticeps* by a more developed vas deferens, which occupies a large area anterior to the cirrus-sac ("Vas deferens bildet von der Bursa cirri ein mächtiges Schlingengewirr"). It seems that all specimens studied by Skrjabin (1913) were strongly contracted; the posterior region of the specimens illustrated on figs. 4 and 8 is very short, especially the uterine region, thus indicating that the worms may have been unnaturally deformed during fixation.

Nybelin (1922) recognised *C. syrdarjensis* as a valid species. Dubinina (1962) and Protasova et al. (1990) did not include this species in their lists of fish cestodes from ex-Soviet Union, but Dubinina (1987) listed *C. syrdarjensis* among the species of *Caryophyllaeus* occurring in the former USSR. In a footnote, she mentioned incorrect synonymy of this species with *C. fimbriceps* by Dogiel and Bykhovsky (1939) and possible conspecificity of *C. syrdarjensis* and *C. brachycollis*. It is true that the scolex of *C. syrdarjensis* (see fig. 3 in Skrjabin 1913) somewhat resembles that of Morphotype 1 of *C. brachycollis* (see figs. 1 and 4A in Barčák et al. 2014); both species also have the anteriormost vitelline follicles and testes situated close to the anterior extremity. However, the posterior end of both species is conspicuously different, including the shape and position of the ovary and cirrus-sac, the latter being much larger in *C. brachycollis* (see figs. 2 and 3 in Barčák et al. 2014 and figs 4, 7 and 8 in Skrjabin 1913). In addition, *C. syrdarjensis* occurs in snowtrouts (species of *Schizothorax* Heckel) that live only in Central and East Asia, whereas *C. brachycollis* is largely a European species.

***Caryophyllaeus chondrostomi* sp. n.**

Figs. 7, 8E

ZooBank number for species:

un:lsid:zoobank.org:act:77D40E4C-CDEC-4B39-87F8-4ACB716C5ECF

Syn.: *Caryophyllaeus laticeps* morphotype 4 of Bazsalovicsová et al. (2014) and Hanzelová et al. (2015).

Material examined. Fifty seven specimens from *Chondrostoma nasus*, River Drau, Austria, collected by F. Jirsa in 2000 and by T.S. and A. Ash in 2009 (IPCAS No.

Fig. 7. *Caryophyllaeus chondrostomi* sp. n. from *Chondrostoma nasus* (Linnaeus), Austria. **A** – outline of whole body, dorsal view (* vitelline follicles in middle part not illustrated); **B** – anterior part of body (note width of scolex and relatively short distance of first testes from anterior margin of body); **C** – posterior part of body with conspicuous vas deferens, ventral view; **D** – longitudinal section of posterior part of body; **E** – cross section of middle part of body; **F** – cross section on level of vas deferens (D–F: note medullary, paramuscular and even cortical position of vitelline follicles). **Abbreviations:** amt – anteriormost testis; amvf – anteriormost vitelline follicle; cs – cirrus-sac; fc – fertilisation canal; ieg – intrauterine eggs; ilm – inner longitudinal musculature; isv – internal seminal vesicle; Mg – Mehlis' gland; mgp – male genital pore; ov – ovary; pvf – postovarian vitelline follicles; sr – seminal receptacle; te – testes; ug – uterine glands; ut – uterus; uvp – uterovaginal pore; va – vagina; vd – vas deferens; vf – vitelline follicles.

Fig. 8. Scanning electron microphotographs of the scoleces of species of *Caryophyllaeus* Gmelin, 1790 (A–H). **A** – flabellate scolex with folds of *C. laticeps* (Pallas, 1781) from *Abramis brama* (Linnaeus) (Slovakia); **B** – cuneicrispate scolex of *C. laticeps* from *Cyprinus carpio* Linnaeus (Italy); **C** – cuneiform scolex with lateral ('auricular') projections of *C. auriculatus* (Kulakovskaya, 1961) from *Leuciscus danilewskii* (Kessler) (Ukraine); **D** – flabellate scolex with wrinkles along front edge of *C. balticus* (Szidat, 1941) from *Tinca tinca* (Linnaeus) (Czech Republic); **E** – flabellate scolex of *C. chondrostomi* sp. n. from *Chondrosoma nasus* (Linnaeus) (Austria); **F** – cuneicrispate scolex of immature *C. fimbriceps* Annenkova-Chlopina, 1919 from *Cyprinus carpio* (Slovakia); **G** – spatulate scolex with tapered edge of Morphotype 1 of *C. brachycollis* Janiszewska, 1953 from *Barbus carpathicus* (Kotlík, Tsigenopoulos, Ráb et Berrebi) (Slovakia); **H** – flabellate scolex with curved margin of Morphotype 2 of *C. brachycollis* from *A. brama* (Slovakia); **I** – acicular filitriches (filiform microtriches) on scolex of *C. laticeps* from *Cyprinus carpio* (Italy).

C-748), and River Hron, Slovakia in 1958 by R. Žitňan (IPSAS Nos. 706/58, 707/58, 718/58, 720/58, 849/58, 863/58).

Diagnosis (based on 15 specimens from *C. nasus*, Austria; see Table 2 for measurements). Body large, robust, with maximum width at level of cirrus-sac, then narrowing towards posterior end. Surface uniformly covered by acicular filitriches (filiform microtriches). Scolex afossate, flabellate, with small wrinkles on anterior margin, much wider than relatively slender neck; its anterior margin with

numerous superficial grooves (wrinkles). Inner longitudinal musculature well developed, formed by small bundles of muscle fibres. Testes medullary, numerous, anteriormost testes always posterior to anteriormost vitelline follicles, in short distance from anterior margin of body and anteriormost vitelline follicles, posteriorly reaching posterior margin of cirrus-sac. Vas deferens very long, strongly coiled, distal (posterior) part not surrounded by vitelline follicles nor testes medially. Cirrus-sac large, pyriform to oval, thin-walled; internal seminal vesicle spherical, large. Pre-

ovarian vitelline follicles small, some of them penetrate to cortex, i.e. paramuscular or even cortical in position. Anteriormost vitelline follicles in relatively short distance from anterior margin of scolex, posteriorly reach ovarian arms. Postovarian vitelline follicles numerous (several dozens). Ovary H-shaped, follicular, close to posterior margin of body. Vagina slightly sinuous tube, ventral to uterus, joins with uterus and forms short common uterovaginal duct; seminal receptacle dorsal to ovarian isthmus. Uterus forms several loops between postovarian vitelline follicles and cirrus-sac; preovarian part surrounded by numerous glands. Genital pores separated, close to one another, male pore always anterior to female (common uterovaginal) pore. Eggs smooth, operculate and unembryonated (without formed oncosphere *in utero*).

Type and only known host: Common nase *Chondrostoma nasus* (Linnaeus) (Cyprinidae: Leuciscinae).

Type locality: River Drau near Rosegg, Carinthia, Austria (46°35'N; 14°01'E).

Type specimens: Holotype – one specimen from host No. AU 2 captured and examined on 28 July 2009, ten paratypes on six slides including three hologenophores (see Pleijel et al. 2008 for terminology) from hosts Nos. AU 2 (one specimen) and AU 3 (nine specimens) captured and examined on 28 July 2009 – all IPCAS C-748; four paratypes from hosts Nos. AU 2 (two specimens) and AU 3 (two specimens) – BMNH 2017.3.20.12–13; four paratypes from hosts Nos. AU 2 (two specimens) and AU 3 (two specimens) – MHNG-PLAT 97005, 97006; four paratypes from hosts Nos. AU 2 (two specimens) and AU 3 (two specimens) – USNM 1422206 and USNM 1422205, respectively.

Etymology: The new species is named after generic name of its type host, i.e. *Chondrostoma*.

Sequence data. Partial *cox1* sequences (KF051128–KF051130; Bazsalovicsová et al. 2014) and partial *lsrD*-NA sequences (KF051178–KF051180; Bazsalovicsová et al. 2014).

Life cycle. Not known.

Distribution. Europe (Austria, Slovakia).

Remarks. Tapeworms from *C. nasus* had been originally considered by the present authors to represent a new, undescribed species related to *C. laticeps*, because of several morphological peculiarities: (i) a large, very robust body (*vs* slender or moderately robust body in other congeners), (ii) scolex significantly wider than neck (*vs* scolex only slightly wider in *C. auriculatus* and *C. syrdarjensis*), (iii) anteriormost testes in a relatively short distance from the anterior extremity (*vs* relatively far distance of anteriormost testes from the anterior extremity in *C. laticeps*, *C. balticus* and *C. fimbriceps*), (iv) anteriormost vitelline follicles located in shorter distance to the anterior extremity (*vs* longer distance from the anteriormost vitelline follicles from the anterior margin of the body in Morphotypes 1, 3 and 5 of *C. laticeps* – see Hanzelová et al. 2015, *C. balticus* and Morphotype 2 of *C. brachycollis* – see Barčák et al. 2014), and (v) long vas deferens not surrounded by vitelline follicles alongside the median line (*vs* vas deferens surrounded by vitelline follicles in its distal, i.e. posterior

part and thus hardly observable in *C. balticus*, *C. brachycollis* and *C. fimbriceps*).

However, Bazsalovicsová et al. (2014) did not find sufficient genetic support for separate status of tapeworms from common nase (see fig. 1 in Bazsalovicsová et al. 2014). As a result, these large-sized tapeworms were designated as Morphotype 4 of *C. laticeps* and Hanzelová et al. (2015) provided their detailed morphological and biometrical characterisation. In contrast, a recent population genetic analysis of isolates originally identified as *C. laticeps* from Austria, Bulgaria, Slovakia, Russia and United Kingdom using microsatellite loci revealed a considerable genetic difference of the population from *C. nasus* in Austria from the remaining isolates found in other fish hosts. The microsatellite data analysed with Structure 2.3.4 and Principal Coordinates Analysis (PCoA) programs demonstrated a significant genetic separation of the Austrian population with no overlaps with other populations of *C. laticeps* (I. Hromadová, Institute of Parasitology of the Slovak Academy of Sciences, Košice – unpubl. data).

Together with the existence of unique morphological traits observed in the cestodes from *C. nasus*, these results of the microsatellite analysis led us to reconsider our previous conclusion. Therefore, tapeworms from common nase in Austria are described herein as a new species. Specimens from the same fish host found by R. Žitňan were strongly flattened, which affected considerably their morphology. However, they possess typical characteristics of *C. chondrostomi* sp. n., i.e. large-sized body, with a very long region filled with loops of sperm ducts (vas deferens), large internal seminal vesicle, vitelline follicles beginning anteriorly near the scolex, and thus are considered conspecific.

Invalid species or taxa of uncertain taxonomic status

Caryophyllaeus kashmirenses Mehra, 1930 – species inquirenda

This species, the name of which was misspelled as *kashmirenses* instead of *kashmirensis*, was insufficiently described in an abstract from the 17th Indian Science Congress held in Allahabad, India, by Mehra (1930). The original description of tapeworms found in *Schizothorax micropogon* Heckel (currently a synonym of *S. curvifrons*) from Srinagar, Kashmir, India, contains only basic data on the worms' morphology (Mehra 1930): Worms large, 30–60 mm long; maximum width 1–2 mm. Scolex always wider than body, devoid of any longitudinal grooves. In ovarian region, 10–13 main excretory canals present. Vas deferens strongly coiled. Vaginal canal tubular, nearly straight. Preovarian vitelline follicles cortical, postovarian follicles medullary; a few vitelline follicles may be present alongside ovary. Uterus forms numerous loops never extending anterior to female gonopore. Genital pores situated at last 10–20% of body length. Eggs 45–53 µm × 30–33 µm.

The original description did not contain any illustration nor explicit differential diagnosis of the new species. Mehra (1930) only stated that “The species apparently connects

the two genera, *Caryophyllaeus* and *Lytocestus*.” Indeed, the cortical position of the preovarian vitelline follicles (but without any evidence in the form of cross sections) is typical of cestodes of the family Lytocestidae, not those of the Caryophyllaeidae (see Mackiewicz 1994).

Caryophyllaeus kashmirenses was found in the same fish host as *C. syrdarjensis* and in a relatively close region. Another caryophyllidean, the capingentid *Adenoscolex oreini* Fotedar, 1958, was found in the congeneric host, *Oreinus sinuatus* (Heckel), in fact misapplied name for *Schizothorax richardsonii* (Gray), from the same region (Kashmir, India) as *C. kashmirenses* (see Fotedar 1958).

However, these three species, for which molecular data are not available, are not synonymised herein because of the differences in their position of vitelline follicles (allegedly cortical in *C. kashmirenses*, but paramuscular in *A. oreini* – see fig. 7 in Fotedar 1958, and medullary in *C. syrdarjensis* – fig. 6 in Skrjabin 1913), body size (the two former taxa are large, robust worms up to 60 mm and 38 mm long, respectively, whereas *C. syrdarjensis* is only 16 mm long), and presumably different shape of the scolex (that of *C. kashmirenses* was reported as always wider than the body, whereas those of *C. syrdarjensis* and *A. oreini* are only slightly wider than the neck region (see fig. 3 in Skrjabin 1913 and fig. 1 in Fotedar 1958)).

Nevertheless, the taxonomic status of *C. kashmirenses* is uncertain and new material is needed to confirm validity of this species. From *A. oreini*, *C. kashmirenses* also differs by having much smaller eggs (45–53 µm × 30–33 µm vs 64–75 µm × 36–48 µm in *A. oreini*), fewer excretory canals (10–13 vs 14–18) and vitelline follicles present alongside the ovary (absent in *A. oreini* – see fig. 2 in Fotedar 1958). However, these differential characteristics cannot be confirmed by a study of type specimens, because only types of *A. oreini* are available at BMNH (1998.10.13.8–10).

***Caryophyllaeus prussicus* (Szidat, 1937) comb. n. – species inquirenda**

Syns.: *Bothrioscolex prussicus* Szidat, 1937; *Khawia prussica* (Szidat, 1937) Markevich, 1951

This species was described as *Bothrioscolex prussicus* by Szidat (1937) from a single specimen found in the intestine of crucian carp, *Carassius carassius*, from Rossitten, Courland Spit (Kuhrische Nehrung), East Prussia (now the Russian enclave of Kaliningrad between Poland and Lithuania). The original description of *B. prussicus* was incomplete and only a very few measurements were provided, namely total length (10 mm), maximum width (0.5 mm) and the size of eggs (51–53 µm × 33–35 µm); however, no true differential diagnosis of the new species was provided by Szidat (1937).

Scholz et al. (2011) considered *K. prussica* (Szidat, 1937) to be *species incertae sedis*, but they assumed that it may belong to *Caryophyllaeus* because it possesses a short uterine region and the preovarian vitelline follicles reaching almost to the ovarian arms. Assignment of *B. prussicus* to *Caryophyllaeus* is accepted in the present paper, but the species is considered to be *species inquirenda* because it differs from both Morphotype 3 of *C. laticeps* (see Han-

zelová et al. 2015 for its morphology), and *C. laticeps* from *Cyprinus carpio* and *Carassius carassius* found in Italy (see Remarks on *C. laticeps* above) in the size of the cirrus-sac and posterior extent of the preovarian vitelline follicles, considering the original description by Szidat (1937) is correct and precise.

***Caryophyllaeus truncatus* von Siebold in Baird, 1853 and *Caryophyllaeus tuba* von Siebold in Baird, 1853 – nomina nuda**

A study of the original paper of von Siebold in Baird (1853) has revealed that the author named these two species found in *Chondrostoma nasus* and *Salmo trutta fario* Linnaeus, respectively, but did not provide their morphological description or other characterisation. Therefore, both taxa are *nomina nuda* according to the Article 12 of the International Code of Zoological Nomenclature (ICZN 1999).

***Caryophyllaeus minutus* Chen, 1973**

This species was mentioned in Chen (1973) together with quite detailed line-drawing. However, the tapeworms identified as *Caryophyllaeus minutus* in fact represent another caryophyllidean species, the lytocestid *Atractolytocestus huronensis*, because they have identical shape of the body and scolex, extensive vitelline follicles uninterrupted alongside the ovarian lobes and the testes reaching posteriorly up to the ovary. Chen (1973) mentioned the date of the first description of *C. minutus* as 1964, but he in fact referred just to an unpublished manuscript of its description.

Interrelationships of species of *Caryophyllaeus* based on molecular data

Mitochondrial *cox1* and nuclear *lsrDNA* sequences of numerous isolates of four of the seven species of the genus *Caryophyllaeus* are available. Concatenated dataset of both partial gene sequences analysed herein contained 2,029 alignable positions. Within the 630 bp long *cox1* dataset 397 (63%) characters were found variable and 349 (88%) of them were parsimony-informative, whereas the 1,399 bp long region of *lsrDNA* offered only 426 (30%) alignable positions, of which 256 (60%) were parsimony-informative. Phylogenetic relationships within the genus *Caryophyllaeus* as well as its position within selected caryophyllidean genera are shown in Fig. 9.

The species of *Caryophyllaeus* form a statistically well-supported monophyletic group, which consists of two clades. The first clade comprises isolates of *C. laticeps* from different hosts including specimens from common carp in Italy, which form just weakly supported group. The position of *Caryophyllaeus chondrostomi* sp. n. within this clade is also uncertain, but this newly described species is distinct from all isolates of *C. laticeps*. The clade also includes isolates preliminary identified as *C. laticeps* morphotype 5 (see fig. 1 in Bazsalovicsová et al. 2014). These samples, designated as *Caryophyllaeus* sp. in the present study (Fig. 9), most probably represent separate species of *Caryophyllaeus*, which is pending formal description. The second group is formed by isolates of *C. brachycollis* and

Fig. 9. Phylogenetic relationships of species of *Caryophyllaeus* Gmelin, 1790 and their position among the species of the Caryophyllidae evaluated by Maximum likelihood method based on concatenated dataset of two genes (*cox1* mtDNA and *lsr*DNA). Bootstrap supports for branch nodes estimated by RAXML and shown if exceed 55. The newly generated sequences are emboldened.

C. balticus, but sister-lineage relationship of the latter taxon with *C. brachycollis* is only weakly supported (Fig. 9).

DISCUSSION

Taxonomic history and species composition of *Caryophyllaeus*

The genus *Caryophyllaeus* was one of the species-rich genera of caryophyllidean cestodes (and in fact of all fish cestodes), with as many as 42 nominal species having been placed in the genus (Table 1). The number of species accommodated in this genus by different authors var-

ied considerably, especially in the 20th century. Whereas Lühe (1910) included only *Caryophyllaeus laticeps* within the genus, Janiszewska (1954) mentioned only *C. laticeps* and *C. brachycollis* as valid species in Europe, and Kulakovskaya (1961) and Dubinina (1962) listed only three and four species, respectively, Hunter (1930), Wardle and McLeod (1952) and Yamaguti (1959) recognised as many as 13, 14 and even 21 possibly valid species of *Caryophyllaeus*, respectively. However, the present authors consider the actual number of valid species of *Caryophyllaeus* to be much lower, with only seven species, including newly described *C. chondrostomi*, recognised as valid. The same

Fig. 10. Geographical distribution of species of *Caryophyllaeus* Gmelin, 1790 (blue dots in A–E). **A** – *C. laticeps* (Pallas, 1781); **B** – *C. brachycollis* Janiszewska, 1953; **C** – *C. fimbriceps* Annenkova-Chlopina, 1919; **D** – *C. balticus* (Szidat, 1941) comb. n.; **E** – *C. chondrostomi* sp. n.; **F** – *C. auriculatus* (Kulakovskaya, 1961) (blue triangle), *C. syrdarjensis* Skrjabin, 1913 (blue dot). Question marks indicate countries with reported occurrence, but exact locality is not known.

situation, i.e. considerable reduction of the number of valid species, was observed in other caryophyllidean genera, especially those in the Oriental and Ethiopian regions (Ash et al. 2011a,b, Schaeffner et al. 2011).

However, validity of some of the seven species listed above still requires confirmation. First, *C. brachycollis* resembles in the shape, size and structure of the cirrus-sac *C. fimbriceps* and both species may be conspecific.

Second, the validity of *C. auriculatus*, which has never been found since its original description, also needs verification; it could be another morphotype of *C. laticeps*. Third, *C. syrdarjensis* from snowtrout (Barbinae) somewhat resembles Morphotype 1 of *C. brachycollis*, which is common in barbels (Barbinae), in the shape of the scolex and the anterior extent of the vitelline follicles and testes. Fourth, the taxonomic status of *C. kashmirenses* is unclear and its conspecificity with *Adenoscolex oreini* found in the same region (Kashmir) cannot be excluded. In contrast, the existence of more, yet undescribed species of *Caryophyllaeus* is probable as documented by the present description of a new species from common nase. Based on the data of Bazsalovicsová et al. (2014), cestodes from *Ballerus sapa* designated as Morphotype 5 also probably represent a new species, but their material is not sufficient for formal, good-quality description as a new species.

Morphotypes and diagnostic characters

Recent morphological and molecular studies of *C. brachycollis* and *C. laticeps* have demonstrated the existence of several morphotypes, which differ from each other mainly in the scolex shape and the anterior extent of the testes and vitelline follicles (Barčák et al. 2014, Bazsalovicsová et al. 2014, Hanzelová et al. 2015). This observation challenges suitability of some of the previously used morphological diagnostic characteristics. In contrast, morphology of the terminal genitalia, especially the shape, size and structure of the cirrus-sac, appeared to be stable and thus suitable for differentiation of species of *Caryophyllaeus* (see Barčák et al. 2014, Hanzelová et al. 2015). In fact, it is sometimes difficult to interpret correctly morphological differences found in cestodes from different fish hosts: do they represent intraspecific variability of polymorphic cestodes with a wide range of definitive hosts such as *C. laticeps* or interspecific differences of separate species specific to their respective fish hosts, e.g. *C. fimbriceps* from common carp or *C. auriculatus* from Danilewski's dace? In such cases, molecular data may help unravel species boundaries between taxa from different hosts. The absence of molecular data on four species (*C. auriculatus*, *C. fimbriceps*, *C. kashmirenses* and *C. syrdarjensis*) impedes reliable assessment of their validity and interrelationships with congeneric taxa.

Assigning *C. balticus* with the exclusively cortical vitelline follicles (a feature typical for members of the Lytocestidae), to a genus of the Caryophyllaeidae, whose taxa are typified by the medullary vitelline follicles, challenges 'classical' classification of the caryophyllidean cestodes (Mackiewicz 1994). However, it has been demonstrated repeatedly over the last decade that the position of the inner longitudinal musculature in relation to the testes and vitelline follicles is a homoplastic character that may not reflect entirely the evolutionary history of these cestodes (Olson et al. 2008, Brabec et al. 2012, Scholz et al. 2015). The possession of paramuscular or even cortical position of vitelline follicles in the newly described species *C. chondrostomi* represents further evidence that the position of the vitelline follicles may vary even between congeneric

species, which makes this taxonomic character problematic for family-level classification.

Host associations

No general pattern in host use by species of *Caryophyllaeus* seems to exist and fidelity of individual cestode species to their definitive hosts differs markedly from each other. Some species such as *C. auriculatus*, *C. balticus*, *C. chondrostomi* and *C. syrdarjensis* are oioxenous (infect only one host species), others (*C. fimbriceps*) stenoxenous, i.e. infect a few related hosts, whereas the remaining species, i.e. *C. laticeps* and *C. brachycollis*, infect a wide spectrum of hosts of different subfamilies. However, it should be pointed out that the actual degree of host specificity is often biased by doubtful host records and/or incorrect identification. This is the main problem of faunal surveys, for which voucher specimens necessary for scrutiny are often not deposited. The absence of molecular data for specimens reported from atypical or uncommon hosts is another obstacle that impedes a more reliable assessment of host associations in *Caryophyllaeus* and other fish tapeworms (Scholz and Kuchta 2017).

Importance of tapeworms of *Caryophyllaeus*

Except for *C. fimbriceps* and *C. laticeps*, almost no data on the veterinary importance and pathology of species of *Caryophyllaeus* are available. *Caryophyllaeus fimbriceps* was considered a pathogenic parasite of cultured common carp (Bauer et al. 1973), but almost no records have been published since the 1970's. This cestode is now extremely rare or may even be extinct in most of its original distribution areas. The pathological impact of *C. laticeps* on wild cyprinid fishes was observed by Karanis and Taraschewski (1993), with the most pronounced pathological effects in freshwater bream; these included the chronic stage of infection, associated with formation of granulomas. Negative effect of *C. laticeps* on host intestinal microflora and physiology of digestion was reported by Izvekova et al. (1997, 2011) and Izvekova and Solovyev (2013).

Caryophyllaeus laticeps served as an important model for pioneer ecological studies including classical papers by Kennedy (1968, 1969), Kennedy and Walker (1969) and Anderson (1974a, 1976), which served as baselines for proposing basic rules of host-parasite relationships and epidemiology of parasite infections. Anderson (1974b) generated a stochastic model to describe one compartment of an indirect parasite life cycle, namely adult *C. laticeps* in the definitive host, cyprinid fishes in Europe. More recently, a few studies using *C. laticeps* as an indicator of ecosystem changes (Kurbanova et al. 2002) or colonisation and re-colonisation potential of some autogenic and allogenic parasite species (Kennedy 1998) have been published.

Concluding remarks

This synoptical review of the formally oldest genus of fish cestodes represents a follow-up of previous revisional studies focused on species-rich genera of the caryophyllidean cestodes such as *Khawia*, *Paracaryophyllaeus*

Kulakovskaya, 1961 and *Wenyonia* Woodland, 1923, and on taxonomically complicated groups such as lytocestids from catfishes (Siluriformes) in the Oriental region (Ash et al. 2011a,b, Schaeffner et al. 2011, Scholz et al. 2011, 2014). Similarly as in some of these studies, an integrated approach has been applied, i.e. combination of morphological and molecular data, to critically review the species composition of the genus that housed as many as 42 nominal taxa over its long and convoluted taxonomic history. Interrelations of only four of the seven recognised species of *Caryophyllaeus* could be assessed using molecular data, but these data were crucial to unravel a high degree of morphological plasticity of the two most common species, namely *C. brachycollis* and *C. laticeps*, in which two and five morphotypes specific to different fish hosts were distinguished (Barčák et al. 2014, Bazsalovicsová et al. 2014, Hanzelová et al. 2015).

To facilitate identification of the species of *Caryophyllaeus*, a simple key based on morphological characteristics is provided. Nevertheless, species identity should be verified by comparing morphological and other information in diagnoses of individual species provided above and in the papers by Barčák et al. (2014) and Hanzelová et al. (2015).

Key to the identification of species of *Caryophyllaeus*

- 1 Cirrus-sac elongated, thick-walled without internal seminal vesicle (Fig. 5B) 2
 - Cirrus-sac oval to subspherical, thin-walled, usually with internal seminal vesicle (Figs. 1B, 2E,F, 7C) 3
- 2 Scolex spatulate or flabellate, without lobes and deep indentations, with tapered or curved anterior margin (Fig. 5A,C, 8G,H); in various cyprinids *C. brachycollis*
 - Scolex cuneicrispate (Fig. 6A, 8F), i.e. flabellate with several short, but conspicuous indentations forming small lobes; in carp, *Cyprinus carpio* *C. fimbriceps*
- 3 Uterine region represents 24–30% of testicular field; vitelline follicles present alongside ovary (Fig. 4B), cirrus-sac difficult to observe; in tench, *Tinca tinca* *C. balticus* comb. n.
 - Uterine region represents 7–25% of testicular field; vitelline follicles absent alongside ovary, cirrus-sac clearly visible 4
- 4 Scolex only slightly wider than neck (Figs. 3A, 6C, 8C); postovarian vitelline follicles small (Figs. 3B, 6D), few in number (16–28) 5
 - Scolex significantly wider than neck (Figs. 1A, 7A,B, 8A,E); postovarian vitelline follicles large (Figs. 1B, 2B,D, 7C), usually numerous (more than 30) 6

- 5 Scolex with lateral ('auricular') projections (Figs. 3A, 8C); ovary at distance from posterior extremity; body slender; internal seminal vesicle absent (Fig. 3B); in Danilewski's dace, *Leuciscus danilewskii* *C. auriculatus*
 - Scolex without lateral ('auricular') projections (Fig. 6C); ovary close to posterior extremity; body robust; internal seminal vesicle present (Fig. 6D); in sattu snowtrout, *Schizothorax curvifrons* *C. syrdarjensis*
- 6 Body slender or moderately robust; anteriormost vitelline follicles in distance from anterior extremity (Figs. 1A, 2A,C), distance of anteriormost testes from anterior extremity represents 17–34% of total body length; in various cyprinids *C. laticeps*
 - Body large, robust (Fig. 7A); distance of anteriormost vitelline follicles close to anterior extremity (Fig. 7A,B), distance of anteriormost testes from anterior extremity represents 4–14% of total body length; in common nase, *Chondrostoma nasus* *C. chondrostomi* sp. n.

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