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Suppression of the tapeworm order Pseudophyllidea (Platyhelminthes: Eucestoda) and the proposal of two new orders, Bothriocephalidea and Diphyllobothriidea

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Abstract

Pseudophyllidea van Beneden in Carus, 1863, a well recognised order of tapeworms (Platyhelminthes: Eucestoda), is suppressed because it is composed of two phylogenetically unrelated groups, for which the new names Bothriocephalidea and Diphyllobothriidea are proposed. The new orders differ from each other in the following characters: (i) position of the genital pore: on the dorsal, dorso-lateral or lateral aspects and posterior to the ventral uterine pore in the Bothriocephalidea versus on the ventral aspect of segments and anterior to the uterine pore in the Diphyllobothriidea; (ii) the presence of a muscular external seminal vesicle in the Diphyllobothriidea, which is absent in the Bothriocephalidea; (iii) the presence of a uterine sac in the Bothriocephalidea, which is absent in the Diphyllobothriidea; and (iv) the spectrum of definitive hosts: mainly teleost fishes, never homoiothermic vertebrates in the Bothriocephalidea, versus tetrapods, most frequently mammals, in the Diphyllobothriidea, with species of *Diphyllobothrium*, *Spirometra* and *Diplogonoporus* parasitic in humans. The Diphyllobothriidea, which includes 17 genera in four families (*Digramma* is synonymised with *Ligula*), is associated with cestode groups that have a range of plesiomorphic characters (Haplobothriidea and Caryophyllidea), whereas the Bothriocephalidea, consisting of 41 genera grouped in four families, is the sister-group to the 'acetabulate' or 'tetrafossate' cestodes, which are generally regarded as having derived characters.

Keywords: Systematics; New classification; Bothriocephalidea new order; Diphyllobothriidea new order; Differential diagnosis; Cestoda

1. Introduction

The order Pseudophyllidea van Beneden in Carus, 1863 (Platyhelminthes: Cestoda) is one of the major groups of tapeworms and consists mostly of parasites of marine and freshwater fish, although some genera are specific to mammals or, more rarely, to birds, reptiles and amphibians (Schmidt, 1986; Bray et al., 1994). The order also includes several important parasites of humans, such as species of *Diphyllobothrium*, *Spirometra* and *Diplogonoporus*, as well as pathogens of fish both in aquaculture and free-living, such as species of *Bothriocephalus*, *Eubothrium*, *Ligula*, *Schistocephalus* and *Triaenophorus* (Williams and Jones, 1994; Kassai, 1999; Muller, 2002; Chai et al., 2005).

The first tapeworm placed in the Pseudophyllidea was the "broad fish tapeworm", *Diphyllobothrium latum*, a large parasite of humans, which was briefly described by Linnaeus (1758) under the name *Taenia lata*. One century later, van Beneden in Carus (1863) proposed the name Pseudophyllidea for one of the five groups, among which he accommodated all previously described genera of tapeworms (Cestoda). The taxon Pseudophyllidea was erected by van Beneden, not by Carus as claimed in the literature (Wardle and McLeod, 1952; Yamaguti, 1959; Schmidt, 1986; Bray

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et al., 1994). Van Beneden should therefore be considered the author of the taxon because it was cited with his name when first proposed (Carus, 1863, p. 482) ("Fam. Pseudophyllidea van Ben.") as a family. Major contributions to the systematics of the group were made by Lühe (1902), Wardle and McLeod (1952), Yamaguti (1959), Protasova (1977), Delyamure et al. (1985), Yurakhno (1992), and more recently by Bray et al. (1994, 1999).

The precise position of the Pseudophyllidea within the 'true' tapeworms (Eucestoda) has changed frequently, but pseudophyllideans have usually been placed close to the most basal orders, such as the Caryophyllidea and Spathebothriidea (see Hoberg et al., 1997, 2001 and references therein). Pseudophyllideans have been treated as a monophyletic group in most classifications and have been typified mainly by the possession of two bothria on the scolex (Schmidt, 1986; Jones et al., 1994).

Hoberg et al. (1997) examined the phylogeny of the Eucestoda based on a suite of 49 characters derived from comparative morphological and ontogenetic studies. In the Pseudophyllidea, these authors found as many as 10 characters of the 49 analysed to be multistate and claimed that the Pseudophyllidea may prove to be paraphyletic or polyphyletic. Indeed, the molecular data of Mariaux (1998), based on partial sequences of the 18S rRNA gene, those of Kodedová et al. (2000), who analysed complete sequences of this gene from cestodes of 'lower' vertebrates, and Olson et al. (2001), who compared sequences of the 18S and 28S rRNA genes of members of all recognised orders, indicated paraphyly or polyphyly of the pseudophyllideans.

Brabec et al. (2006) provided evidence that the Pseudophyllidea actually consisted of two unrelated clades, differing markedly from each other in their phylogenetic position within the Eucestoda. An analysis of sequences of the 18S and 28S rRNA genes of 25 representatives of all of the pseudophyllidean families recognised by Bray et al. (1994) has shown that one group, provisionally named 'Diphyllobothriidea' therein, formed a sister group to the Haplobothriidea, a very small group composed of two species in one genus (Brabec et al., 2006). In turn, these taxa were closely related to monozoic caryophyllideans and the putatively most basal spathebothriideans (Brabec et al., 2006). The second clade, 'Bothriocephalidea', is apparently derived, because it appeared as a sister group to the 'higher' ('acetabulate' or 'tetrafossate') tapeworms (Brabec et al., 2006; Waeschenbach et al., 2007) (Fig. 1).

Therefore, the order Pseudophyllidea is formally suppressed in this paper and new orders are proposed to accommodate two unrelated clades possessing dorsal and ventral longitudinal grooves on the scolex called bothria (Bray et al., 1994). In addition, both new orders are characterised and their differential diagnoses, based on morphological and life-cycle characteristics found during a systematic revision of the order (Kuchta, 2007; Kuchta and Scholz, 2007), are provided to reflect the results of recent phylogenetic studies.

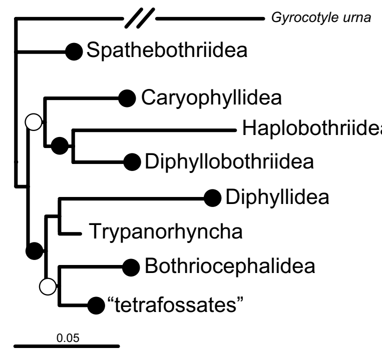

Fig. 1. Phylogenetic tree of basal tapeworms (Eucestoda) inferred from SSU + LSU data (sequences of the small and large subunits of the rRNA gene; modified from Brabec et al., 2006). Bayesian majority rule consensus tree with nodal support based on Bayesian posterior probabilities. Nodal support of 1.00 and >0.90 indicated by filled and open circles, respectively.

2. Results

2.1. Proposal of new orders

2.1.1. ***BOTHRIOCEPHALIDEA new order*** *Figs. 1 and 2a, c–f*

2.1.1.1. Synonyms: Pseudophyllidea van Beneden in Carus (1863) *in part*; Pseudophyllidea van Beneden in Carus (1863) *sensu* Wardle et al. (1974); Bothriocephalata Freze (1974); Bothriocephalinea Euzet (1982).

2.1.1.2. Diagnosis. Cestoda: Eucestoda. Small to large tapeworms. Strobila usually segmented. Segmentation complete, incomplete, or rarely absent. Segments usually craspedote, wider than long, anapolytic. Two pairs of main osmoregulatory canals; ventral canals usually wider, thin-walled; dorsal canals narrow, thick-walled. Scolex variable in shape, unarmed, or rarely with hooks, may be replaced by pseudoscolex or *scolex deformatus*. Scolex with dorsal and ventral longitudinal grooves, termed bothria. Apical disc present or absent. Neck present or absent. Reproductive organs single in segment, rarely two symmetrical sets of proglottids present in segment. Testes numerous, medullary, usually in two lateral fields. Sperm ducts convoluted; external seminal vesicle absent. Cirrus-sac with or without internal seminal vesicle; cirrus unarmed or armed with spines or tegumental bulbs. Genital pores on dorsal surface (median or submedian) or lateral, irregularly alternating. Ovary medullary, usually bilobed, compact, folliculate or dendritic, posterior. Vitellarium follicular, extensive, exceptionally single, cortical, less often medullary or paramuscular (between bundles of inner longitudinal muscles). Uterus variable in shape, divided into tubular, convoluted uterine duct that may enlarge and compact or diverticulate (branched) uterine sac; ventral uterine pore present or absent. Eggs with or without operculum, egg may be embryonated in uterus; free ciliated coracidium may be present, usually when eggs are not embryonated in uterus. One or two intermediate hosts: procercoids develop in copepods (Crustacea), plerocercoids, if present, in fish.

Adults in intestine of fish, exceptionally in amphibians (newts).

2.1.2. ***DIPHYLLOBOTHRIIDEA new order*** *Figs. 1 and 2b, g*
2.1.2.1. Synonyms: Pseudophyllidea van Beneden in Carus (1863) *in part*; Diphyllidea Wardle et al. (1974) (*nec* van Beneden in Carus, 1863); Diphyllobothriata Freze (1974); Diphyllobothriinea Euzet (1982); Polygonoporiata Yurakhno (1992).

2.1.2.2. Diagnosis. Cestoda: Eucestoda. Medium-sized to large tapeworms. Strobila usually segmented. Segmentation complete or incomplete; rarely absent. Segments craspedote or acraspedote, usually wider than long, anapolytic. Two pairs of main osmoregulatory canals; ventral canals usually wider, thin-walled; dorsal canal narrow, thick-walled. Scolex variable in shape, always unarmed, with dorsal and ventral longitudinal grooves, termed bothria. Apical disc absent, or rarely present. Neck present or absent. Reproductive organs single in segment, rarely double or multiple proglottids in segment. Testes numerous, medullary, usually in single field. Sperm ducts convoluted, with thick-walled, muscularised external seminal vesicle attached to proximal part of cirrus-sac. Cirrus-sac usually thick-walled; cirrus unarmed. Internal seminal vesicle occasionally present. Genital pore ventral (median or submedian). Ovary medullary, usually bilobed, posterior. Vitelline follicles numerous, cortical, rarely paramuscular (between bundles of inner longitudinal muscles), circum-medullary. Uterus tubular, variable in shape, opening to exterior through uterine pore situated posterior to genital pore; uterine sac absent. Eggs usually operculate, unembryonated; free, ciliated coracidium present. Usually two intermediate hosts: procercoids develop in copepods (Crustacea), plerocercoids in vertebrates. Adults in intestine of tetrapods, most frequently in mammals.

2.2. Differential diagnosis

The new orders, previously included within the Pseudophyllidea, were differentiated from other cestode orders currently recognised as valid (Khalil et al., 1994; Olson et al., 2001; Caira et al., 2005) by the morphology of the scolex which possesses dorsal and ventral longitudinal grooves (i.e. bothria) serving as attachment organs, external segmentation, proglottization and a follicular vitellarium (Jones et al., 1994).

The Bothriocephalidea differs from the Diphyllobothriidea in the following characteristics:

(i) The genital pores (openings of the cirrus-sac and vagina) are median, submedian or sublateral on the dorsal surface or are lateral, whereas they are on the ventral surface in the Diphyllobothriidea;
(ii) The uterine pore is anterior to the genital pore, whereas it is posterior in the Diphyllobothriidea;
(iii) An external seminal vesicle is absent, but is present in the Diphyllobothriidea;
(iv) A uterine sac is present, but is lacking in the Diphyllobothriidea;
(v) The spectrum of definitive hosts includes fish, with a few taxa found in newts, which contrasts with that of the Diphyllobothriidea which are found only in tetrapods, never in fish.

Both new orders belong among the ‘bothriate’ groups (previously also named less appropriately ‘difossate’ – see Olson et al., 2001), the attachment organs of which are not separated from the surrounding tissue by a well demarcated plasma membrane (*lamina basalis*) (Caira et al., 1999, 2001; Jones et al., 2004). However, the position of the Bothriocephalidea and Diphyllobothriidea among other major groups of the ‘bothriate’ tapeworms remains unclear, as do the relationships among basal tapeworms (Olson and Caira, 1999; Kodedová et al., 2000; Olson et al., 2001; Olson and Tkach, 2005; Waeschenbach et al., 2007). Therefore, putative sister groups of the Bothriocephalidea and Diphyllobothriidea are not unequivocally identifiable.

Nevertheless, recent molecular data indicate that the Diphyllobothriidea are associated with the taxa that have a range of plesiomorphic characters, namely the Haplobothriidea and Caryophyllidea (Fig. 1) (Waeschenbach et al., 2007). All three groups share the following characters, some of them, however, being present also in other ‘bothriate’ groups (for more data see Khalil et al., 1994; Hoberg et al., 1997, 2001; Olson et al., 2001): (i) the genital pores and uterus open on the ventral side of the segment; (ii) the vitellarium consists of numerous follicles usually distributed throughout the segment; (iii) the operculate, unembryonated eggs; (iv) the male genital pore is anterior to the uterine pore. The last character, present also in the Spathebothriidea and Gyrocotylidea, might represent a symplesiomorphy retained by the basal tapeworms (Cestoda).

Besides possessing a strobila with well-developed external segmentation, the polyzoic Diphyllobothriidea can also be distinguished from the monozoic (non-segmented) Caryophyllidea by scolex morphology (see Mackiewicz, 1994, 2003), the anterior or equatorial position of the uterus (confined to the posterior part of the body in the Caryophyllidea), parasitism in tetrapods, never in fish (versus teleost fish as the only definitive hosts in the latter group), a two-host life cycle involving copepods (versus tubificid oligochaetes in the Caryophyllidea), and other morphological, ultrastructural, spermiological and biological characters reviewed by Mackiewicz (1972, 1994, 2003) and Hoberg et al. (1997, 2001).

The order Haplobothriidea contains only two species in one genus, *Haplobothrium*, parasitic in a relict fish species, the bowfin (*Amia calva*), and its affinities and systematic position have been controversial (Jones, 1994). As an independent family, the Haplobothriidae Cooper, 1917, was placed within the Pseudophyllidea by Wardle and McLeod (1952), Yamaguti (1959) and Schmidt (1986), whereas

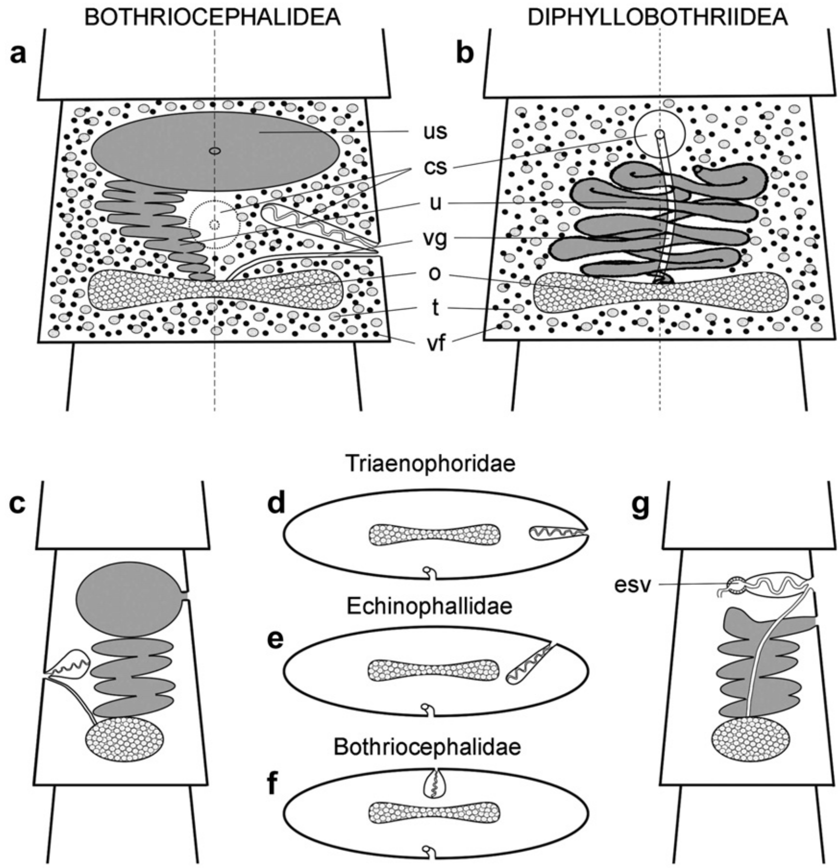

Fig. 2. Schematic drawings of differential morphological characteristics of the new orders Bothriocephalidea (a, c–f) and Diphyllobothriidea (b and g). (a) and (b), ventral view; (c) and (g), lateral view; (d–f), cross-section. *Abbreviations:* cs, cirrus-sac; esv, external seminal vesicle; o, ovary; t, testes; u, uterus; us, uterine sac; vf, vitelline follicles; vg, vagina.

Euzet (1959, 1974) and Dubinina (1980) considered haplobothriideans to be a sister group of the Pseudophyllidea. The anatomy of the segments and the life-cycle patterns are characteristic of the Diphyllobothriidea (Jones, 1994), but haplobothriids differ markedly in possessing a tentacle-bearing primary scolex (absent in the Diphyllobothriidea), an undivided secondary scolex depressed on four sides and a dilated uterine sac (a uterine sac is absent in diphyllobothriideans) (Bray et al., 1994; Jones, 1994).

The phylogenetic position of the Bothriocephalidea is also not resolved satisfactorily (Waeschenbach et al., 2007), but molecular data indicate that it may be a sister-group to the 'acetabulate' ('tetrafossate') tapeworms, which are generally regarded as having derived characters (Hoberg et al., 1997, 2001; Olson et al., 2001; Brabec et al., 2006; Waeschenbach et al., 2007). 'Acetabulate' cestodes differ from bothriocephalideans in possessing acetabulate attachment organs, i.e. bothridia, suckers or both (Caira et al., 1999, 2001).

Molecular analyses have also indicated possible relationships between bothriocephalideans, diphyllideans and trypanorhynchs, the latter being parasites of elasmobranchs (Brabec et al., 2006; Waeschenbach et al., 2007). Although members of the latter two orders also possess bothria or bothria-like attachment organs (Olson et al., 2001; Jones et al., 2004), they are markedly different in their scolex morphology. The scolex of diphyllideans consists of a 'head' and a cephalic peduncle (Khalil, 1994), whereas that of the Trypanorhyncha possesses a unique rhyncheal apparatus with four armed, retractable tentacles (Campbell and Beveridge, 1994).

2.3. List of families and genera recognised in the new orders

2.3.1. **Order BOTHRIOCEPHALIDEA new order**

2.3.1.1. Bothriocephalidae Blanchard, 1849.

Synonyms: Ptychobothriidae Lühe, 1902; Acompsocephalidae Rees, 1969.

Type-genus: Bothriocephalus Rudolphi, 1808.

Other valid genera: Anantrum Overstreet, 1968; *Clestobothrium* Lühe, 1899; *Ichthybothrium* Khalil, 1971; *Oncodiscus* Yamaguti, 1934; *Penetrocephalus* Rao, 1960; *Plicatobothrium* Cable & Michaelis, 1967; *Polyonchobothrium* Diesing, 1854; *Ptychobothrium* Lönnberg, 1889; *Senga* Dollfus, 1934; *Taphrobothrium* Lühe, 1899; *Tetracampos* Wedl, 1861.

2.3.1.2. Echinophallidae Schumacher, 1914.

Synonym: Parabothriocephalidae Yamaguti, 1934.

Type-genus: Echinophallus Schumacher, 1914.

Other valid genera: Bothriocotyle Ariola, 1900; *Neobothriocephalus* Mateo & Bullock, 1966; *Parabothriocephaloides* Yamaguti, 1934; *Parabothriocephalus* Yamaguti, 1934; *Paraechinophallus* Protasova, 1975; *Pseudamphicotyla* Yamaguti, 1959.

2.3.1.3. Philobythiidae Campbell, 1977.

Type-genus: Philobythos Campbell, 1977.

Other valid genus: Philobythoides Campbell, 1979.

2.3.1.4. Triaenophoridae Lönnberg, 1889.

Synonyms: Amphicotylidae Lühe, 1889; Ancistrocephalidae Protasova, 1974.

Type-genus: Triaenophorus Rudolphi, 1793.

Other valid genera: Abothrium van Beneden, 1871; *Ailinella* Gil de Pertierra & Semenas, 2006; *Amphicotyle* Diesing, 1863; *Anchistrocephalus* Monticelli, 1890; *Anonchocephalus* Lühe, 1902; *Australicola* Kuchta & Scholz, 2006; *Bathybothrium* Lühe, 1902; *Bathycestus* Kuchta & Scholz, 2004; *Eubothrioides* Yamaguti, 1952; *Eubothrium* Nybelin, 1922; *Fistulicola* Lühe, 1899; *Galaxitaenia* Gil de Pertierra & Semenas, 2005; *Glossobothrium* Yamaguti, 1952; *Marsipometra* Cooper, 1917; *Metabothriocephalus* Yamaguti, 1968; *Parabothrium* Nybelin, 1922; *Pistana* Campbell & Gartner, 1982; *Pseudeubothrioides* Yamaguti, 1968; *Probothriocephalus* Campbell, 1979.

Remarks. A detailed revision of the order with amended generic diagnoses and keys to identification is in preparation (Kuchta et al., in preparation).

2.3.2. Order ***DIPHYLLOBOTHRIIDEA*** **new order**

2.3.2.1. Diphyllobothriidae Lühe, 1910.

Synonyms: Baylisiidae Yurakhno, 1992; Baylisiellidae Yurakhno, 1992; Ligulidae Claus, 1868; Glandicephalidae Yurakhno & Maslev, 1995; Schistocephalidae Yurakhno, 1992.

Type-genus: Diphyllobothrium Cobbold, 1858.

Other valid genera: Baylisia Markowski, 1952; *Baylisiella* Markowski, 1952; *Diplogonoporus* Lönnberg, 1892; *Flexobothrium* Yurakhno, 1979; *Glandicephalus* Fuhrmann, 1921; *Ligula* Bloch, 1782; *Plicobothrium* Rausch & Margolis, 1969; *Pyramicocephalus* Monticelli, 1890; *Schistocephalus* Creplin, 1829; *Spirometra* Faust, Campbell & Kellogg, 1929; *Tetragonoporus* Skriabin, 1961.

Remarks. Based on molecular data (Luo et al., 2003; Logan et al., 2004), *Digramma* Cholodkovsky, 1914 is synonymised with *Ligula*, in agreement with Wardle and McLeod (1952), who considered *Digramma* to be merely a rare diplogonadic type of *Ligula*. *Multiductus* Clarke, 1962 was synonymised with *Tetragonoporus* Skriabin, 1961 by Delyamure and Skriabin (1968). Bray et al. (1994) considered *Polygonoporus* Skriabin, 1967 to be a synonym of *Hexagonoporus* Gubanov in Delyamure, 1955, which, however, is considered herein to be a *genus inquirendum* because the original description is incomplete (no data on the scolex, etc.).

2.3.2.2. Cephalochlamydidae Yamaguti, 1959.

Type-genus: Cephalochlamys Blanchard, 1908.

Other valid genus: Paracephalochlamys Jackson & Tinsley, 2001.

2.3.2.3. Scyphocephalidae Freze, 1974.

Type-genus: Scyphocephalus Riggenbach, 1898.

Other valid genera: Bothridium Blainville, 1824; *Duthiersia* Perrier, 1873.

3. Discussion

Molecular data (Brabec et al., 2006; Waeschenbach et al., 2007) provided evidence that both new orders, previously placed in the Pseudophyllidea, are phylogenetically distinct. The present study includes the results of molecular analyses and a subsequent morphology-based evaluation of most 'pseudophyllidean' genera in proposing a new ordinal classification. Several morphological characters typical of each of these groups were found, which enabled us to distinguish them from one another. They were also distinguishable based on their host groups. In contrast, the presence of paired, dorsal and ventral grooves, termed bothria, on the scolex may represent a homoplastic character, because it appears in phylogenetically distinct cestode groups. However, the possible homologies of bothria and bothrium-like attachment organs present in the so-called 'bothriate' eucestodes, including diphyllideans and trypanorhynchs, are yet to be identified (Caira et al., 1999, 2001; Olson et al., 2001; Jones et al., 2004).

The Pseudophyllidea has previously been split into two or three groups by some authors (Freze, 1974; Euzet, 1982; Yurakhno, 1992; Bray et al., 1999; Hoberg et al., 2001), but none of them suppressed the order as such and both of the taxa here raised to ordinal level have almost always been considered to be members of the monophyletic order Pseudophyllidea (Hoberg et al., 1997, 2001). Wardle et al. (1974) were the first to separate genera of the current diphyllobothriideans (referred to as 'Diphyllidea') from bothriocephalideans, for which the original name of the order ('Pseudophyllidea') was used. However, these authors provided neither justification for the separation of the groups, nor a differential diagnosis. In addition, the nomenclature they proposed was confusing, especially in the case of the former group, because the name Diphyllidea, considered by Wardle et al. (1994) to be a *nomen oblitum*, has been widely used for cestodes parasitic in elasmobranchs (Khalil et al., 1994; Tyler, 2006).

The term 'Pseudophyllidea' has been used for a long time for those segmented tapeworms that possessed paired attachment organs formed by dorsal and ventral longitudinal grooves or tubes in the case of the genus *Bothridium*. However, the composition of the order has changed considerably, as has its delimitation from other cestode orders. Several cestode groups now recognised as independent ordinal taxa (Khalil et al., 1994), such as the monozoic caryophyllideans, the non-segmented spathebothriideans and the haplobothriideans, have previously been placed in the Pseudophyllidea (Lühe, 1899, 1902; Nybelin, 1922; Fuhrmann, 1931; Wardle and McLeod, 1952; Brooks et al., 1991). Mola (1921, 1928) even included lecanicephalideans from elasmobranchs in the order. Since retaining the name 'Pseudophyllidea' for only one of the groups previously considered to constitute the pseudophyllidean tapeworms could potentially cause great confusion, this name is suppressed and two new names are proposed to accommodate the newly erected orders.

Similarly, two suborders erected by Freze (1974), Diphyllobothriata and Bothriocephalata, are not elevated to ordinal status in order to prevent possible confusion, based on the following reasons: (i) Freze (1974) did not provide any justification for his new classification nor did he present differential diagnoses of component taxa (suborders, superfamilies, families and subfamilies), some of which were proposed as new taxa; (ii) the revised classification of the Pseudophyllidea appeared only as abstract from an international congress; the text contains only one introductory sentence and then a list of the higher taxa included; (iii) the names of the suborders erected by Freze (1974) did not follow widely accepted rules and did not end with "-idea"; thus, Freze's (1974) names would cause confusion; (iv) the International Code of Zoological Nomenclature does not apply for taxon names above the family level.

The Bothriocephalidea was considered to be composed of four families by Bray et al. (1994), but molecular data indicate that some families may be paraphyletic or polyphyletic (Brabec et al., 2006). Similarly, several genera, including the largest genus *Bothriocephalus*, may include unrelated species groups (Škeříková et al., 2004; Kuchta, 2007).

Regarding the patterns of host associations, a putatively more basal position of the Diphyllobothriidea compared with that of the Bothriocephalidea, most members of which are parasites of teleost fish, indicates that diphyllobothriideans may represent an example of early colonization of tetrapods (Hoberg et al., 1999).

Bray et al. (1999) suggested that egg morphology and development, as described by Freeman (1973), could be integrated into phylogenetic appraisals of 'pseudophyllidean' cestodes. However, it should be emphasized that the data on egg morphology and development, although potentially very promising (see Beveridge, 2001), are difficult to use in the systematics of the 'Pseudophyllidea', as argued by Bray et al. (1994), because reliable information is absent on the most significant characters previously used to delimit genera and families, such as the presence or absence of an operculum and embryonation of eggs (Freze, 1974; Protasova, 1977; Schmidt, 1986). In addition, almost no data are available on the life-cycles and postembryonic development of marine species that form a major part of the Bothriocephalidea (see Kuchta and Scholz, 2007).

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References

Beveridge, I., 2001. The use of life-cycle characters in studies of the evolution of cestodes. In: Littlewood, D.T.J., Bray, R.A. (Eds.), Interrelationships of the Platyhelminthes, The Systematics Association Special Volume Series 60. Taylor & Francis, London and New York, pp. 250–256.

Brabec, J., Kuchta, R., Scholz, T., 2006. Paraphyly of the Pseudophyllidea (Platyhelminthes: Cestoda): circumscription of monophyletic clades based on phylogenetic analysis of ribosomal RNA. Int. J. Parasitol. 36, 1535–1541.

Bray, R.A., Jones, A., Andersen, K.I., 1994. Order Pseudophyllidea Carus, 1863. In: Khalil, L.F., Jones, A., Bray, R.A. (Eds.), Keys to the Cestode Parasites of Vertebrates. CAB International, Wallingford, UK, pp. 205–247.

Bray, R.A., Jones, A., Hoberg, E.P., 1999. Observations on the phylogeny of the cestode order Pseudophyllidea Carus, 1863. Syst. Parasitol. 42, 13–20.

Brooks, D.R., Hoberg, E.P., Weekes, P.J., 1991. Preliminary phylogenetic systematic analysis of the major lineages of the Eucestoda (Platyhelminthes, Cercomeria). Proc. Biol. Soc. Washington 104, 651–668.

Caira, J.N., Jensen, K., Healy, C.J., 1999. On the phylogenetic relationships among tetraphyllidean, lecanicephalidan and diphyllidean tapeworm genera. Syst. Parasitol. 42, 77–151.

Caira, J.N., Jensen, K., Healy, C.J., 2001. Interrelationships among tetraphyllidean and lecanicephalidean cestodes. In: Littlewood, D.T.J., Bray, R.A. (Eds.), Interrelationships of the Platyhelminthes, The Systematics Association Special Volume Series 60. Taylor & Francis, London and New York, pp. 135–158.

Caira, J.N., Mega, J., Ruhnke, T.R., 2005. An unusual blood sequestering tapeworm (*Sanguilevator yearsleyi* n. gen., n. sp.) from Borneo with description of *Cathetocephalus resendezi* n. sp. from Mexico and molecular support for the recognition of the order Cathetocephalidea (Platyhelminthes: Eucestoda). Int. J. Parasitol. 35, 1135–1152.

Campbell, R.A., Beveridge, I., 1994. Order Trypanorhyncha Diesing, 1863. In: Khalil, L.F., Jones, A., Bray, R.A. (Eds.), Keys to the Cestode Parasites of Vertebrates. CAB International, Wallingford, pp. 51–148.

Chai, J.-Y., Murrell, K.D., Lymbery, A.J., 2005. Fish-borne parasitic zoonoses: status and issues. Int. J. Parasitol. 35, 1233–1254.

Carus, J.V., 1863. Räderhiere, Würmer, Echinodermata, Coelenterata und Protozoen. In: Handbuch der Zoologie 11. Peters, Carus and Gerstaecker, Leipzig.

Delyamure, S.L., Skriabin, A.S., 1968. Origin and systematic position of diplogonal and polygonadal diphyllobothriids. Helminths of man, animals and plants and measures of their control. Izd. Nauka (in Russian).

Delyamure, S.L., Skriabin, A.S., Serdiukov, A.M., 1985. Diphyllobothriata – Flatworms of Man, Mammals and BirdsPrinciples of Cestodology, Vol. 9. Akademia Nauk SSSR, Moscow, in Russian.

Dubinina, M.N., 1980. Importance of attachment organs for phylogeny of tapeworms. Parazitologiya 29, 65–83, in Russian.

Euzet, L., 1959. Recherches sur les cestodes Tétraphyllides des sélaciens des côtes de France. Thèse, Faculté des Sciences de l'Université de Montpellier, France.

Euzet, L., 1974. Essai sur la phylogenèse des cestodes a la lumière de faits nouveaux. In: Proceedings of the Third International Congress of Parasitology, Munich, 25–31 August 1974, vol. 1. Facta Publication, Vienna, pp. 378–379.

Euzet, L.M., 1982. Problèmes posés par la spécificité parasitaire des cestodes Proteocephalidea et Pseudophyllidea parasites de poissons. Deuxième Symposium sur la Spécificité Parasitaire des Parasites de Vertebrés. Mém. Mus. Natl. Hist. Nat. 123, 279–287.

Freeman, R.S., 1973. Ontogeny of cestodes and its bearing on their phylogeny and systematics. Adv. Parasitol. 11, 481–557.

Freze, V., 1974. Reconstruction of the systematics of cestodes of the order Pseudophyllidea Carus, 1863. In: Proceedings of the Third International Congress of Parasitology, Munich, 25–31 August 1974, vol. 1. Facta Publication, Vienna, pp. 382–383.

Fuhrmann, O., 1931. Dritte Klasse des Cladus Plathelminthes. Cestoidea. In: Kükenthal, W. (Ed.), Handbuch der Zoologie, vol. 2, pp. 141–416.

Hoberg, E.P., Jones, A., Bray, R.A., 1999. Phylogenetic analysis among the families of the Cyclophyllidea (Eucestoda) based on comparative morphology, with new hypotheses for co-evolution in vertebrates. Syst. Parasitol. 42, 51–73.

Hoberg, E.P., Mariaux, J., Brooks, D.R., 2001. Phylogeny among orders of the Eucestoda (Cercomeromorphae): integrating morphology, molecules and total evidence. In: Littlewood, D.T.J., Bray, R.A. (Eds.), Interrelationships of the Platyhelminthes, The Systematics Association Special Volume Series 60. Taylor & Francis, London and New York, pp. 122–126.

Hoberg, E.P., Mariaux, J., Justine, J.L., Brooks, D.R., Weekes, P.J., 1997. Phylogeny of the orders of the Eucestoda (Cercomeromorphae) based on comparative morphology: historical perspectives and a new working hypothesis. J. Parasitol. 83, 1128–1147.

Jones, A., 1994. Order Haplobothriidea Joyeux & Baer, 1961. In: Khalil, L.F., Jones, A., Bray, R.A. (Eds.), Keys to the Cestode Parasites of Vertebrates. CAB International, Wallingford, pp. 249–251.

Jones, A., Bray, R.A., Khalil, L.F., 1994. Key to the orders of the Cestoda. In: Khalil, L.F., Jones, A., Bray, R.A. (Eds.), Keys to the Cestode Parasites of Vertebrates. CAB International, Wallingford, pp. 1–2.

Jones, M.K., Beveridge, I., Campbell, R.A., Palm, H.W., 2004. Terminology of the sucker-like organs of the scolex of trypanorhynch cestodes. Syst. Parasitol. 59, 121–126.

Kassai, T., 1999. Veterinary Helminthology. Butterworth & Heinemann, Oxford.

Khalil, L.F., 1994. Order Diphyllidea van Beneden in Carus, 1863. In: Khalil, L.F., Jones, A., Bray, R.A. (Eds.), Keys to the Cestode Parasites of Vertebrates. CAB International, Wallingford, pp. 45–49.

Khalil, L.F., Jones, A., Bray, R.A., 1994. Keys to the cestode parasites of vertebrates. CAB International, Wallingford.

Kodedová, I., Doležel, D., Broučková, M., Jirků, M., Hypša, V., Lukeš, J., Scholz, T., 2000. On the phylogenetic positions of the Caryophyllidea, Pseudophyllidea and Proteocephalidea (Eucestoda) inferred from 18S rRNA. Int. J. Parasitol. 30, 1109–1113.

Kuchta, R., 2007. Revision of the paraphyletic "Pseudophyllidea" (Eucestoda) with description of two new orders Bothriocephalidea and Diphyllobothriidea. Ph.D. Thesis. Faculty of Biological Sciences, University of South Bohemia, České Budějovice, Czech Republic.

Kuchta, R., Scholz, T., 2007. Diversity and distribution of fish tapeworms of the "Bothriocephalidea" (Eucestoda). Parassitologia 49, 129–146.

Linnaeus, C., 1758. Systema naturale per regna tria naturale, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decimal, reformata 1.

Logan, F.J., Horák, A., Štefka, J., Aydogdu, A., Scholz, T., 2004. The phylogeny of diphyllobothriid tapeworms (Cestoda: Pseudophyllidea) based on ITS-2 rDNA sequences. Parasitol. Res. 94, 10–15.

Lühe, M., 1899. Zur Anatomie und Systematik der Bothriocephaliden. Verhandl. Deutsch. Zool. Gesellschaft 9, 30–55.

Lühe, M., 1902. Revision meines Bothriocephaliden Systeme. Centralbl. Bakteriol. Parasitenkd. Infektionskrankh. 31, 318–331.

Luo, H.Y., Nie, P., Yao, W.J., Wang, G.T., Gao, Q., 2003. Is the genus Digramma synonymous to the genus *Ligula* (Cestoda: Pseudophyllidea)?. Parasitol. Res. 89 419–421.

Mackiewicz, J.S., 1972. Caryophyllidea (Cestoidea): a review. Exp. Parasitol. 34, 417–512.

Mackiewicz, J.S., 1994. Order Caryophyllidea van Beneden in Carus, 1863. In: Khalil, L.F., Jones, A., Bray, R.A. (Eds.), Keys to the Cestode Parasites of Vertebrates. CAB International, Wallingford, UK, pp. 21–43.

Mackiewicz, J.S., 2003. Caryophyllidea (Cestoidea): molecules, morphology and evolution. Acta Parasitol. 48, 143–154.

Mariaux, J., 1998. A molecular phylogeny of the Cestoda. J. Parasitol. 84, 114–124.

Mola, P., 1921. Une nueva classifica di cestode. Sassari.

Mola, P., 1928. Per una nuova classifica dei cestode. Sassari.

Muller, R., 2002. Worms and human disease, 2nd ed. CABI Publishing, Wallingford, UK.

Nybelin, O., 1922. Anatomisch-systematische Studien über Pseudophyllideen. Göteborgs kungl. Vetenskaps-och Vitterhets-Samhälles Handlingar 26, 1–128.

Olson, P.D., Caira, J.N., 1999. Evolution of the major lineages of tapeworms (Platyhelminthes: Cestoidea) inferred from 18S ribosomal DNA and elongation factor-1α. J. Parasitol. 85, 1134–1159.

Olson, P.D., Littlewood, D.T.J., Bray, R.A., Mariaux, J., 2001. Interrelationships and evolution of the tapeworms (Platyhelminthes: Cestoda). Mol. Phylogenet. Evol. 19, 443–467.

Olson, P.D., Tkach, V.V., 2005. Advances and trends in the molecular systematics of the parasitic Platyhelminthes. Adv. Parasitol. 60, 165–243.

Protasova, E.N., 1977. Cestodes of fish – Bothriocephalata. Principles of Cestodology, Vol. VIII. Akademia Nauk SSSR, Moscow, in Russian.

Schmidt, G.D., 1986. CRC handbook of tapeworm identification. CRC Press, Inc, Boca Raton, Florida.

Škeříková, A., Hypša, V., Scholz, T., 2004. A paraphyly of the genus *Bothriocephalus* Blanchard, 1852 (Cestoda: Pseudophyllidea) inferred from ITS2 and partial 18S rDNA sequences. J. Parasitol. 90, 612–617.

Tyler, G.A., 2006. Tapeworms of elasmobranchs (Part II). A monograph on the Diphyllidea (Platyhelminthes, Cestoda). Bull. Univ. Nebraska State Mus. 20.

Wardle, R.A., McLeod, J.A., 1952. The Zoology of Tapeworms. The University of Minnesota Press, Mineapolis.

Wardle, R.A., McLeod, J.A., Radinovsky, S., 1974. Advances in the Zoology of Tapeworms 1950–1970. University of Minnesota Press, Minneapolis.

Waeschenbach, A., Webster, B.L., Bray, R.A., Littlewood, D.T.J., 2007. Added resolution among ordinal level relationships of tapeworms (Platyhelminthes: Cestoda) with complete small and large subunit nuclear ribosomal RNA genes. Mol. Phylogenet. Evol. 45, 311–325. doi:10.1016/j.ympev.2007.03.019.

Williams, H., Jones, A., 1994. Parasitic worms of fish. Taylor & Francis, London.

Yamaguti, S., 1959. Systema Helminthum, Vol. II. The cestodes of vertebrates. Keigaku Publishing House, Tokyo.

Yurakhno, M.V., 1992. On the taxonomy and phylogeny of some groups of cestodes of the order Pseudophyllidea. Parazitologiya 26, 449–461, in Russian.