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VERSITA

Egg ultrastructure of the amabiliid cestode *Tatria biremis* Kowalewski, 1904 (Cyclophyllidea, Amabiliidae), with an emphasis on the oncospheral envelopes**

Vasyl Tkach[1,2]*, Zdzisław Świderski[2,3] and Daniel Młocicki[2,3]

[1]Department of Biology, University of North Dakota, 10 Cornell street, Grand Forks, ND 58202-9019, USA;
[2]W. Stefański Institute of Parasitology, Polish Academy of Sciences, Twarda Street 51/55, 00-818, Warszawa, Poland;
[3]Department of General Biology and Parasitology, Medical University of Warsaw, Chałubińskiego 5, 02-004 Warszawa, Poland

Abstract

This is the first report on the ultrastructure of eggs in the cestode family Amabiliidae Braun, 1900. The gravid proglottides of *Tatria biremis* easily detach from the strobila. Their thick-walled saccate uterus contains numerous rounded or oval eggs measuring about 30–32 μm in diameter. In the early preoncospheral phase, three primary embryonic envelopes are formed around the developing and differentiating embryos, namely: (1) vitelline capsule originating from vitellocyte material; (2) outer envelope formed by two macromeres, and (3) inner envelope originating from a fusion of three mesomeres. Thus, both the outer and inner envelopes of *T. biremis* eggs are cellular in origin and syncytial in nature. During egg maturation, the three primary embryonic envelopes undergo differentiation into fully formed oncospheral or egg envelopes. Most significant changes were observed in the inner envelope which becomes progressively subdivided into 3 sub-layers: the extra-embryophoral sub-layer, the embryophore, and the intra-embryophoral sub-layer, containing mesomere nuclei. The mature hexacanth is covered by a thin layer of the oncospheral tegument. Within the infective hexacanth larva, five cell types were distinguished: (1) a binucleated subtegumental cell; (2) U-shaped penetration gland; (3) nerve cells; (4) somatic cells representing the myocytons of both somatic and hook musculature, and (5) large germinative cells. Ultrastructural characteristics of *T. biremis* eggs are compared with those described in representatives of other cestode taxa. Since the functional ultrastructure of cestode egg envelopes is defined by multiple factors such as the type of life cycles, habitats and behaviour of the intermediate hosts, mode of the intermediate host infection, etc., ultrastructural studies of the greater diversity of cestodes are needed to obtain comparative data for fruitful analysis of cyclophyllidean cestode adaptations to their diverse life cycles.

Keywords

Tatria biremis, Cestoda, Amabiliidae, ultrastructure, eggs, oncospheral envelopes

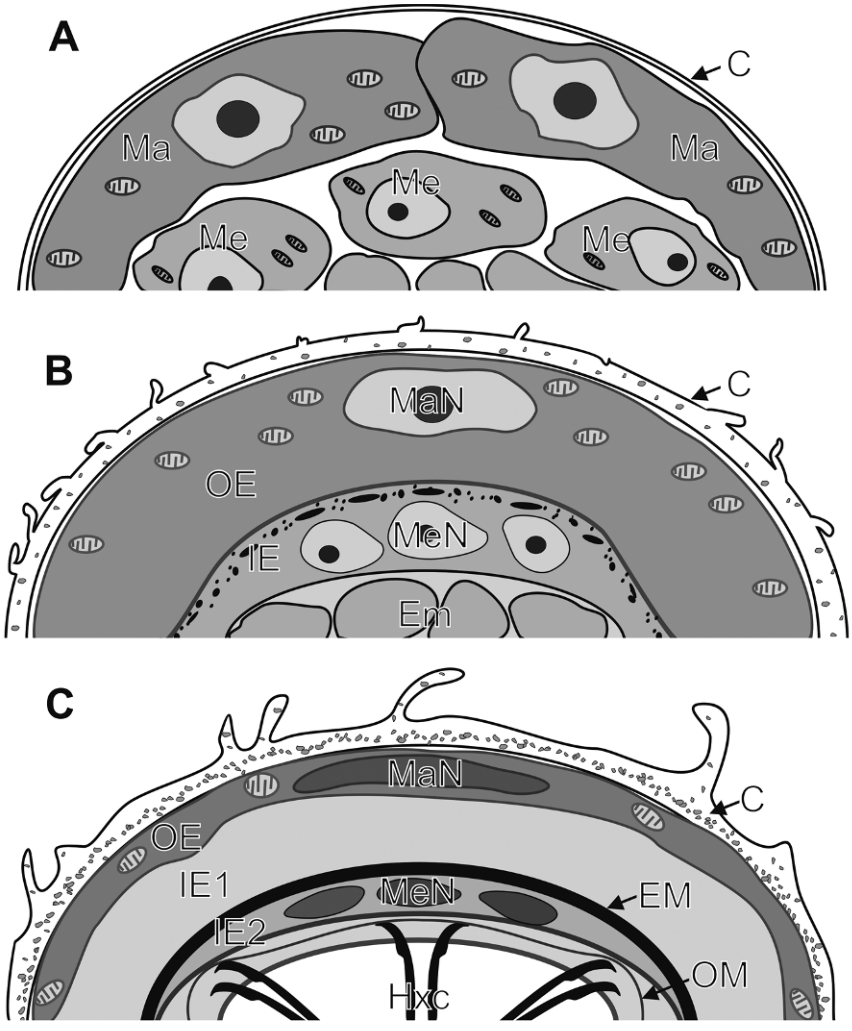
Introduction

The cestode family Amabiliidae Braun, 1900 includes small to medium-size tapeworms parasitic in birds and belonging to only six or seven genera, according to different taxonomic views. This family, initially established as a subfamily within Taeniidae by Braun (1900) and raised to family rank by Fuhrmann (1907), is characterized by the presence of secondary supplementary ducts associated with female reproductive organs. No information was available until now on the egg ultrastructure in any member of the Amabiliidae. The oncospheral or egg envelopes play an important role in protection, nutrition, and metabolism of the developing embryo and infective oncospheres (Rybicka

****This paper is dedicated to the memory of Professor Mieczysław Kowalewski (1857–1919), the founder of the Polish school of parasitology, who erected the genus *Tatria* Kowalewski, 1904, reflecting his great attachment to the Tatra Mountains**

*Corresponding author: vasyl.tkach@email.und.edu

1966). They exhibit a great variety in the ultrastructure and differentiation patterns in different groups of cestodes. These differences are usually related to particular aspects of the cestode life cycle and their adaptations to different hosts and environmental conditions (Świderski 1968, 1981; Gabrion 1981; Chomicz *et al*. 1995a, b; Swiderski and Tkach 1997a, b, 2002; Tkach and Swiderski 1997, 1998; Chomicz and Świderski 2004; Młocicki et al. 2005, 2010a). All known life cycles of amabiliids include aquatic arthropods, i. e., insects such as Odonata and Hemiptera, as intermediate hosts (Ryjikov and Tolkacheva 1981, Storer 2000), and it is important to investigate the morphological and bi-



Abbreviations to all figures: C – vitelline capsule; CJ – cell junctions; Em – embryo; EM – embryophore; GC – germinative cells; GV – Golgi vesicles; GER – granular endoplasmic reticulum; H – oncospheral hooks; HM – hook muscles; Hxc – hexacanth larva; IE1 – extra-embryophoral layer of inner envelope; IE – inner envelope; IE1 – intra-embryophoral layer of inner envelope; m – mitochondria; Ma – macromere; MaN – macromere nucleus; mc – mitochondrial cristae; Me – mesomere; MeN – mesomere nucleus; N – nucleus; n – nucleolus; OC – outer coat; OE – outer envelope; OM – oncospheral membrane; OT – oncospheral tegument; PG – penetration glands, sg – secretory granules; SM – somatic muscles; sv – secretory vesicles

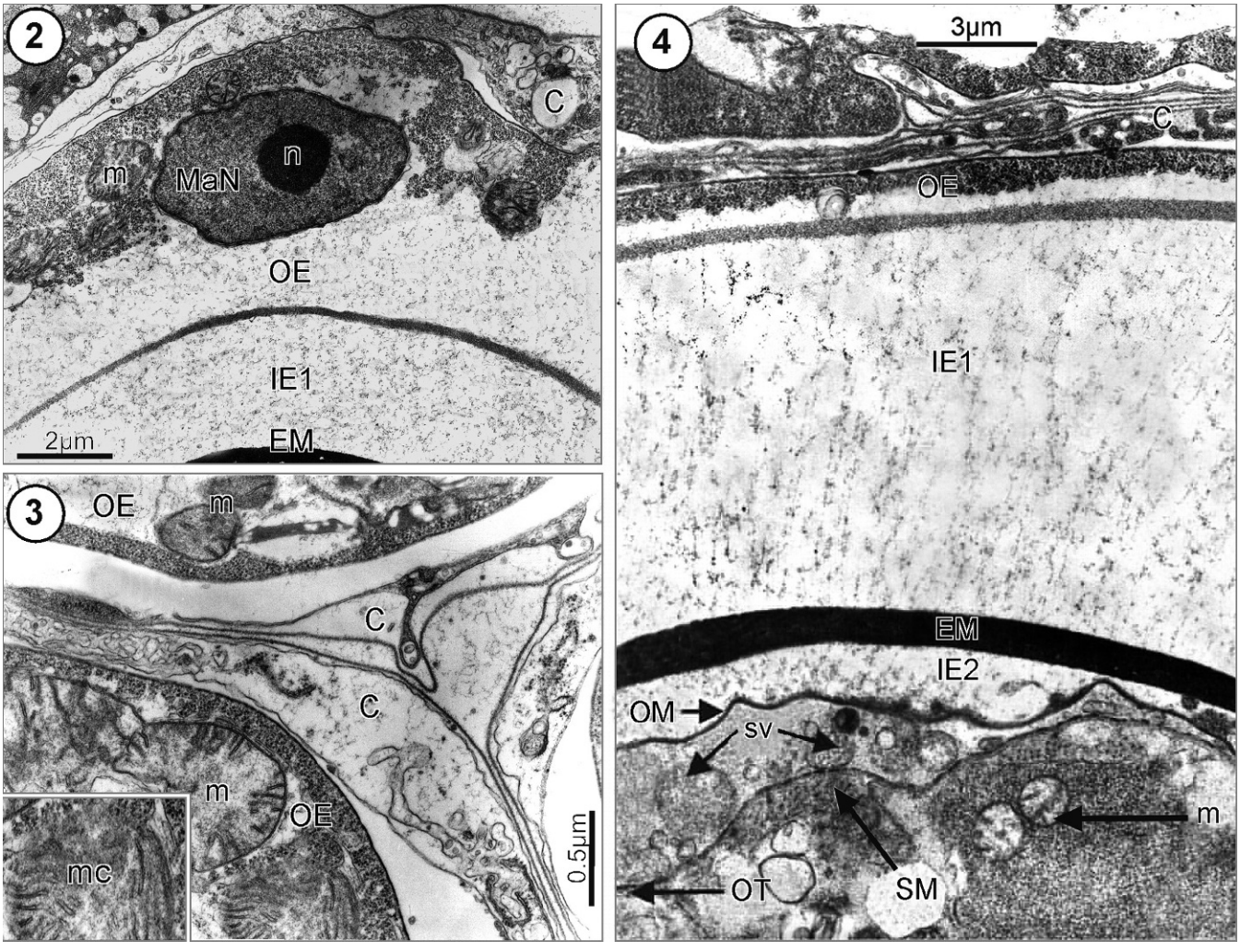
Fig. 1. Diagram showing changes in the thickness of the preoncospheral and oncospheral envelopes in *T. biremis* at different stages of their development. **A** – early stage showing the vitelline capsule and initial stage of macromere fusion, with three mesomeres situated underneath. **B** – intermediate stage: egg from pregravid proglottis showing the enlarged layer of vitelline capsule, thick layer of the outer envelope with large macromere nucleus; the inner envelope is at the beginning of its differentiation. Note: accumulation of dense islands of embryophore material situated below the outer membrane of the inner envelope and three mesomere nuclei localized within the cytoplasmic layer under the newly formed embryophore. **C** – fully formed oncospheral envelopes in mature eggs. Note: (1) Persisting relatively thick layer of the vitelline capsule with its elongated processes; (2) much reduced volume of the outer envelope with flattened electron-dense macromere nucleus and several large mitochondria; and (3) evident differentiation of the inner envelope into three sub-layers: the thick extra-embryophoral sub-layer, the continuous embryophore and the thin intra-embryophoral sub-layer containing degenerating mesomere nuclei

ological adaptations of amabiliids to these particular hosts. There are also some long-standing problems in the systematics of the group, most importantly the relationship of the type genus *Amabilia* Diamare 1893 parasitic in flamingos, to all other members of the family, parasitic in grebes. Although this is not a subject of the present study, ultrastructural data may have the potential to contribute positively to the resolution of this problem as well.

The aim of the present study is to describe the egg ultrastructure of the amabiliid cestode *Tatria biremis* Kowalewski, 1904, with an emphasis on the characteristics of their oncospheral envelopes.

Materials and Methods

Adult specimens of *T. biremis* Kowalewski, 1904 were obtained from the Black-necked Grebe *Podiceps nigricollis* (Brehm) collected in the Kherson Region, Ukraine. For morphological examination, the tapeworms were killed with hot 4% formalin, postfixed in 70% ethanol and stained with iron acetocarmine after Georgiev *et al.* (1986). For TEM study, tissue samples from mature and gravid proglottides were quickly rinsed in saline and fixed for 2 h in 2.5% glutaraldehyde, buffered to pH 7.4 with 0.1 M sodium cacodylate buffer, washed for 2 hours in the same buffer and postfixed for 1 h in



Figs 2. Part of the egg in advanced preoncospheral phase showing high magnification of the vitelline capsule enlarged and infolded in some regions and the syncytial layer of the outer envelope containing in its outermost part a large nucleus of macromere with prominent electron-dense nucleolus, numerous free ribosomes and several large mitochondria. Note: the difference in ultrastructure of the internal and external part of outer envelope; its internal part becomes amorphous and showing randomly dispersed flocculent material. **Fig. 3.** High power magnification of the peripheral part of three closely adjacent eggs at preoncospheral phase. Note: (1) extended regions of the vitelline capsules showing presence of much infolded lamellae and GER-like cisternae; (2) the external part of outer envelope showing high concentration of free ribosomes and several large mitochondria with numerous elongated cristae. Inset: details of elongated mitochondrial cristae and its matrix. **Fig. 4.** Enlarged details of all oncospheral envelopes in a mature egg showing (1) evident differences in the volume of the outer envelope and three sub-layers of the inner envelope; (2) the presence of the vesicles and granules of different size and electron-density situated between oncospheral membrane and oncospheral tegument. Note: somatic musculature closely adjacent to oncospheral tegument

2% osmium tetroxide. They were then dehydrated in an ethanol series, infiltrated with propylene oxide and embedded in Spurr's epoxy resin. Ultrathin sections were mounted on uncoated copper grids, double stained with lead citrate and uranyl acetate and examined with a JEM-1200EX electron microscope operated at an accelerating voltage of 80 kV.

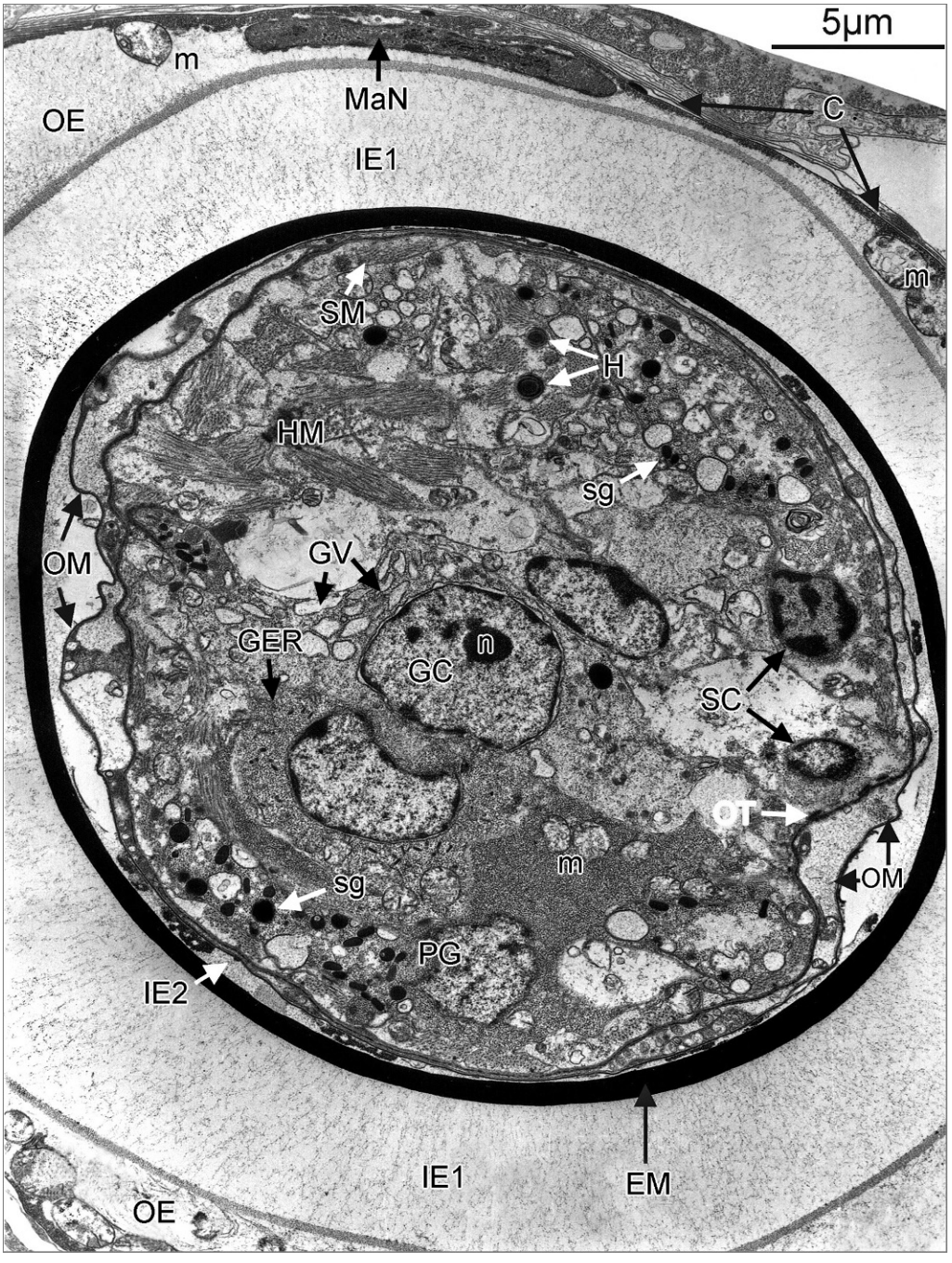


Fig. 5. General topography of the entire fully formed, invasive, egg. Note: (1) the outer vitelline capsule of different thickness; (2) relatively thin, much reduced, layer of the outer envelope, still containing flattened, elongated, moderately electron-dense macromere nucleus and several large mitochondria adjacent to limiting plasma membrane of this envelope; (3) the inner envelope subdivided into three layers of different thickness and ultrastructure: a thickest extra-embryophoral part, containing only an amorphous, flocculent material; relatively thick, highly electron-dense and homogeneous embryophore; and very thin sub-layer of intra-embryophoral part; (4) the oncospheral membrane consisting of two closely apposed plasma membranes frequently adjacent to the oncospheral tegument or to the inner plasma membrane of the inner envelope; (5) the fully formed hexacanth larva covered by oncospheral tegument, armed with oncospheral hooks, and containing different cell types and structures such as: somatic and germinative cells, somatic and hook musculature, penetration gland with characteristic secretory granules

The terminology of cestode embryonic envelopes in different developmental stages is after Conn and Świderski (2008).

Results

The uterus of *Tatria biremis* is usually saccate and relatively thick-walled; gravid proglottides easily detach from the strobila. They contain numerous rounded or oval eggs which measure about 30–32 μm in diameter/length. In the early preoncospheral phase (Fig. 1A-B), three primary embryonic envelopes are formed: (1) vitelline capsule originating from vitellocyte material; (2) outer envelope is formed by two macromeres, and (3) inner envelope originating from a fusion of three mesomeres. Thus, both outer and inner envelopes in this species are cellular in origin and syncytial in nature. During advanced stages of the oncospheral differentiation these three primary envelopes undergo further differentiation and transform into oncospheral or egg envelopes surrounding invasive hexacanth larvae (oncospheres). The maturation of each envelope is described below.

Egg envelopes

The delicate membranous vitelline capsule, formed of the material originating from vitelline cells, is initially thin and delicate, (Figs 1A-C, 2–4), but always remains visible in the fully formed eggs at the outer surface of the outer envelope, as a more or less thick region (Figs 2–5). In the advanced preoncospheral stage the vitelline capsule becomes enlarged and infolded (Figs 1B, 2–3). Its extended regions show presence of folded lamellae and GER-like cisternae (Figs 2–3). The capsule persists in fully formed eggs as a continuous outermost layer of different thickness surrounding oncospheres.

The outer envelope is formed by a fusion of two large macromeres in the preoncospheral phase of the egg formation; it is the thickest of all oncospheral envelopes at this stage of egg development (Fig. 1B and 2). It consists of a thick layer of syncytial cytoplasm containing large nuclei of macromeres with prominent electron-dense nucleoli (Fig. 2). The peripheral layer of the outer envelope also contains numerous large mitochondria with long cristae (Figs 2–4), free ribosomes and polyribosomes localized mainly in the external layer of its cytoplasm. At the same time, the inner layer becomes progressively amorphous and only shows minute randomly dispersed granules of flocculent material (Fig. 2). Along with the maturation of the egg, the volume of the outer envelope undergoes reduction and its organelles, such as nuclei and mitochondria, progressively degenerate. In the fully mature egg, this envelope appears as a relatively thin layer of amorphous structure, containing much flattened, moderately electron-dense macromere nuclei, several mitochondria and very thin granular layer of tightly packed ribosomes (Figs 1C, 4–5).

The inner envelope of *T. biremis* in the preoncospheral phase undergoes differentiation and transformation in both its ultrastructure and volume. At the beginning of its differentiation the inner envelope is thinner than the outer envelope (Figs 1B and 2). However, with the egg maturation, the inner envelope increases in volume and forms three evident sub-layers of different thickness and ultrastructural characteristics (Fig. 2). In mature eggs it is generally amorphous, much thicker than the outer envelope and subdivided into following sub-layers: (1) the thickest extra-embryophoral part, containing only amorphous flocculent material; (2) a relatively thick, highly electron-dense and homogeneous embryophore; and (3) a very thin intra-embryophoral sub-layer containing usually flattened nuclei of mesomeres and remnants of other cell organelles (Figs 1C, 5).

The oncospheral membrane is formed in the late preoncospheral phase by delamination of the inner membrane of the inner envelope. In the mature eggs of *T. biremis* the oncospheral membrane (Figs 1C, 4–5) is well defined, but not always clearly visible when observed or examined on the micrographs of eggs at low magnification. It frequently adheres to two adjacent surfaces and appears not well separated from the inner membrane of the inner envelope and/or from the oncospheral surface. The oncospheral membrane consists of two closely apposed plasma membranes. In the mature eggs, it is usually detached from the inner envelope (Figs 4 and 5). In some regions it can be closely adjacent to the oncospheral surface or to the inner plasma membrane of the inner envelope.

Oncosphere

The infective oncosphere of *T. biremis* shows evident bilateral symmetry in its cellular organization. The mature hexacanth is armed with three pairs of oncospheral hooks of a heterogeneous electron density (Figs 1C, 5). It is covered by a thin layer of the oncospheral tegument (Figs 4–5). Within the infective hexacanth larva five cell types were distinguished: (1) a binucleated subtegumental cell; (2) a U-shaped penetration gland with characteristic secretory granules; (3) nerve cells; (4) two types of somatic cells representing myocytons of both somatic and hook musculature, and (5) large germinative cells with characteristic prominent nucleoli in their large spherical nuclei (Fig. 5). Functions of all the cell types are described on the basis of their ultrastructural characteristics and comparison with previously published data on other cestode species. The mode of the penetration gland secretion is classified as apocrine.

Discussion

Tatria Kowalewski, 1904 is the most speciose genus in the family Amabiliidae (Ryjikov and Tolkacheva 1981, Storer 2000, Vasileva *et al.* 2003a, b). The life cycles of the mem-

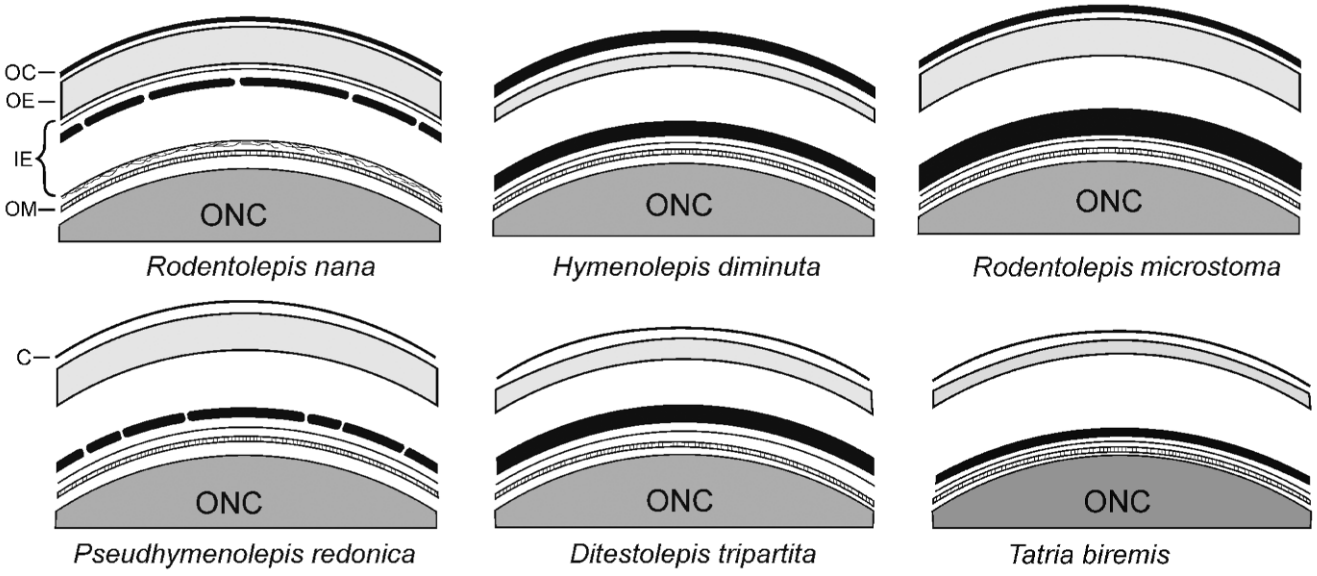


Fig. 6. Comparative diagram of the embryonic envelopes in five mammalian hymenolepidids with terrestrial life cycles and *T. biremis*: *Rodentolepis nana* (after Fairweather and Threadgold 1981), *Hymenolepis diminuta* (from Fairweather and Threadgold 1981, after Lethbridge 1976, Pence 1970, Rybicka 1972), *Rodentolepis microstoma* (after Świderski 1975, 1981), *Pseudhymenolepis redonica* (after Tkach and Świderski 1997), *Ditestolepis tripartita* (after Świderski and Tkach 1997) and *Tatria biremis* (present study). Note the difference and thickness of corresponding layers of different species, unusual position of the embryophore in *R. nana* and presence of thick egg outer coat in species from rodents (upper row) and its absence in hymenolepidids of soricomorphs (lower row) and *T. biremis*. Modified after Tkach and Świderski (1998)

bers of the genus involve grebes as obligate definitive hosts and aquatic arthropods as intermediate hosts. Unlike the majority of other cestodes with aquatic life cycles that usually use crustaceans as intermediate hosts, members of *Tatria* normally use insects in this role. In the case of *Tatria biremis*, the only known intermediate host is the aquatic hemipteran *Sigara concinna* of the family Corixidae (Kukashev 1983). The gravid uterus in members of *Tatria* is thick-walled with eggs tightly packaged in the middle of the proglottis (Fig. 7) and it is likely that in most cases the intermediate host consumes the whole proglottis rather than individual eggs, thus causing multiple infections in the host. The proglottides morphology of *T. biremis* (and a majority of other *Tatria*) is highly peculiar and characterized by the presence of contractile lateral extensions (Fig. 7; also see Ryjikov and Tolkacheva 1981, Vasileva *et al*. 2003a, b) as an adaptation to attract a potential intermediate host (corixid hemipterans and odonate larvae are active predators). Probably, because of this mode of transmission, eggs of *T. biremis* do not demonstrate any obvious morphological or ultrastructural adaptations to the aquatic life cycle and/or dispersion as described in some hymenolepidid cestodes with aquatic life cycles (Jarecka 1961; Chomicz and Świderski 2004). In spite of the fact that the detached gravid proglottides of this tapeworm are also deposited in aquatic environments, its egg envelopes surrounding mature hexacanths are quite different. In our opinion, the oncospheral envelopes of *T. biremis* show greater resemblance to egg envelopes typical of hymenolepidids with terrestrial life cycles, mainly parasites of mammals (Fig. 6). It should be noticed that the majority of previous studies on the functional ultrastructure of oncospheral envelopes in cestodes were done on this family of cestodes. The schematic comparison of the ultrastructure of mammalian hymenolepidids studied so far is presented on Fig. 6. Notably, the egg envelopes of *T. biremis* are more similar to the envelopes of *Pseudhymenolepis redonica* and *Ditestolepis tripartita* that have capsule-like egg-protecting structures of uterine origin (Tkach and Swiderski, 1997, 1998), than to the envelopes of *Rodentolepis nana*, *Rodentolepis microstoma* and *Hymenolepis diminuta* lacking any additional egg protection.

The general pattern of the oncospheral envelope origin, formation and early differentiation in *T. biremis* is similar to that described in other cyclophyllideans (Świderski 1968, 1975, 1981; Swiderski and Tkach 1997a, b; Rybicka 1972; Tkach and Świderski 1998, Młocicki *et al*. 2005) and some proteocephalideans (Świderski and Subilia 1988, Młocicki *et al*. 2010a). In spite of a great similarity observed in the early stages of the embryonic development, the mode of differentiation of the three primordial embryonic envelopes (the vitelline capsule, outer and inner envelopes) into the fully formed egg envelopes appears somewhat different in each species. In the egg envelopes of *T. biremis*, the most evident changes take place in the ultrastructure of the inner envelope. This initially homogeneously structured layer becomes progressively subdivided into 3 sub-layers: the extra-embryophoral sub-layer, the hard, electron-dense embryophore and the intra-embryophoral sub-layer.

The egg envelopes of *T. biremis* differ from those described in several other cyclophyllidean families which exhibit types of egg envelope differentiation and ultrastructure

that are frequently characteristic for each family. For example, the ultrastructure of anoplocephalid eggs with very robust and thick protective envelopes as described in *Anoplocephaloides dentata* by Świderski *et al.* (2001) and in *Mosgovoyia ctenoides* by Młocicki *et al.* (2005), shows differentiation of a characteristic embryophore in the form of the pyriform apparatus. Development and ultrastructure of a similar type of the embryophore was described by Świderski (1968, 1972) in the eggs of *Catenotaenia pusilla*. In contrast, a certain degree of reduction of one or more egg envelopes is evident in cestode species possessing special uterine and/or parenchymatic protective capsules, e.g., nematotaeniids *Cylindrotaenia hickmani* (see Jones 1988) and *Nematotaenia dispar* (see Świderski and Tkach 1997b), mesocestoidid *Mesocestoides lineatus* (see Conn 1988), inermicapsiferine anoplocephalid *Inermicapsifer madagascariensis* (see Świderski and Tkach 2002), a dipylidiid *Dipylidium caninum* (see Pence 1967) or two linstowiids *Oochoristica anolis* (see Conn 1985) and *Oochoristica agamae* (see Świderski and Subilia 1988).

The so-called "hook-region membrane" described in the eggs of numerous cestode species (Świderski 1968, 1972,

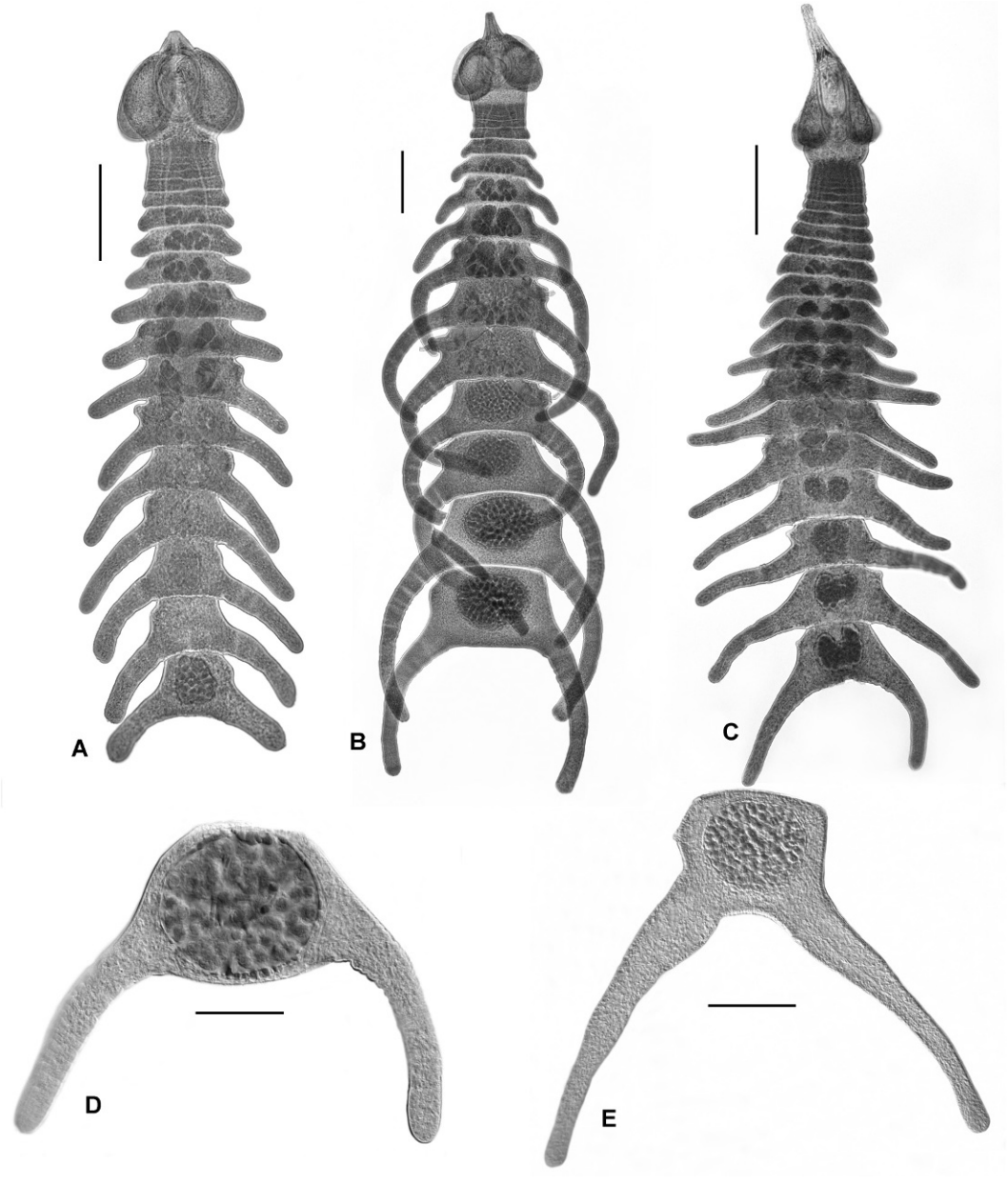


Fig. 7. Strobilae (A-C) and detached gravid proglottides (D, E) of representatives of *Tatria*. **A, D** – *T. biremis*. **B, E** – *T. gulyaevi*, **C** – *T. minor*. Note the unique shape of the proglottides possessing contractile lateral extensions that most likely serve to attract predatory intermediate hosts; also note eggs tightly packed in the middle of pre-gravid and gravid proglottides and relatively thick uterine envelope. Scale-bars: **A-C**, **E** – 200 µm, **D** – 100 µm

1975, 2008, Młocicki *et al*. 2006, Jabbar *et al*. 2010a, b) was not observed in the eggs of *T. biremis*. However, the exact origin and nature of membranous vesicles and granules frequently observed in this species between the oncospheral membrane and the oncosphere surface remains unclear. They may potentially represent the remnants of a degenerating hook-region membrane as previously described in *N. dispar* (see Świderski and Tkach 1997b), penetration gland secretion (Swiderski and Tkach 2002; Młocicki *et al.* 2006, 2010b) or a by-product of the oncospheral tegument formation (Fairweather and Threadgold 1981).

The ultrastructure of hexacanth larvae was not examined here in detail. Detailed studies of the oncospheral cell types and their numbers should be always based on serial semi-thin and, if possible, serial thin sections. However, the preliminary results allow us to conclude that the general topography and ultrastructure of cell types in the eggs of *T. biremis* correspond to those previously described in oncospheres of other cyclophyllideans (Świderski 1972, 2008; Świderski and Tkach 1997b, Tkach and Świderski 1997, Młocicki *et al.* 2006, 2010b, Jabbar 2010a).

The functional ultrastructure of cestode egg envelopes is defined by multiple factors, such as type of life cycle (aquatic or terrestrial), habitats and behaviour of the intermediate hosts, mode of the intermediate host infection, etc. Due to this complexity it is difficult to evaluate potential phylogenetic implications of certain characteristics in individual species or higher taxa. Future ultrastructural studies of a greater diversity of amabiliids and other presently neglected cestode families are needed to obtain additional comparative data for fruitful analysis of cyclophyllidean cestode adaptations to their diverse life cycles.

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References

Braun M. 1900. Cestodes. In: *H.G. Bronn*, *Klassen und Ordnungen des Tierreichs*, *Band IV Vermes*; *Abtheilung I.B.*, Leipzig, 927–1731.

Chomicz L., Świderski Z. 2004. Functional ultrastructure of the oncospheral envelopes of twelve species of the family Hymenolepididae, Ariola, 1899, with aquatic life cycles. *Acta Parasitologica*, 49, 177–181.

Chomicz L., Świderski Z., Czubaj A. 1995a. Ultrastructure of the oncospheral envelopes in Hymenolepididae (Cestoda) with aquatic life cycles. *Hydrobiologia*, 305, 213–216. DOI: 10.1007/BF00036389.

Chomicz L., Świderski Z., Grytner-Zięcina B. 1995b. Ultrastructure of the oncospheral envelopes and their differentiation in the cestode, *Dicranotaenia coronula* (Dujardin, 1845) (Cyclophyllidea, Hymenolepididae). *Acta Parasitologica*, 40, 31–36.

Conn D.B. 1985. Fine structure of the embryonic envelopes of *Oochoristica anolis* (Cestoda: Linstowiidae). *Zeitschrift für Parasitenkunde*, 71, 639–648. DOI: 10.1007/BF00925597.

Conn D.B. 1988. Development of the embryonic envelopes of *Mesocestoides lineatus* (Cestoda: Cyclophyllidea). *International Journal of Invertebrate Reproduction and Development*, 14, 119–130. DOI: 10.1080/01688170.1988.10510372.

Conn D.B., Świderski Z. 2008. A standardised terminology of the embryonic envelopes and associated developmental stages of tapeworms (Platyhelminthes: Cestoda). *Folia Parasitologica*, 55, 42–52. DOI: http://folia.paru.cas.cz/detail.php?id=20884.

Fairweather I., Threadgold L.T. 1981. *Hymenolepis nana*: The fine structure of the embryonic envelopes. *Parasitology*, 82, 429–443. DOI: http://dx.doi.org/10.1017/S0031182000066968.

Fuhrmann O. 1907. Die systematic der ordnung der Cyclophyllidea. *Zoologischer Anzeiger*, 32, 289–297.

Gabrion C. 1981. Ontogenèse de Cestodes Cyclophyllides. Etude Morphogénétique du Développement Post-oncosphéral. Thèse, Academie de Montpellier.

Georgiev B.B., Biserkov V., Genov T. 1986. *In toto* staining method for cestodes with iron acetocarmine. *Helminthologia*, 23, 279–281.

Jabbar A., Swiderski Z., Mlocicki D., Beveridge I., Lightowlers M.W. 2010a. The ultrastructure of taeniid cestode oncospheres and localization of host-protective antigens. *Parasitology*, 137, 521–535. DOI: http://dx.doi.org/10.1017/S0031182009991260.

Jabbar A., Crawford S., Młocicki D., Swiderski Z., Conn D.B, Jones M.K., Beveridge I., Lightowlers M.W. 2010b. Ultrastructural reconstruction of *Taenia ovis* oncospheres from serial sections. *International Journal for Parasitology*, 40, 1419–1431. DOI: 10.1016/j.ijpara.2010.04.011.

Jarecka L. 1961. Morphological adaptations of tapeworm eggs and their importance in the life cycles. *Acta Parasitologica Polonica*, 9, 409–426.

Jones M.K. 1988. Formation of the paruterine capsules and embryonic envelopes in *Cylindrotaenia hickmani* (Jones, 1985) (Cestoda: Nematotaeniidae). *Australian Journal of Zoology*, 36, 545–563. DOI: 10.1071/ZO9880545.

Kukashev D.S. 1983. [*Sigara concinna* Fieb., an intermediate host of *Tatria biremis*, (Cestoda: Amabiliidae)]. *Parazitologiya*, 17, l65–168. (In Russian).

Młocicki D., Świderski Z., Eira C., Miquel J. 2005. An ultrastructural study of embryonic envelope formation in the anoplocephalid cestode *Mosgovoyia ctenoides* (Railliet, 1890) Beveridge, 1978. *Parasitology Research*, 95, 243–251. DOI: 10.1007/s00436-004-1276-4.

Młocicki D., Świderski Z., Miquel J., Eira C., Conn D.B. 2006. Cellular organization of the oncosphere of *Mosgovoyia ctenoides* (Cestoda, Anoplocephalidae). *Journal of Parasitology*, 92, 953–961. DOI: http://dx.doi.org/10.1645/GE-790R1.1.

Młocicki D., Swiderski Z., Conn D.B. 2010a. Ultrastructure of the early embryonic development of *Corallobothrium fimbriatum* (Cestoda: Proteocephalidea). *Journal of Parasitology*, 96, 839–846. DOI: http://dx.doi.org/10.1645/GE-2438.1.

Młocicki D., Świderski Z., Bruňanská M., Conn D.B. 2010b. Functional ultrastructure of the hexacanth larvae in the bothriocephalidean cestode *Eubothrium salvelini* (Schrank, 1790) – phylogenetic implications. *Parasitology International*, 59, 539–548. DOI: http://dx.doi.org/10.1016/j.parint.2010.07.001.

Pence D.B. 1967. The fine structure and histochemistry of the infective eggs of *Dipylidium caninum*. *Journal of Parasitology*, 53, 1041–1054. Stable URL: http://www.jstor.org/stable/3276834.

Rybicka K. 1966. Embryogenesis in cestodes. *Advances in Parasitology*, 4, 107–186. DOI: http://dx.doi.org/10.1016/S0065-308X(08)60449-2

Rybicka K. 1972. Ultrastructure of embryonic envelopes and their differentiation in *Hymenolepis diminuta* (Cestoda). *Journal of Parasitology*, 58, 849–863. Stable URL: http://www.jstor.org/stable/3286572.

Ryjikov K.M., Tolkacheva L.M. 1981. [Principles of Cestodology. Vol. X. Acoleata – Cestodes of Birds.] Moscow, USSR, Akademiya Nauk, 215 pp. (In Russian).

Storer R.W. 2000. The metazoan parasite fauna of grebes (Aves: Podicipediformes) and its relationship to the birds' biology. *Miscellaneous Publications*, *Museum of Zoology*, *University of Michigan*, No. 188, 90 pp. ON-LINE ACCESS: http://deepblue.lib.umich.edu/bitstream/handle/2027.42/56431/MP188.pdf;jsessionid=2F2CF00B0FA37B611D9791B3A65AD20F?sequence=1.

Świderski Z. 1968. Electron microscopy of embryonic envelope formation by the cestode *Catenotaenia pusilla. Experimental Parasitology*, 23, 104–113. DOI: http://dx.doi.org/10.1016/0014-4894(68)90048-9.

Świderski Z. 1972. La structure fine de l'oncosphère du cestode *Catenotaenia pusilla* (Goeze, 1782) (Cyclophyllidea, Catenotaeniidae). *La Cellule*, 69, 207–237.

Świderski Z. 1975. Comparative fine structure of cestode embryos. In: *Proceedings of the Second European Multicolloquium of Parasitology*, *September 1–6*, *1975*, *Trogir*, 265–273.

Świderski Z. 1981. Reproductive and developmental biology of the cestodes. In: *Advances in Invertebrate Reproduction*. (Eds. W.H. Clark, Jr and T.S. Adams). Elsevier/North Holland, New York, Amsterdam, Oxford.

Świderski Z. 2008. Biodiversity of parasite eggs: their importance for disease dissemination and diagnostics. In: *Commemorative Volume of Proceedings Published on the Occasion of the International Conference Dedicated to the 130th Anniversary of the Birthday of Academician K.I. Skrjabin*, 453–459.

Świderski Z., Ndiaye P.I., Miquel J., Tkach V., Marchand B., Chomicz L., Sereda M. 2001. Ultrastructural study of the embryonic development of the anoplocephalid cestode *Anoplocephaloides dentata*, an intestinal parasite of Arvicolidae rodents I. Egg envelope formation. *Acta Parasitologica*, 46, 171–185.

Świderski Z., Subilia L. 1988. Embryonic development of the cestode *Oochoristica agamae* Baylis, 1919 (Cyclophyllidea: Anoplocephalidae). In: *Electron Microscopy – 1988* (Ed. V. Mangclaviraj). *Proceedings of the 6th Asia-Pacific Congress and Workshop on Electron Microscopy*, July 26-August 4, 1988, Bangkok, Thailand, 699–700.

Świderski Z., Tkach V.V. 1997a. Ultrastructure of the infective eggs of the hymenolepidid cestode, *Ditestolepis tripartita* (Zarnowski, 1955), a parasite of shrews. *Acta Parasitologica*, 42, 46–54.

Świderski Z., Tkach V.V. 1997b. Differentiation and ultrastructure of oncospheral and uterine envelopes in the nematotaeniid cestode, *Nematotaenia dispar* (Goeze, 1782). *International Journal for Parasitology*, 27, 1065–1074. DOI: http://dx.doi.org/10.1016/S0020-7519(96)00185-3

Świderski Z., Tkach V.V. 2002. Ultrastructure of embryonic development of *Inermicapsifer madagascariensis* (Cestoda, Anoplocephalidae) with emphasis on the cellular organisation of the infective eggs. *Acta Parasitologica*, 47, 105–120.

Tkach V.V., Świderski Z. 1997. Late stages of egg maturation in the cestode *Pseudhymenolepis redonica* Joyeux et Baer, 1935 (Cyclophyllidea, Hymenolepididae), a parasite of shrews. *Acta Parasitologica*, 42, 97–108.

Tkach V.V., Świderski Z. 1998. Differentiation and ultrastructure of the oncospheral envelopes in the hymenolepidid cestode *Staphylocystoides stefanskii* (Zarnowski, 1954). *Acta Parasitologica*, 43, 222–231.

Vasileva G.P., Gibson D.I., Bray R.A. 2003a. Taxonomic revision of *Tatria* Kowalewski, 1904 (Cestoda: Amabiliidae): redescriptions of *T. biremis* Kowalewski, 1904 and *T. minor* Kowalewski, 1904, and the description of *T. gulyaevi* n. sp. from Palaearctic grebes. *Systematic Parasitology*, 54, 177–198. DOI: 10.1023/A:1022641426066.

Vasileva G.P., Gibson D.I., Bray R.A. 2003b. Taxonomic revision of *Tatria* Kowalewski, 1904 (Cestoda: Amabiliidae): redescriptions of *T. appendiculata* Fuhrmann, 1908 and *T. duodecacantha* Olsen, 1939, a key and an amended diagnosis of *Tatria* (*sensu stricto*). *Systematic Parasitology*, 55, 97-113. DOI: 10.1023/A:1024042616966

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