DOI: 10.2478/s11686-007-0009-0

Acta Parasitologica, 2007, 52(1), 31–50; ISSN 1230-2821

VERSITA

Post-embryonic development and ultrastructural characteristics of the polycephalic larva of *Taenia parva* Baer, 1926 (Cyclophyllidea, Taeniidae)**

Zdzisław Świderski[1,2*], Jordi Miquel[3], Daniel Młocicki[1,4], Boyko B. Georgiev[5,6], Catarina Eira[3], Barbara Grytner-Zięcina[2] and Carlos Feliu[3]

[1]W. Stefański Institute of Parasitology, Polish Academy of Sciences, 51/55 Twarda Street, 00-818 Warsaw, Poland; [2]Department of General Biology and Parasitology, Medical University of Warsaw, 5 Chałubińskiego Street, 02-004 Warsaw, Poland; [3]Laboratori de Parasitologia, Departament de Microbiologia i Parasitologia Sanitàries, Facultat de Farmàcia, Universitat de Barcelona, Av. Joan XXIII s/n, E-08028 Barcelona, Spain; [4]Department of Medical Biology, Medical University of Warsaw, 73 Nowogrodzka Street, 02-004 Warsaw, Poland; [5]Central Laboratory of General Ecology, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria; [6]Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

Abstract

Post-embryonic development and fully-formed polycephalic larvae of *Taenia parva* Baer, 1926 were examined by light (LM) and transmission electron microscopy (TEM). Three developmental stages were recognised: (1) an early stage of exogenous budding at the surface of the central vesicle; (2) a stage of polycephalic cyst development accompanied by segmentation of the growing larval strobile and an obvious decrease in the size of the central vesicle; (3) fully-formed larval strobile and invaginated scoleces. In fully-developed encysted polycephalic larvae, there are usually 14–24 segmented larval strobilae, each terminating with an invaginated scolex; larval strobilae arise from a common central vesicle and remain attached posterior to it during the entire development. The number of segments varies between 109 and 120 per larval strobila. The polycephalic larvae examined closely resemble the strobilocercus type of taeniid larvae. The structure of developing and fully-formed larvae was examined by TEM. The tegument, scolex, subtegumental musculature of the strobilar segments, protonephridial system, calcareous corpuscles and medullary parenchyma of larvae exhibit general similarity with the same structures in adults at both LM and TEM levels. The morphogenesis of the larva of *T. parva* is compared with that of the polycephalic larvae of other *Taenia* spp. (*T. krepkogorski*, *T. twitchelli* and *T. endothoracica*) and with other asexually-multiplying cestode larvae (mesocestoidids, hymenolepidids and dilepidids).

Key words

Cestoda, *Taenia parva*, polycephalic larva, post-embryonic development, ultrastructure

Introduction

The post-embryonic developmental stages of taeniid cestodes deserve particular attention. This family comprises 44 species, including 5 of medical importance and about 20 of veterinary importance (Abuladze 1964, Verster 1969, Loos-Frank 2000). Because of this, some taeniids such as *Echinococcus granulosus* (Batsch, 1786) and *E. multilocularis* (Leuckart, 1863) have already been studied extensively (see Smyth 1964; Morseth 1967; Sakamoto and Sigimura 1969, 1970; Šlais 1973; Mehlhorn *et al*. 1983; Thompson 1986; Eckert *et al*. 2002). Their larvae show the highest rate of asexual reproduction among cestodes, resulting in the proliferation of thousands of scoleces from a single oncosphere. They cause, respectively, cystic and alveolar echinococcosis and are a major current problem of medical parasitology. However, the larvae of *Echinococcus* spp. are essentially different from those of other taeniids.

Ultrastructural features of larval cestodes can provide useful characters for phylogenetic and evolutionary analyses.

*Corresponding author: z.swider@twarda.pan.pl

**Dedicated to the memory of Professor Konstanty Janicki, on the occasion of the 75th anniversary of his death

Until now, however, they have been relatively little utilised (Beveridge 2001, Chervy 2002). Earlier reviews by Freeman (1973) and Jarecka (1975) on the post-embryonic developmental stages of cestodes provided important comparative data for phylogenetic analyses. Studies on the histology and ultrastructure of larval cestodes have been "largely restricted to the classical 'cysticerci' and 'cysticercoids' limiting the possibilities of making comparison across all taxa within the Cyclophyllidea, let alone the wider array of cestode orders" (Beveridge 2001; p. 253). A far greater diversity of ultrastructural data on a variety of metacestodes is needed before we can apply them successfully in analyses of cestode phylogeny.

During the last 20–30 years, the ultrastructure of the post-embryonic developmental stages of *Taenia* spp. has been neglected. Apart from five rather old papers describing the fine morphology of the post-embryonic larvae of *T. multiceps* Leske, 1780 by Race *et al*. (1965), *T. taeniaeformis* (Batsch, 1786) by Nieland and Weinbach (1968), *T. crassiceps* (Zeder, 1800) by Baron (1968) and Mount (1970) and *T. saginata* Goeze, 1782 by Šlais *et al*. (1972), there is apparently no other ultrastructural information on the taeniid larvae. In addition to these five papers, some details on the ultrastructure of the outer cytoplasmic layer of the metacestode tegument of *Anoplotaenia dasyuri* Beddard, 1911 have been presented (Beveridge *et al*. 1975); however, the position of this species is controversial and it probably does not belong within the Taeniidae (Khalil *et al*. 1994). Unfortunately, in many old papers, the ultrastructural preparations were made with the fixation and embedding procedures of 20–30 years ago which caused artifacts, including shrinkage of tissues, separation of organelles and failure to preserve glycogen and lipids.

In other cestode groups, there are numerous more recent LM and TEM studies on larvae, mostly in other cyclophyllidean families; some have been reviewed by Ubelaker (1980, 1983) and Jarecka *et al*. (1981). Other studies on various types of larval cestodes (Caley 1974, 1976; Burt and Jarecka 1984; Jarecka and Burt 1984; Jarecka *et al*. 1984; Krasnoshchekov and Pluzhnikov 1984; Burt 1987; Conn 1986, 1988a, 1990, 2005; Conn *et al*. 2002; Galán-Puchades *et al*. 2002; Świderski *et al*. 2002a; Georgiev *et al*. 2005) have yet to be reconsidered in a broader comparative context.

No information on the ultrastructure of the polycephalic larvae of taeniids is available. In order to obtain such data, we selected *Taenia parva* Baer, 1926 for the present study. With the single exception of the classification of Wardle and McLeod (1952), who included it in *Hydatigera* Lamarck, 1816, it has always been considered a species of *Taenia* L., 1758 (see Baer 1926, Abuladze 1964, Verster 1969, Loos-Frank 2000). Adults of *T. parva* are frequent parasites of the Viverridae carnivores in Africa. This parasite has also been found in the Iberian Peninsula and is believed to be progressively expanding its range into Europe (Mas-Coma and Feliu 1977, Feliu 1980, Alvarez *et al*. 1990, Casanova *et al*. 2000). The intermediate hosts include several species of African and European rodents (Verster 1969, Loos-Frank 2000). Polycephalic larvae identified as *T. parva* were described by Campana-Rouget (1950) and Bernard (1961, 1963) from the abdominal cavity of *Apodemus sylvaticus* L., 1758 (Rodentia, Muridae). Dollfus and Saint Girons (1958) reported behavioural modifications in wood mice infected with *T. parva*, which probably resulted from the increase of the parasite cyst volume. Our material was obtained from *A. sylvaticus,* the intermediate host of *T. parva* in the Iberian Peninsula.

The aim of this study is to describe the development and ultrastructural characteristics of the post-embryonic larva of *T. parva* and to compare it with other polycephalic larvae of *Taenia* spp. and other asexually-multiplying cestode larvae.

Materials and methods

Larvae of *Taenia parva* were obtained from the abdominal cavity of naturally-infected wood mice, *Apodemus sylvaticus*, captured in Quiaios, Portugal. Live specimens were placed in 0.9% NaCl solution. For TEM examination, they were dissected and fixed in cold (4°C) 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer at pH 7.2 for 1 h, rinsed in 0.1 M sodium cacodylate buffer at pH 7.2, postfixed in cold (4°C) 1% osmium tetroxide in the same buffer for 1 h, dehydrated in an ethanol series and propylene oxide and embedded in Spurr's resin. Semithin sections stained with 1% methylene blue in borax solution were used for LM examination. Ultrathin sections were obtained using a Reichert-Jung Ultracut E ultramicrotome, placed on copper grids and double-stained with uranyl acetate and lead citrate. Ultrathin sections were examined using a Jeol 1010 transmission electron microscope.

Results

Development and general topography of the polycephalic larva of T. parva

Encysted polycephalic larvae of *T. parva* were found in the body cavity of the intermediate host (Fig. 1). Individual cysts reached ~3.5 cm in diameter. The number of cysts per host individual was 1–3; a single cyst per host was most frequent. Each cyst was covered with a thin, semitransparent envelope. The outer part of the cyst wall (*tunica adventitia*), originating from the host connective tissue, had a network of small blood vessels. In the early stage, an exogenously-budding central vesicle was situated inside the cyst wall (Fig. 2A). Subsequent stages showed elongation of the buds and gradual transformation into segmented strobilae, each terminating with an invaginated scolex (Fig. 2B). In the developed encysted larvae (Fig. 2C), 14–24 larval strobile, arising from the central vesicle, were recorded. During their growth and development, the larval strobile remained connected posteriorly to the central vesicle (or bladder). The size of the latter gradually decreased and it was gradually transformed into a vestigial structure that did not completely disappear. Each invaginated larval scolex of *T. parva* had four suckers and a rostellum with two alter-

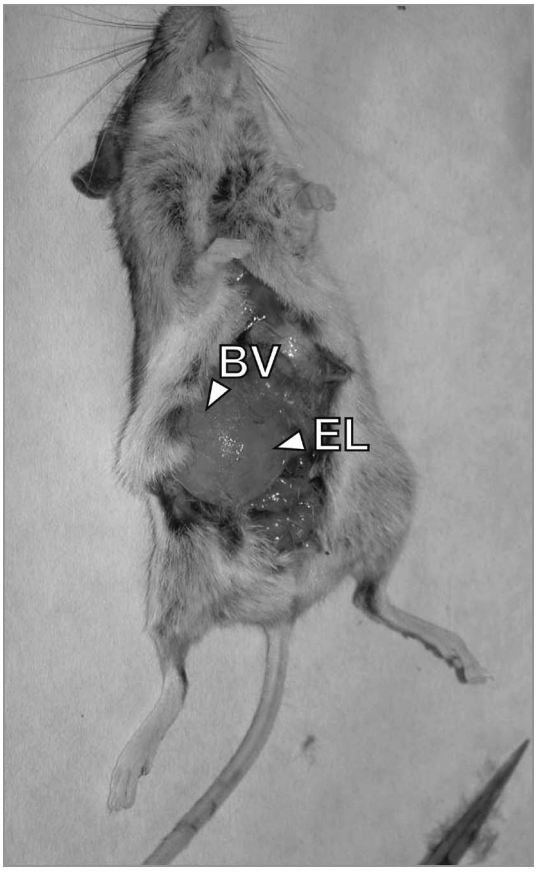


Fig. 1. Dissected *Apodemus sylvaticus* with a very large (~3 cm in diameter) encysted larva of *Taenia parva* of strobilocercus-type in the abdominal cavity. The larva is surrounded by a thin layer of host connective tissue (*tunica adventitia*) with several small blood vessels

nating crowns of large and small rostellar hooks (Figs 3 and 4). Fully-formed strobile were 2.35–3.25 cm long and 2.00–2.15 mm wide. The number of segments ranged from 109–120. The scoleces examined were 569–619 μm wide at the level of the rostellar hooks and 1139–1423 μm wide at the level of the suckers. The average diameter of suckers was 227–258 μm. The rostellum was armed with 32–44 μm rostellar hooks. The lengths of the large and small rostellar hooks were 340–356 and 213–231 μm, respectively. Each developed larval strobila, except for the invaginated scolex, resembled a miniature adult cestode. However, no primordia of genital organs were observed.

The development and general topography of the larvae were examined mainly by LM, and the fine morphology of developing (Fig. 2B) and fully-formed metacestodes (Fig. 2C) was studied by TEM.

Ultrastructure of the larval tegument

The electron micrographs of the surface of the larval strobila and the scolex (Figs 5–7) showed that the larval tegument resembled that of adult worms. The essential feature of the external surface was the brush border comprising microtriches (Figs 6 and 7). Their tips were typically pointed and filled with a keratinous, electron-opaque matrix of densely-packed fibrils or rods; their proximal shafts tended to be cylindrical, with a core of microfilaments (Fig. 7). The keratinous spike was set off from the shaft by a multilaminate baseplate (Fig. 7). Microtriches appeared polymorphic, as seen in different anatomical regions of the same individual. The distal cytoplasm of the tegument contained mitochondria and a substantial population of membrane-bound vesicles and granules of various sizes, shapes and electron densities. The great majority of vesicles and granules appeared to have arisen from the Golgi apparatus of the cytons and transported to the distal cytoplasm via the cytoplasmic bridges uniting both parts of the tegument. The perinuclear cytoplasm of the cytons (Fig. 8) contained abundant free ribosomes, a few cisternae of granular endoplasmic reticulum (GER) and numerous vesicles. The distal cytoplasmic layer of the tegument covering the suckers was continuous with that of the strobila but somewhat thinner in some regions.

Ultrastructure of muscle system

The musculature of the larvae studied consisted of subtegumental longitudinal and circular fibres, longitudinal medullary fibres, cortical transverse fibres and highly specialised arrangements of fibres associated with the suckers and rostellum. The strobilar myofibrils were smooth (Figs 9–14). Each muscle cell consisted of two major components: (1) the contractile myofibril, containing actin and myosin myofibrils (Figs 9–12) and (2) the myocyton, the non-contractile perikaryon (Fig. 10). The myocytons were typically lateral to and at some distance from the myofibrils (Fig. 10), with cytoplasmic continuity established via tendrillar processes. Lacking intact Z-discs, there was no division of the myofibril into sarcomeres. Nevertheless, both thick (myosin) and thin (actin) myofilaments were present (Figs 9–14); their arrangement was not ordered to an extent showing clear demarcation of A and I bands.

The sucker musculature was characterised by a very compact arrangement of fibres (Fig. 9). The cavity of each sucker (Fig. 9) was lined by a thin layer of tegument that was continuous with that of the scolex proper. The intrinsic sucker musculature (Fig. 9) consisted of circular, radial and longitudinal fibres, with the radial fibres predominating. The circular fibres (Fig. 9) were generally oriented around the rim of the sucker, as a purse string regulating its aperture. The strongly developed radial muscles extended from the tegument of the base of the sucker. The highly-branched transverse muscle fibrils surrounded the myocytons and tegumental perikarya (Fig. 10). The extrinsic sucker musculature was inserted at the lateral margins and interconnected with adjacent suckers. The predominant extrinsic muscles at the base of each sucker consisted of transverse fibres (Figs 10 and 12–15) and undoubtedly were responsible for most of the mobility of the sucker.

Two types of secretory granules were observed within long cytoplasmic processes associated with extensive muscu-

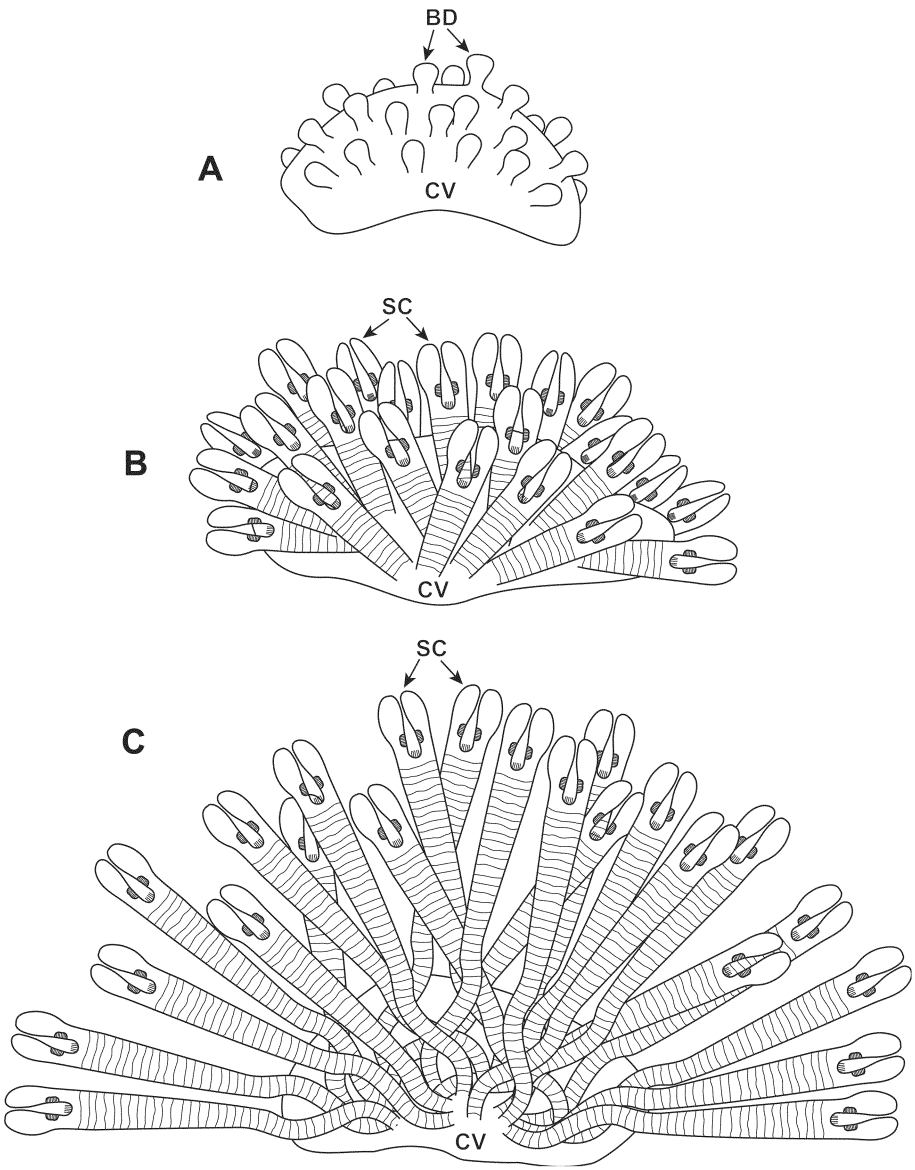
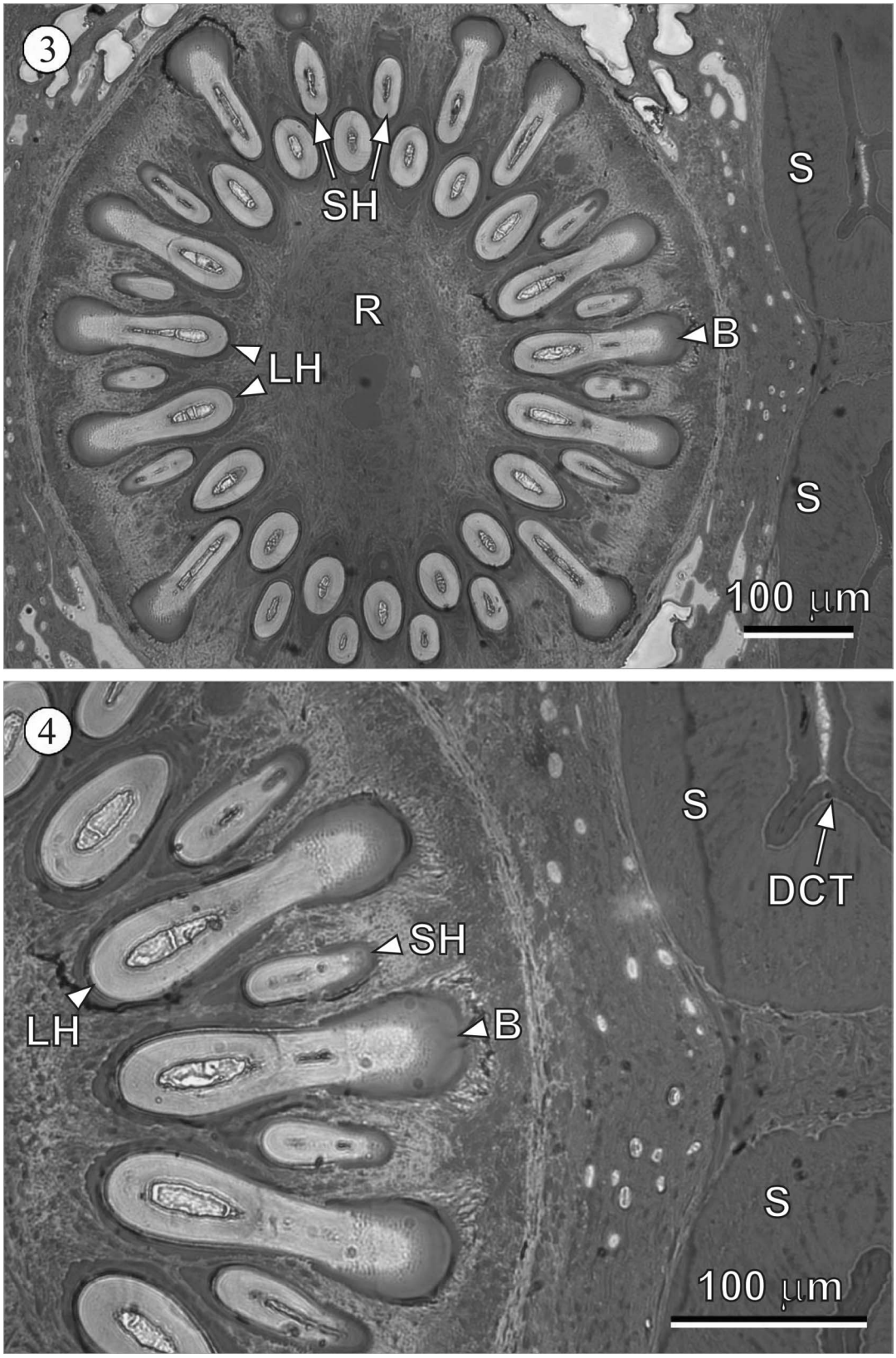


Fig. 2A-C. Three consecutive stages of development of a polycephalic cyst of *T. parva*: **A** – early stage of exogenous budding at the surface of the central vesicle; **B** – stage of polycephalic cyst maturation, accompanied by (1) invagination of scoleces, (2) segmentation of growing strobilocerci, and (3) decrease in size of the central vesicle; **C** – fully-formed, mature strobilocerci with invaginated scoleces. Note presence of much elongated strobile with obvious segmentation and the residual central vesicle serving as an attachment point for the posterior ends of all larval strobile, which always remain united. **Abbreviations to all figures:** AD – amorphous diaphragms between external and internal rods of the nephridial chamber, AF – actin filaments, B – basal region of the hook blade, BD – buds or primordia of scoleces, BL – basal lamina, BM – bases of microtriches, BP – baseplates of microtriches, BV – blood vessels in cyst wall of host origin, C – core of hook, CB – cytoplasmic bridges, CC – calcareous corpuscles, CM – circular muscles, CS – surface of calcareous corpuscle, CT – connective tissue fibrils, CV – central vesicle or bladder, Cx – cortex of rostellar hook, D – desmosomes, DC – dense caps of microtriches, DCT – distal cytoplasm of tegument, EL – encysted polycephalic larva, ER – external rods of the nephridial chamber, F – "flame" or bundle of cilia, G – Golgi complex, GER – granular endoplasmic reticulum, Gl – glycogen-like rosettes of α-glycogen or individual particles of β-glycogen, HDZ – hook differentiation zone, IR – internal rods of the nephridial chamber, IS – concentric rings of inorganic substances in calcareous corpuscles, L – lipid droplet, LCD – large collecting duct, LH – large hooks, LM – longitudinal muscles, Lt – leptotriches, M – mitochondria, Mc – myocytons, MF – myosin filaments, Mt – microtriches, Mx – matrix of calcareous corpucle, Mv – microvilli, N – nucleus, n – nucleolus, NCh – nephridial chamber, NF – nephridial funnel, R – rostellum, r – ribosomes, S – sucker, SC – strobilocerci, SG1 – secretory granules of type-1, SG2 – secretory granules of type-2, SH – small hooks, TC – tegumental collars surrounding rostellar hooks, TD – terminal collecting duct, TM – transverse muscles of sucker, TP – tegumetal perikaryons, V – vesicles, V1 – dense, flattened vesicles, V2 – clear, spherical or elongated vesicles



Figs 3 and **4**. Semithin sections showing cross-sectioned apical regions of the invaginated scoleces of *T. parva.* Note two alternating crowns of large and small rostellar hooks and rostellar tissue in the centre. **Fig. 4.** Slightly enlarged lateral part of the above micrograph showing, in addition, parts of sucker at the right side

lature of the scolex region. One type of the secretory granules was frequently observed in the elongated cytoplasmic projections within the scolex and, in particular, within the sucker musculature (Figs 12, 14 and 15). They were much larger and less dense than the second type of granules. The latter were represented by characteristic very small, highly electron-dense spherical granules resembling the so-called "neurosecretory granules" (Figs 16–19).

Ultrastructure of protonephridial system

All the three main components of the protonephridial system were studied. These included (1) terminal structures ("flame

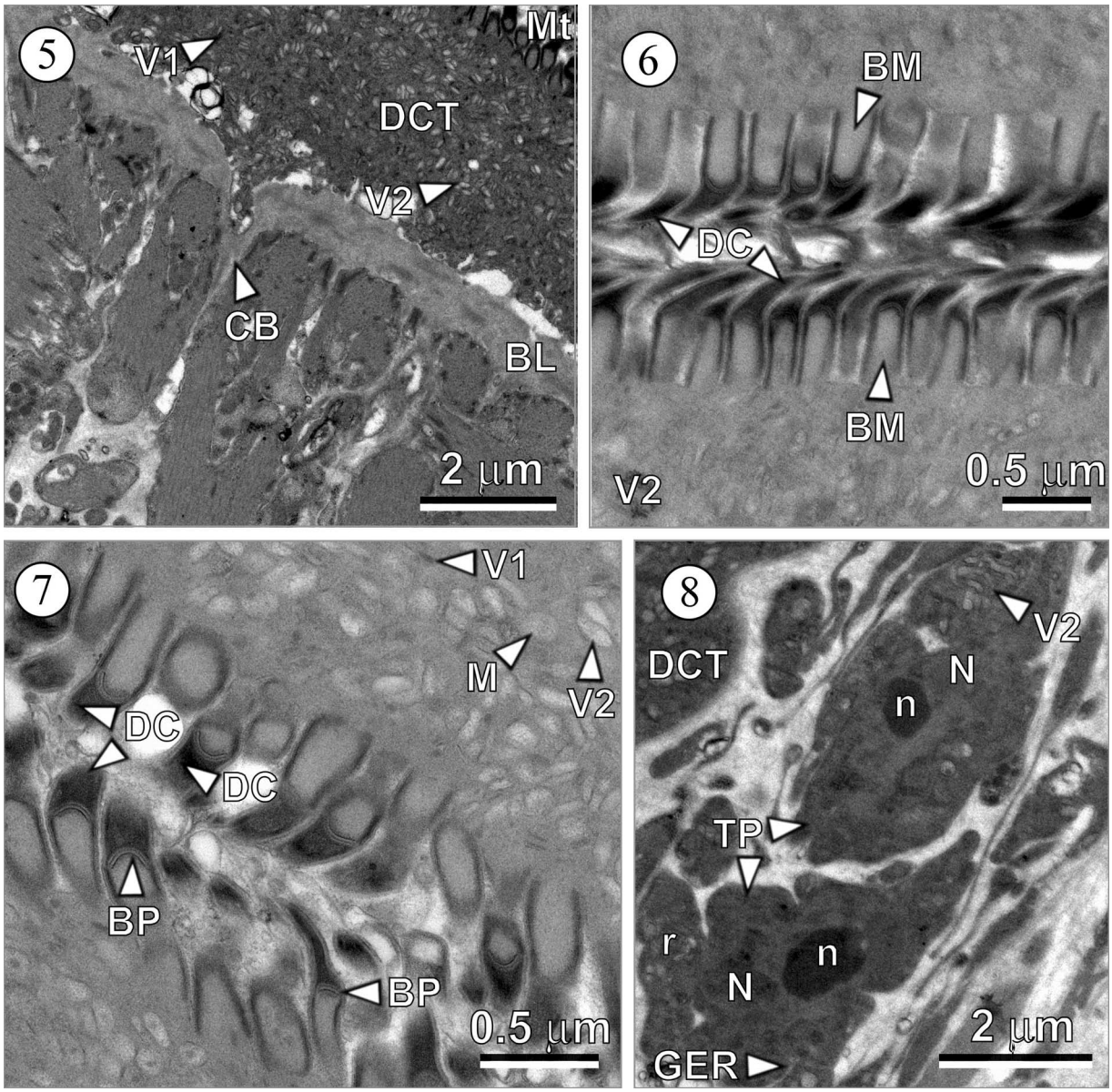


Fig. 5. Low power TEM-micrograph showing general topography of the distal cytoplasm of the tegument with underlying basal lamina and large, compact bands of longitudinal and circular muscle fibres. Note: (1) numerous microtriches, (2) densely granular nature of the distal cytoplasm of the tegument containing a high accumulation of ribosomes, two types of membranous vesicles (clear and dense vesicles), and (3) part of cytoplasmic bridge providing connection with the tegumental perikaryon situated below muscle layers. **Fig. 6.** Enlarged detail of two adjacent parts of the distal cytoplasm of the tegument with numerous microtriches at their surfaces. **Fig. 7.** High-power TEM-micrograph showing sagitally oblique section of tegumental microtriches. Note: (1) electron-opaque cap separated from the base by a multilaminar baseplate, (2) microfilaments regularly arranged within base, (3) tegumental plasmalemma extending over entire length of each microthrix, and (4) two types of membrane-bound vesicles: flat, electron-dense vesicles and elongate clear vesicles. **Fig. 8.** Low power TEM-micrograph showing general topography of two tegumental perikarya. Note: (1) densely granular cytoplasm of the tegumental cytons containing high accumulation of free ribosomes, few profiles of GER and mitochondria, and (2) numerous dark and clear vesicles in the upper part of the cell, which provides connection with the distal cytoplasm of the tegument

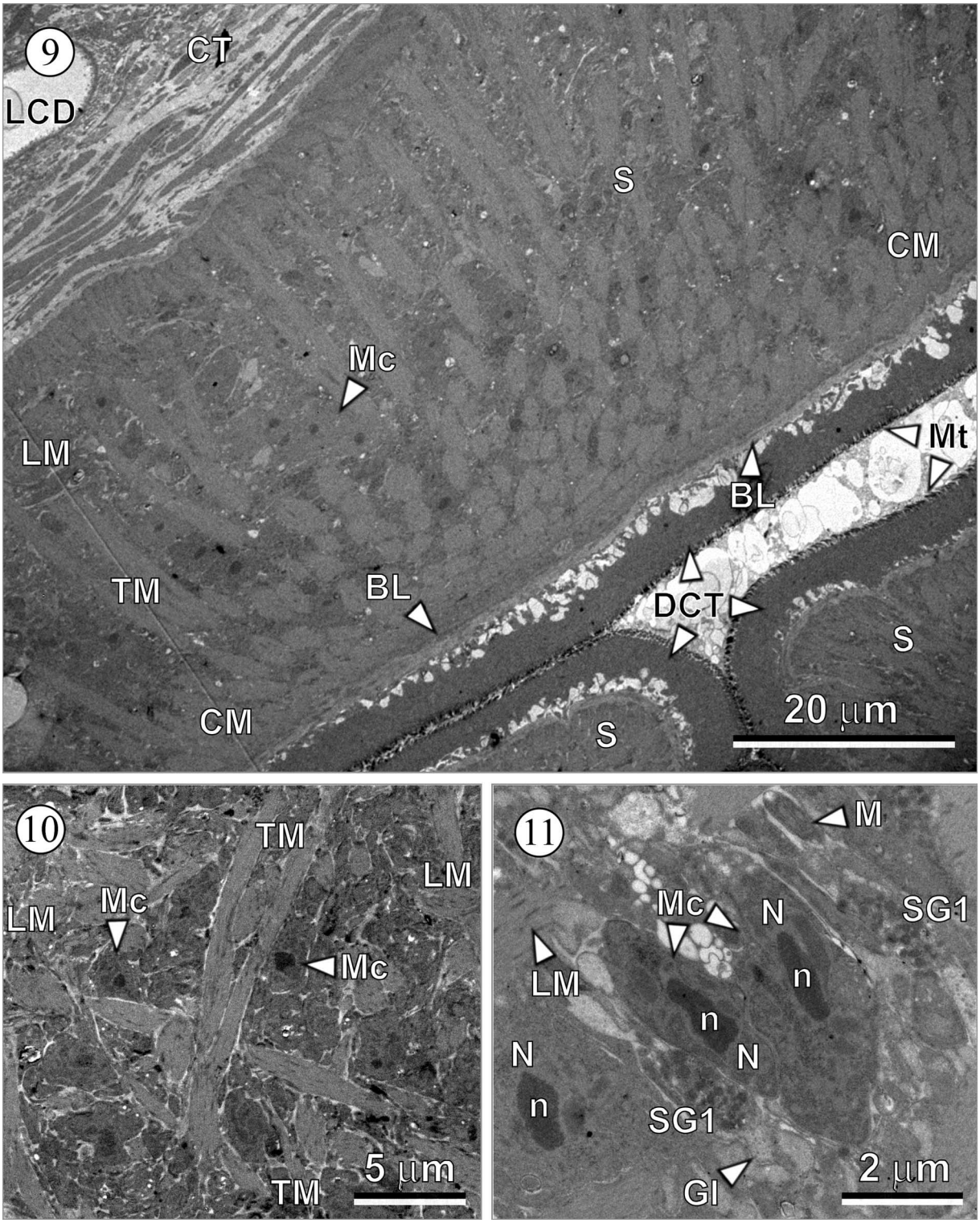
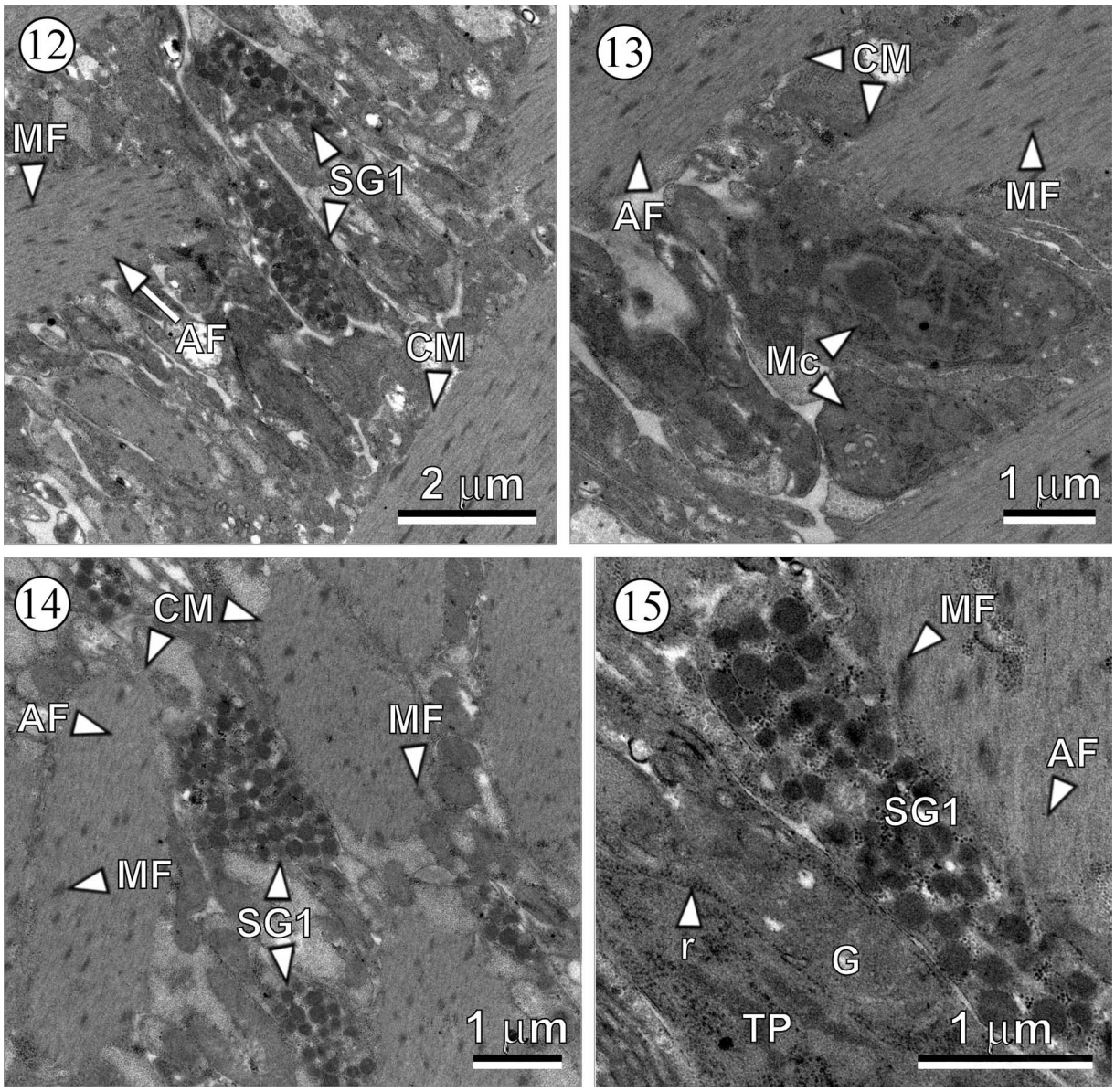


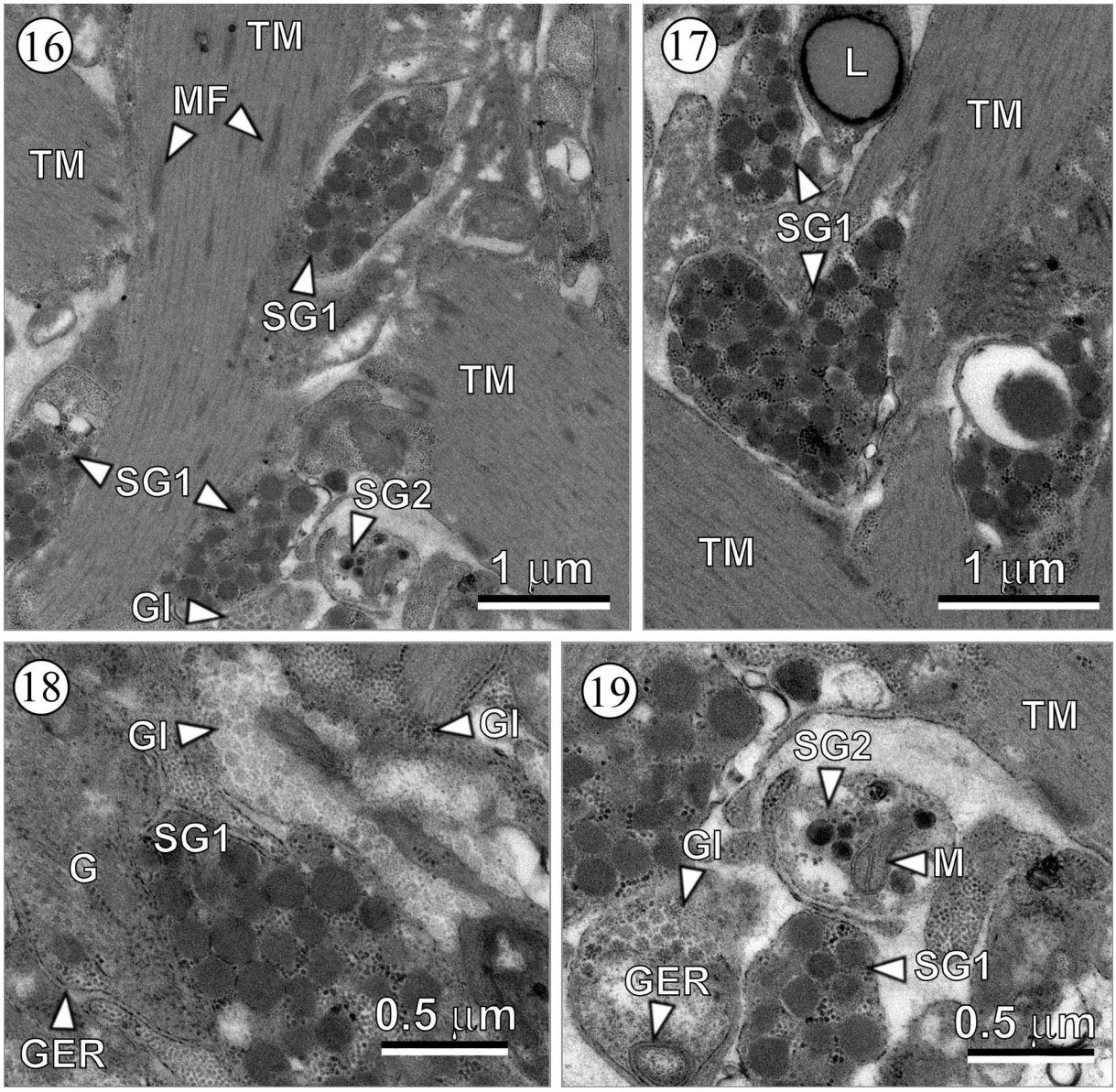
Fig. 9. Low power TEM micrograph showing general topography of sucker ultrastructure. Note: (1) thin layers of the distal cytoplasm of the tegument covered by microtriches, composed of granular, moderately electron-dense cytoplasm; (2) infolded basal lamina consisting of connective tissue fibres; and (3) a compact arrangement of the sucker musculature composed of large bands of longitudinal, transverse, radial and circular muscle fibres. **Fig. 10.** Characteristic crossing pattern of longitudinal and transverse muscle fibres and their myocytons. Note that each muscle cell consists of two major components: (1) the contractile myofibril, containing the actin and myosin myofibrils; and (2) the myocyton, the noncontractile perikaryon. **Fig. 11.** Details of myocyton ultrastructure: Note: (1) large, irregularly-shaped nuclei with elongate, electron-dense nucleoli and granular cytoplasm rich in free ribosomes; (2) myocytons are typically positioned lateral to the longitudinal muscles and localised at some distance from the myofibrils, with cytoplasmic continuity established via tendrillar processes which contain mitochondria; (3) cytoplasmic processes with characteristic type-1 dense secretory granules are situated on both sides of myocytons



Figs 12–15. Ultrastructure of muscle system. Note: (1) two parallel bands of circular muscles, (2) thick myofibrils of myosin, (3) thin myofibrils of actin, (4) elongate cytoplasmic processes containing a heavy accumulation of the secretory granules of type-1. Note that in addition to the above details, **Fig. 13** shows in its central part the myocyton of circular muscles and **Fig. 15**, in its lower left corner, a part of tegumental perikaryon with numerous free ribosomes and Golgi complex, adjacent to cytoplasmic process containing a large amount of type-1 secretory granules (**Figs 12, 14** and **15**) and in the upper right corner thick fibrils of myosin and thin fibrils of actin

cells"), scattered throughout the strobila and the scolex, acting as filters for the entrance of extracellular fluid into the system and responsible for the propulsion of fluid through the protonephridium (Figs 20 and 22); (2) system of terminal tubules of various sizes (Fig. 20) and collecting tubules connecting flame cells with the major canals; and (3) the major collecting canals, with their surface extended by numerous short microvilli and often containing small calcareous corpuscles within the lumen (Fig. 21).

The flame cells were studied in cross and oblique sections (Figs 20 and 22). The concave surface of the cup-shaped flame cell was facing the enlarged part of the collecting tubule ("nephridial funnel"). This surface supported the "flame" consisting of a tuft of about 70 or more closely apposed cilia (Figs 20 and 22). Each cilium contained a typical 9 + 2 axoneme composed of nine double peripheral microtubules surrounding a pair of central single microtubules. The basal 1/3 of the flame was surrounded by the so-called "nephridial chamber" delimited by a double row of digitiform cytoplasmic processes (Figs 20 and 22), each about 110–150 nm in diameter, which were parallel to the longitudinal axes of the cilia. The processes comprising the outer row arose from the distal end



Figs 16–19. Ultrastructural details of strobilocercus musculature. Note: (1) several accumulations of large, moderately electron-dense granules of type-1 in the cytoplasmic processes situated usually between muscle bifurcations (see **Figs 16** and **17**), (2) different type of cell processes containing heavy accumulations of α-glycogen rosettes or lipid droplets, (3) very characteristic cell processes with mitochondria and less granular cytoplasm containing the second type of secretory granules represented by very small, typical highly electron-dense spherical granules, resembling the so-called "neurosecretory granules" (see **Fig. 16** for their localization and **Fig. 19** for their ultrastructural details)

of the enlarged collecting tubule or so-called "nephridial funnel", but those of the inner row arose from the leading edge of the flame cell (Figs 20 and 22). These overlapping processes were separated from one another by about 40 nm but were interconnected by a thin, continuous, amorphous diaphragm (Fig. 20). Circularly-arranged, minute pores ("nephrostomes") were evident between the endings of the outer row of digitiform processes arising from the nephridial funnel and the surface of the leading edge of the flame cell, providing direct communication between the nephridial chamber and intercellular spaces of the medullary parenchyma.

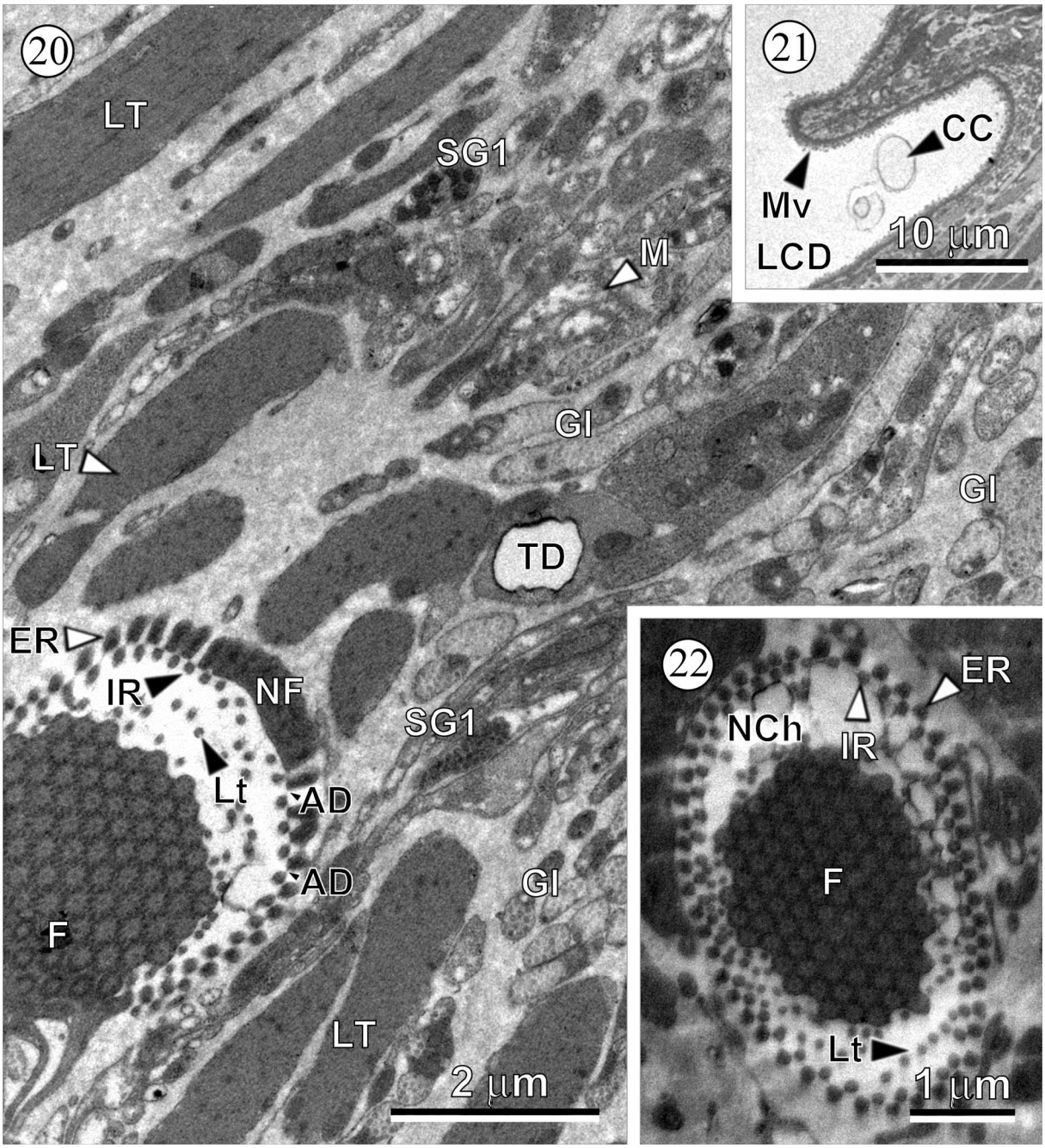
Ultrastructure of medullary parenchyma

Interstitial material was rather abundant in the parenchyma of the body segments. Loosely-arranged muscle fibres were surrounded by fibrous zones separating them from tegumental perikarya and loosely-packed parenchymal cells rich in α-rosettes and β-particles of glycogen. They represented a syncytium of anastomosing cells, which formed a meshwork around muscle fibres and/or fluid-filled intercellular spaces. The medullary parenchyma was visualised as the major site for polysaccharide and lipid deposition. The ultrastructurally-detectable components of extracellular connective tissue

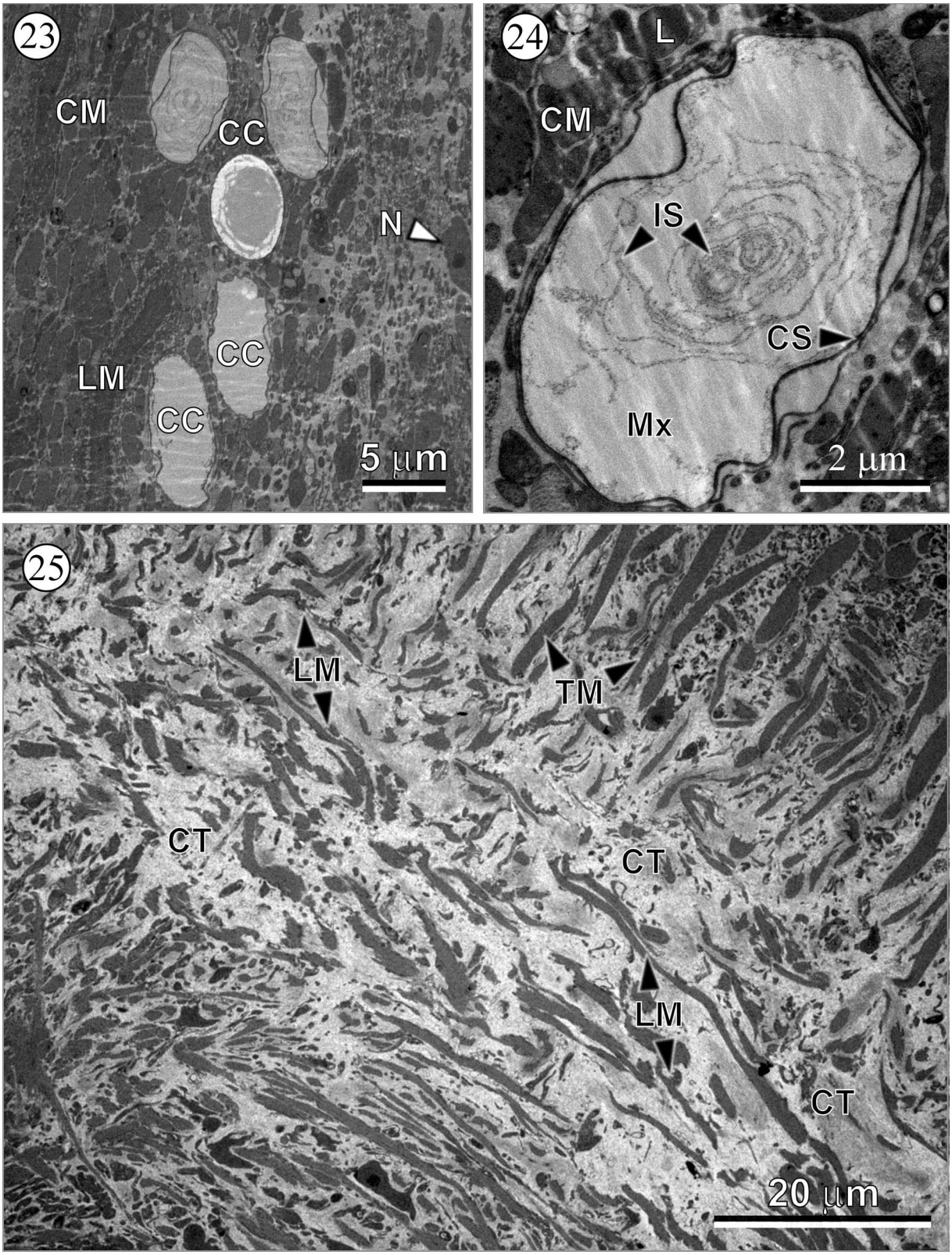
were fine fibrils supporting the tegumentary basal lamina (Fig. 5) and muscle fasciculi (Figs 12–19); they resembled the protein elastin. Most of the central part of larval segments was occupied by medullary parenchyma and the so-called "interstitial matrix". The medullary parenchymal interstitium of larval strobile was voluminous (Fig. 25). Close associations and interconnections between parenchymal cells, myofibrils and myocytons, supporting the interpretation of cestode parenchyma as musculo-parenchymal tissue, were frequently observed.

Ultrastructure of calcareous corpuscles

In the polycephalic larvae of *T. parva*, the calcareous corpuscles occurred in the central vesicle, the larval strobilae and the scole-

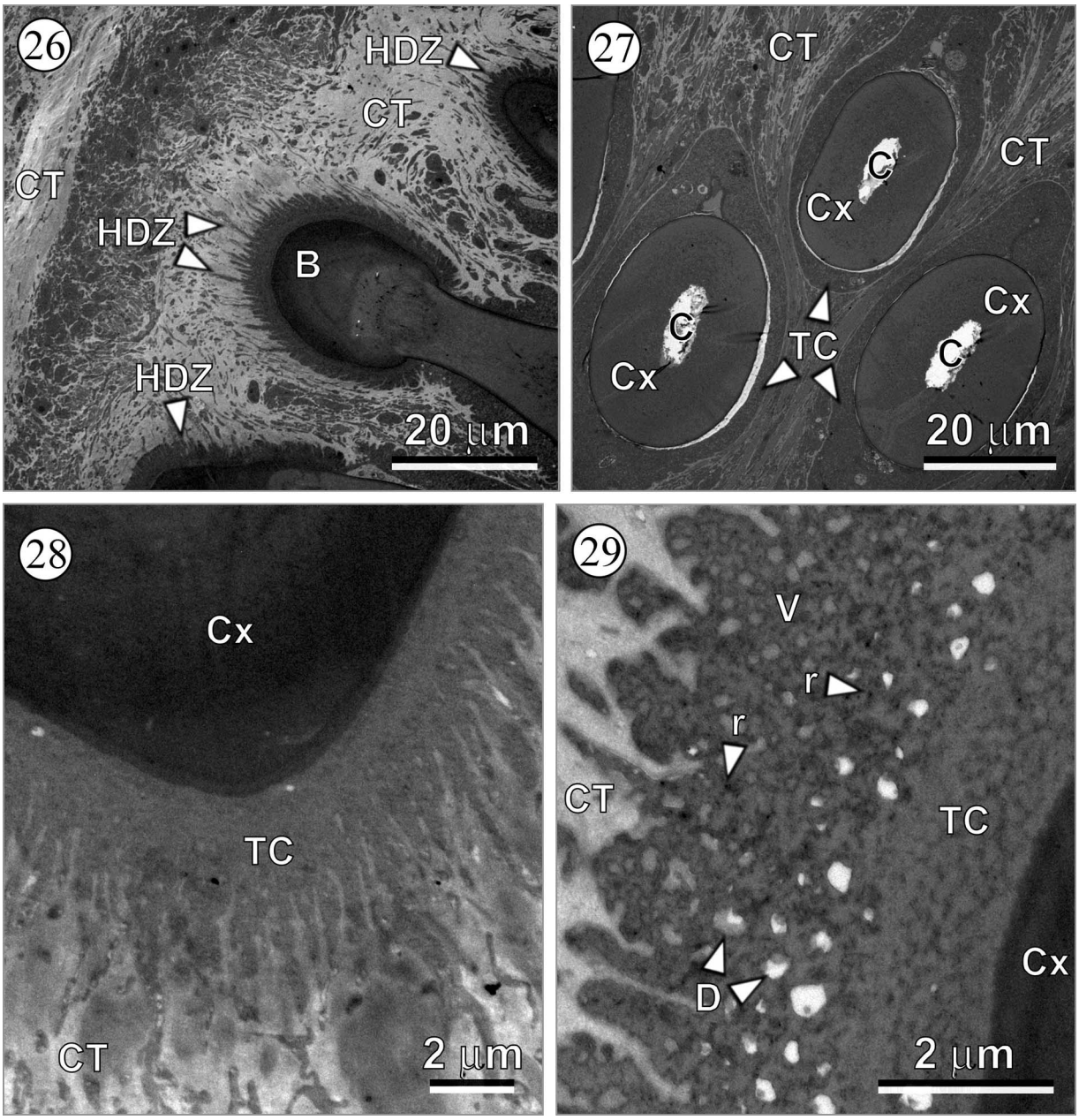


Figs 20–22. Ultrastructure of the protonephridial system. **Figs 20** and **22**. Cross-sections of the terminal organs, at the levels of the nephridial chambers showing interdigitations of flame cells and cytoplasmic digitiform projections of the nephridial funnel. Internal finger-like processes from flame cells and external processes of the nephridial funnel interconnected by dense, amorphous material. Note: (1) leptotriches from flame cells extending into lumen of terminal organ, and (2) about 70 cilia of flame tightly packed within the central part of the lumen of the terminal organ. **Fig. 21.** Note oblique section through the longitudinall collecting duct with numerous short microvilli at it surface and small calcareous corpuscles in its lumen



Figs 23–25. Ultrastructure of calcareous corpuscles of *T. parva* larvae. Note: (1) five fully-formed, elongate calcareous corpuscles embedded in the larval parenchyma (**Fig. 23**), and (2) a single, irregularly-shaped calcareous corpuscle showing several concentric layers of inorganic substances (**Fig. 24**). **Fig. 25.** Ultrastructure of the medullary parenchyma**.** Note loosely arranged muscular fibres and elongate cell processes embedded in an electron-lucent, fine-fibrillar connective tissue and large intercellular spaces (i.e., extracellular matrices)

ces (Fig. 23). They first appeared in the cytoplasm of specialised corpuscle-forming cells situated among various other cell types of the parenchyma. Each corpuscle-forming cell contained a single, peripherally situated nucleus, mitochondria, ribosomes, few profiles of GER and Golgi complexes. These cells were enlarged by the accretion of organic homogeneous matrix and of granular inorganic materials in concentric layers, with progressive compression of the surrounding cytoplasm (Fig. 24). They were usually spherical, oval or irregularly-shaped and, when fully-developed, ranged 10–35 μm in diameter (Figs 23 and 24). In fully-developed corpuscles, their ground substance showed several concentric rings visible at both LM and TEM levels. TEM examination revealed that the electron-dense concentric rings were composed of opaque gran-



Figs 26–29. Ultrastructure of rostellar hooks of the strobilocercus of *T. parva* larvae. **Fig. 26.** Enlarged basal part of the rostellar hook. Note highly electron-dense outer layer of hook material and numerous thin elongate strands of pro-keratin in hook differentiation zones at the surface of hook base, surrounded by a finely-fibrillar connective tissue. **Fig. 27.** Cross-sections through 3 rostellar hooks. Note: (1) homogeneously electron-dense cortex in hook material, (2) large holes in their core region, and (3) collars of tegumental layer surrounding each hook. **Fig. 28.** Detail of hook peripheral layer of cortex surrounded by tegumental collar of granular cytoplasm rich in free ribosomes, forming around elongate processes of striated appearance, surrounded by a connective tissue. **Fig. 29.** Peripheral part of the handle of a mature hook surrounded by granular cytoplasm of tegumental collar rich in free ribosomes and anchored in position by numerous, small hemidesmosomes in the form of button-like structures

ular material, but the remaining ground substance was homogeneous (Fig. 24). As the corpuscle continued to enlarge, it displaced the nucleus and cytoplasm to the cell periphery.

All organelles of the corpuscle-forming cells degenerated at the final stage of corpuscle development (Figs 23 and 24).

Origins and ultrastructure of the rostellar hooks

Ultrastructure of rostellar of *T. parva* larvae was examined on cross and oblique sections (Figs 26–29). The enlarged basal part of the rostellar hook shows an electron-dense outer layer of hook material and numerous thin elongate strands of prokeratin in hook differentiation zones at the surface of hook base, surrounded by a finely-fibrillar connective tissue (Fig. 26). On the cross-sections through rostellar hooks there are distinct: (1) homogeneous electron-dense cortex in hook material, (2) large holes in their core region, and (3) collars of tegumental layer surrounding each hook (Fig. 27). The hook peripheral layer of cortex is surrounded by a tegumental collar of granular cytoplasm, rich in free ribosomes, which forms around elongate processes of striated appearance, surrounded by a connective tissue (Fig. 28). The handle of mature hooks is anchored in a correct position by numerous, small hemidesmosomes in the form of button-like structures (Fig. 29). All the developmental stages of the rostellar hook morphogenesis were not examined here in detail and they will be a subject of a separate paper.

Nervous system

The work on the differentiation and ultrastructure of the nervous system of post-embryonic larvae of *T. parva* is still in progress and will be published elsewhere.

Discussion

Developmental pattern

The oncosphere carries the germinative cells, which are the primordium of the second larval stage, post-embryonic larva or metacestode (Świderski 1972, 1981, 1983; Świderski *et al*. 2002b; Młocicki *et al*. 2006). However, most of the larval attributes of the oncosphere are lost during development, and structures such as the somatic musculature, the hook musculature and the penetration glands do not persist in the metacestode. Our study on the development of the larvae of *T. parva* confirmed that all the metacestode structures are formed *de novo* and none of them is inherited from the oncosphere. Therefore, the formation of the metacestode is a true metamorphosis (for detailed discussions see Stunkard 1962, Conn 2005).

Asexual multiplication

Larval asexual multiplication is not common among cestodes. It is restricted to cyclophyllideans (some members of the families Taeniidae, Hymenolepididae and Dilepididae), a few unidentified pseudophyllideans (Nobrega-Lee *et al*. 2007) and to the Mesocestoididae. The position of the latter family in the order Cyclophyllidea has been questioned by proposing the division of the latter order into two groups: "mesocestoidatans + cyclophyllideans" (Mariaux 1998). However, it appears that the status of the mesocestoidids as a distinct order or as the basal member of the Cyclophyllidea may require further examination (Mariaux 1998; Miquel *et al*. 1999, 2007; Hoberg *et al*. 1999, 2001).

The unique feature of the asexual multiplication in some species of the Mesocestoididae, which distinguishes them from all other cestodes, is their capability of asexual reproduction not only in the intermediate host but also in the gut of the definitive host. According to Eckert *et al*. (1969), asexual reproduction in adult *Mesocestoides corti* Hoeppli, 1925 should be interpreted as the completion of larval reproduction while in the definitive host. A recent study on metacestodes of *Mesocestoides* sp. described a new type of endogenous asexual proliferation, in addition to two other previously described types, longitudinal fission and exogenous budding (Galán-Puchades *et al*. 2002). However, the fact that most *Mesocestoides* spp. are not known to reproduce asexually remains an enigmatic feature of this group (Conn 1986, 1988a, 1990; Conn *et al*. 2002).

Of all the cestodes, larval asexual reproduction is most common in the family Taeniidae, many species of which have the capacity for exogenous and/or endogenous budding. The greatly-increased rate of asexual reproduction in *Echinococcus* larval cysts has potential unsurpassed by any other cestode. For details and references on the larvae of *E. granulosus*, see Smyth (1964), Morseth (1967) and Sakamoto and Sigimura (1969, 1970); for reviews, see Šlais (1973), Thompson (1986) and Eckert *et al*. (2002); for details and references on the larvae of *E. multilocularis*, see Mehlhorn *et al*. (1983), Thompson (1986) and Eckert *et al*. (2002).

In the genus *Taenia*, asexually multiplying larvae of the cysticercus type occur in eight species [*T. crassiceps*, *T. endothoracica* (Kirschenblatt, 1948), *T. martis* (Zeder, 1803), *T. multiceps*, *T. mustelae* Gmelin, 1790, *T. polyacantha* Leuckart, 1856, *T. serialis* (Gervais, 1847) and *T. twitchelli* Schwartz, 1924] and polycephalic larvae of the strobilocercus type occur in three species [*T. krepkogorski* (Schulz et Landa, 1934), *T. selousi* Mettrick, 1962 and *T. parva*]. For a brief characteristic of the metacestodes of the eleven above-mentioned taeniid species, see Loos-Frank (2000).

Polycephalic larvae developing in the abdominal and thoracic cavities of small mammals, mainly rodents, greatly resemble larvae of *T. parva*. Rausch (1952, 1959, 1977) examined experimentally the life cycle and post-embryonic development of *T. twitchelli*, including the differentiation of the intermediate stages. The exogenous budding in *T. crassiceps* was studied by Freeman (1962). He also examined *T. mustelae*, in which a single oncosphere may give rise to more than one metacestode by the formation of multiple scoleces (Freeman 1956). Gvozdev and Agapova (1963) studied experimentally the life cycle of *T. endothoracica*, a species with metacestodes resembling greatly those of *T. parva*. Like the

post-embryonic larva of *T. parva*, those of *T. endothoracica*, *T. twitchelli*, *T. crassiceps* and *T. mustelae* have scoleces that are invaginated. In contrast, evaginated scoleces have been reported in two species of taeniids with polycephalic larvae (Loos-Frank 2000), *T. krepkogorski* and *T. selousi* (see below for discussion on the significance of the scolex retraction or invagination).

In the Hymenolepididae, asexual reproduction of metacestodes was described in *Urocystis prolifer* Villot, 1880 (see Joyeux 1922, Kisielewska 1960) and *Staphylocystis pistillum* (Dujardin, 1845) (see Joyeux and Baer 1936). Intermediate hosts of both species are glomerid diplopods (*Glomeris* spp.). The oncosphere of *U. prolifer* gives rise to an irregular cellular mass in the body cavity of the intermediate hosts; it produces numerous cysticercoids by budding (Kisielewska 1960). The larval stage of *S. pistillum* is a polycephalic larva with individual cysticercoids in the form of a bunch of grapes, for which the name *Staphylocystis* has been proposed (Villot 1877). In an attempt to unify the cestode larval names, Chervy (2002) proposed for these two types of larvae the terms "urocysticercoid" and "staphylocysticercoid", respectively.

In the Dilepididae, asexual reproduction leading to formation of polycephalic larvae was found in earthworms and described either as *Polycercus lumbrici* Villot, 1883 or *Paricterotaenia paradoxa* (Rudolphi, 1802) (= *Polycercus paradoxa*, *Sacciuterina paradoxa*). The development of the larvae ("polycercus cysts") was examined by LM (Metchnikov 1869, Scott 1965, Gulyaev 2000) and by TEM (Crowe *et al*. 1974). Their ultrastructure shows a great similarity to the hydatid larvae of *E. granulosus* with respect to asexual multiplication and the presence of a PAS-positive layer of surrounding tissue. It is clearly different from the polycephalic larva of *T. parva*. Therefore, our ultrastructural results confirm that the asexual multiplication of metacestodes does not reflect close phylogenetic relationships among the species (Moore and Brooks 1987, Hoberg *et al*. 2000, Trouve *et al*. 2003).

Types of larvae occurring in the genus Taenia *and their terminology*

Two general terms are currently used for the post-embryonic, post-oncospheral larvae of cestodes in the intermediate host: "metacestode" (see Wardle and McLeod 1952, Freeman 1973) and "cercoid" (see Jarecka 1970a,b, 1975). Both Freeman (1973) and Jarecka (1975) have commented on coexisting terminology and their criticisms are instructive. Conn (2005) pointed out that the true metamorphosis of oncospheres, into stages that are ultrastructurally like immature adults, makes the metacestode stage of cestodes ontogenetically like the "juveniles" of other animal phyla (see Conn 2000). Although the term "metacestode" seems to be controversial and etymologically may appear inappropriate (Jarecka 1975, Pojmanska 1986, Chervy 2002), it remains still the most commonly-used term and it is impossible to avoid it. Whenever possible, however, because of the above-mentioned differences of opinion, neutral terms such as "post-embryonic larvae" and "post-embryonic development" are used here.

The polycephalic larvae of *T. parva* are characterised by a segmented body and, therefore, they are very similar to the strobilocercus type. The similar polycephalic and segmented larva of *T. krepkogorski* has been described as "coenurostrobilocercus" (Agapova 1950). However, according to Abuladze (1964) and Ryzhikov *et al*. (1978), there are no grounds for introducing this term because (1) Agapova (1950) did not observe the stages of coenurus development and (2) her observations require confirmation as "she has not described her biological experiment" (Abuladze 1964; p. 236). According to Hoberg *et al*. (2000), the strobilocercus is considered to be derived from the cysticercus and is postulated as independent of other larval forms of *Taenia* spp.; it is defined as a strobilate metacestode with well-developed scolex and prominent segmentation, which is present in life cycles of *T. taeniaeformis* and *T. parva*. The "coenurostrobilocercus" of *T. parva* has been considered homologous with strobilocercus (Murai *et al*. 1989, Hoberg *et al*. 2000).

The following six types of taeniid cestode larvae can be distinguished (Hoberg *et al*. 2000, Chervy 2002, Georgiev *et al*. 2006): (1) cysticercus, the most common type among *Taenia* spp., e.g. *T. crassiceps*, *T. pisiformis* (Bloch, 1780); (2) strobilocercus (= "strobilated cercoid"), e.g. *T. taeniaeformis*; (3) fimbriocercus (= armatetrathyridium), with an elongated unsegmented body, e.g. *T. martis*; (4) coenurus, forming a large bladder full of liquid, lined by a germinative membrane budding off multiple scoleces, e.g. *T. serialis*; (5) hydatid, structurally resembling a coenurus but producing daughter cysts, which can also form both daughter cysts and scoleces; and (6) polycephalic, with numerous scoleces on elongated, segmented or non-segmented strobile, arising by exogenous budding from a central vesicle, which later degenerates, e.g. *T. twitchelli*.

The post-embryonic larva of *T. parva* possesses multiple scoleces and has consequently to be referred to as a polycephalic larval form. On the other hand, it closely resembles the strobilocercus type of taeniid larvae by having a segmented larval body. However, the term "strobilocercus" has been proposed to be used for monocephalic larvae only (Chervy 2002) and, therefore, no existing term explicitly describes the larval traits of the species studied. This contradiction indicates the necessity of further improvement of the unified terminology of larval cestodes proposed by Chervy (2002). Hoberg *et al*. (2000) identified the larva of *T. parva* as a "polycephalic strobilocercus", which more effectively reflects its morphology.

Loos-Frank (2000), in her valuable taxonomic survey of *Taenia*, subdivided all multiplying larvae into two types, cysticerci and strobilocerci. In our opinion, it is not entirely clear why the larvae of *T. endothoracica* ("superficially annulated anteriorly") and *T. twitchelli* ("with pseudosegmentation at the anterior end") are not included as belonging to the strobilocercus type. The metacestodes of these two species exhibit a great resemblance to the larva of *T. parva*.

Significance of scolex invagination or retraction

As summarised by Beveridge (2001), the larval scolex of lower cestodes develops externally, whilst the scolex is either

inverted or withdrawn during post-embryonic development in higher cestodes. The significance of evagination and invagination of the scolex remains unclear. In the classical definitions of cysticercoids and cysticerci, it has always been an essential characteristic whether fully-developed scoleces were invaginated or retracted, although these terms were used interchangeably by Wardle and McLeod (1952). In their reviews on cestode post-embryonic development, Voge (1967) and Šlais (1973) considered scolex retraction or invagination as prominent, key developmental features. Freeman (1973), on the other hand, did not include this character in his phylogenetic analysis because he considered the scolex as a labile structure, stating that "there is some evidence that the scolex of the metacestode may evert and retract as need be…" (Freeman 1973; p. 502).

This character of scolex retraction or invagination is of greatest potential use in the Dilepididae. Hoberg *et al*. (1999) used this metacestode character in their analysis and supported the division of dilepidids into Dilepididae *sensu stricto* and Gryporhynchidae, with dilepidids having a withdrawn scolex and gryporhynchids with an invaginated scolex (see Beveridge 2001).

Apparently, all taeniids are characterised by scolex morphogenesis in an invaginated condition. They differ from higher cyclophyllideans such as the hymenolepidids and dilepidids, in which scolex morphogenesis takes place in an evaginated condition. As the results of the present study also indicate, the scoleces of *T. parva* remain invaginated during the morphogenesis of the post-embryonic larva. A similar condition has been described for two other taeniids with polycephalic larvae, *T. twitchelli* (see Rausch 1959) and *T. endothoracica* (see Gvozdev and Agapova 1963). However, in the polycephalic larvae of *T. krepkogorski*, as described by Agapova (1950), when the early buds reach a certain size, their scoleces evaginate and remain so during the entire further development (including the formation of the larval strobila). These observations of Agapova (1950) may still require confirmation because, according to Abuladze (1964), her data were incomplete. In *T. selousi*, the larva is composed of several larval strobila arising from a common bladder, each of them with ~50 segments and having an evaginated scolex (see Loos-Frank 2000). Unfortunately, we have been unable to verify this detail.

As summarised by Chervy (2002; p. 19), "careful examination of the fully-developed larval cestode must reveal whether or not the scolex is invaginated or withdrawn and developmental stages are not required to demonstrate this feature". We concur with Beveridge (2001; p. 253) that "further clarification of this character may assist in phylogenetic analysis within the Cyclophyllidea, since, if the proteocephalideans are used as an outgroup, the withdrawn scolex would represent a synapomorphy linking the hymenolepidids, anoplocephalids, davaineids and dilepidids".

Larval strobilation

The polycephalic larva of *T. parva* shows distinct strobilation. However, as in *T. taeniaeformis* strobilocerci (Rees 1951; Georgiev, unpublished information), no primordia of genital organs were observed in the larval strobila, even in stained specimens. It seems that it may be a general rule for the taeniids having "larval strobila" (e.g. *T. taeniaeformis*, *T. krepkogorski*, *T. parva*) that genital systems never develop in the larval segments. For this reason, Loos-Frank (2000) generally used the term "pseudostrobila" for the polycephalic larvae of *Taenia* spp., including *T. parva*.

In *Dioecocestus asper* (Mehlis, 1831) (Cyclophyllidea, Dioecocestidae), the strobilate metacestodes show the presence of a cirrus sac in the male specimens and the absence of terminal genitalia in the females. However, when these tapeworms become mature in the intestine of the final host, the "larval proglottides" do not mature. The strobilar portion consisting of "larval proglottides" remains at the end of the growing strobila as a sterile series before the beginning of apolysis (data of Yogis presented by Ryzhikov and Tolkacheva 1981). On the basis of these studies and our observations on the lack of genital primordia in the strobilate larva of *T. parva*, it may be concluded that the "larval strobila" of the cyclophyllideans is not an adaptation for rapid maturation. Apparently, it is rather an adaptation for a better feeding of the juvenile cestodes during the first days after infecting the final host, when the larval strobila can provide a larger absorptive surface. Thus, the strobilate larval cestodes in cyclophyllideans are basically different from those of pseudophyllideans [e.g. *Ligula intestinalis* (L., 1758), *Digramma interrupta* (Rudolphi, 1810) and *Schistocephalus solidus* (Mueller, 1776)], where the plerocercoid consists of proglottides at a very advanced stage, which mature rapidly and start egg production within 2–5 days after infecting the final host (Dubinina 1966, Smyth and McManus 1989). It is worth mentioning that in *Lateriporus* sp. (Cyclophyllidea, Dilepididae) there is a segmented cysticercoid termed strobilocysticercoid by Freeman (1973).

Tegument

The tegument of the larvae of *T. parva* resembles that of other adult (Threadgold 1962, Lumsden 1975, Młocicki *et al*. 2004) and larval tapeworms (Morseth 1967; Baron 1968, 1971; Crowe *et al*. 1974; Jarecka *et al*. 1981, 1984; Burt and Jarecka 1984; Jarecka and Burt 1984; Świderski *et al*. 2002a). It is composed of an anucleate layer of peripheral cytoplasm covered by a great number of microtriches and connected by cytoplasmic projections with tegumental perikarya situated below the muscle layers. Our studies on *T. parva* corroborate those mentioned above and support the concept that the microtriche borders of both adult and larval cestodes should be regarded as a digestive-absorptive surface with specialised functional components (Threadgold 1962, Lumsden 1975).

Parenchyma

The nature of cestode parenchyma (and even its existence) remains unresolved. For example, a major question for a long time has been whether the "parenchymal space" represents an intra- or intercellular space. It has been shown that much of

the volume of parenchymal tissue is made up of both voluminous lipid- and/or glycogen-rich cytoplasm and extracellular matrices (ECM) in cyclophyllideans (Conn and Etges 1984) and proteocephalideans (Conn and Rocco 1989), and that the dynamic interaction between parenchymal cells and ECM is involved in histogenesis in some cestodes (Conn 1988b). The close association of parenchymal cells with myocytes and muscle fibres has led to the conclusion that most of the "parenchymal cells" of cestodes are in fact myocytons (reviewed by Conn 1993). Later study on cyclophyllidean parenchyma similarly reported two types of "parenchymal cells": "typical parenchymal cells" having numerous large outgrowths and exhibiting great storage capacity for lipids and glycogen, and "muscular cells" (Kornakova 1994), thus characterising the cestode parenchyma as "musculo-parenchymal" tissue. If this interpretation is confirmed by further studies, then the musculo-parenchymal tissue could be considered a kind of syncytial structure. Our study also confirms classical works (Lumsden 1965, 1966) demonstrating that the medullary parenchyma is the major site for polysaccharide and lipid deposition.

Muscle system

In general, the fine structure of cestode muscles is fairly uniform, except for the highly-specialised ones associated with the suckers and the rostellum (Lumsden and Hildreth 1983). Our observations are in agreement with the conclusion of Lumsden and Byram (1967) that cestode muscles are of a non-striated type and are rather a variety of smooth muscles.

Functional correlates: *possible role of regulatory peptides in neuromuscular interactions*

The cytoplasmic projections with characteristic large, electron-dense, spherical granules (type-1) observed between scolex muscles and, in particular, within the sucker musculature of *T. parva* (see Figs 12, 14–19) resemble those described in the proximity of the acetabular myocytons of *Hymenolepis diminuta* (Rudolphi, 1819) (see Specian *et al*. 1979, Lumsden and Specian 1980); they were believed to originate from the multipolar cells filled with the same type of electron-opaque secretory granules found in perinuclear regions. Initially, these cells were interpreted as unicellular endocrine glands (Specian *et al*. 1979), probably because of their epithelial origin; however, at the ultrastructural level, these glands were considered as exhibiting many "non-neural" characteristics. According to Specian *et al*. (1979) and Lumsden and Specian (1980), the activity of these cells was of a neuroendocrine-type that had the possibility of establishing a direct communication with the adjacent muscular tissue via a gap junction. The secreted material might function as a long-acting modulator of acetabular muscle activity (Specian *et al*. 1979). The recent rapid development of research in this field has shown that the borderline between the platyhelminth nervous system and endocrine system has become indistinct and that the two parts should now be considered under the name neuroendocrine system. The last 16 years have witnessed, in addition to cholinergic and aminergic elements, the identification of a third element to the nervous system of helminths, namely the peptidergic component (Halton *et al*. 1990, 1994, 1999; Halton and Gustafsson 1996). The three types of nerve fibres (cholinergic, aminergic and peptidergic) are sometimes registered in close association as in the innervation of the rostellum musculature of davaineid cestodes (Stoitsova *et al*. 2001). Neuropeptides are ubiquitous intercellular signalling molecules in all Metazoa. There is increasing evidence, derived mainly from light and electron microscope immunocytochemistry, that regulatory peptides and classical transmitters (catecholamines, 5-HT and acetylcholine) coexist in certain populations of neurons and endocrine cells. The peptidergic neuron is a multifunctional cell which probably has an important integrative function in platyhelminths since they do not have true endocrine organs.

The second type of very small, highly electron-dense secretory granules (type-2), embedded in less granular cytoplasm with mitochondria and observed within adjacent cytoplasmic processes among muscle fibres of scolex and neck region of *T. parva* larvae, resemble typical neurosecretory granules (Świderski 1997, Świderski and Tkach 2002).

Origins and ultrastructure of the rostellar hooks

The general characteristics of rostellar histogenesis in taeniids have been described at LM (Crusz 1947, 1948; Bilqees and Freeman 1969) and TEM level (Mount 1970). Initial disagreement concerning the origin of the primary rostellar hooklets was resolved by the convincing visual evidence provided by Mount (1970); he showed that the primordia of the rostellar hooks originate through enlargement of specialised microtriches. Subsequently, hook protein is deposited along the edges of these microtriches to form the blade of the definitive hook. The handle and guard are formed as a secondary thickening from the deposition of hook protein along the blade. The larval tegument of *T. parva*, which surrounds the developing hooks, is modified by the presence of large accumulations of ribosomes and polyribosomal clusters as described for *T. crassiceps* (see Mount 1970). The abundant rod-like bodies in the tegument forming the hook sheath in *T. parva* and *T. crassiceps* may represent the same hook-forming material described in *Polycercus paradoxa* (see Crowe *et al*. 1974).

Calcareous corpuscles

The calcareous corpuscles (CC) observed in the larvae of *T. parva* are characteristic for many cestode species, in particular for their post-embryonic larvae (Conn 1993, Conn *et al*. 2002). They are of cellular origin and are formed in specialised parenchymal cells, the so-called "CC-forming cells" (Nieland and Von Brand 1969, Świderski *et al*. 1970). Each calcareous corpuscle is composed of concentric lamellae and is made up of an organic basis together with inorganic material. Initially, they remain and grow in the cytoplasm of the "CC-forming cell" but, after reaching a certain size, they destroy the cells and remain as a large accumulation in the intercellular space of the parenchyma. The major inorganic components of calcareous corpuscles are calcium, magnesium,

carbonate and phosphorus, with small traces of other elements; these constituents can vary considerably in relation to metabolic conditions and cestode species (Etges and Marinakis 1991). Their role is still not entirely understood. It has been suggested that they buffer anaerobically-produced acids or help to buffer gastric hydrochloric acid during larval passage through the host stomach, or they may also have an immunological role. Other hypotheses are that they play an important role in: (1) the metabolism of early developing intestinal worms; (2) lipid metabolism; (3) tissue repair and osmotic balance; and finally (4) may act as rudimentary skeletal structures (Chung *et al*. 2003). Calcareous corpuscles have been the subject of numerous studies (see Von Brand *et al*. 1969, Smyth and McManus 1989) but their formation, composition and function are still not completely clear.

Protonephridial system

The protonephridial system of *T. parva* larvae resembles, to a great extent, that described from adult (Świderski *et al*. 1973, Lumsden and Specian 1980, Lumsden and Hildreth 1983) and larval cestodes (Xylander 1987, 1992; Świderski *et al*. 2002a; Świderski and Mackiewicz 2004). Circularly-arranged, minute pores or "nephrostomes", as described from three species of cyclophyllideans (Świderski *et al*. 1973), are between the endings of the outer row of digitiform processes arising from the nephridial funnel and the surface of the leading edge of the flame cell. These pores provide a direct communication between the nephridial chamber and intercellular spaces of the medullary parenchyma and, therefore, play an important role in the so-called "filtration apparatus".

Concluding remarks

Both asexual reproduction and formation of polycephalic larvae, as observed in *T. parva* and in other taeniids as well as in three other cestode families, are considered here as the results of multiple and independent origins and should be regarded as a good example of convergent evolution. Asexual proliferation plays an important role in effective group infestation of the final hosts and undoubtedly increases the chances of completing the parasite life cycle.

As concluded by Beveridge (2001) in his review on the application of life-cycle characters in cestode phylogeny, new LM and TEM data on a great variety of cestode species are urgently needed to provide novel characters to examine in seeking a better understanding of cestode evolution. In his opinion, histology and the ultrastructure of metacestodes offer "considerable opportunities and appear to be a field which has, until now, not been exploited in a systematic fashion" Beveridge (2001; p. 256), but which offers considerable scope for future analysis. Unfortunately, such studies are not common, despite the fact that they can clearly provide direct evidence that might help to resolve many disputed questions concerning interrelationships between cestode taxa and major evolutionary lineages. Nevertheless, ultrastructural and histological studies on metacestodes appear to have considerable promise for providing new characters for phylogenetic analysis. As Beveridge (2001; p. 254) has concluded, "until more comprehensive studies become available, the current data are not amenable to analysis".

Acknowledgements. We are grateful to A. Jones, J.S. Mackiewicz, I. Beveridge and D.B. Conn for kindly commenting on an earlier version of the manuscript. We also thank "Serveis Científics i Tècnics" of the University of Barcelona for their support in the preparation of samples. This study was financially supported by the Spanish grant 2005-SGR-00576 from the "DURSI (Generalitat de Catalunya)". The completion of results, analysis of TEM-micrographs, and preparation of the manuscript of this paper for publication was supported by a Sabbatical Grant (SAB2005-0068) from the "Secretaría de Estado de Universidades e Investigación, Ministerio de Educación y Ciencia" of Spain for Z.S.

References

Abuladze K.I. 1964. Taeniata – tapeworms of animals and man, and diseases caused by them. In: *Osnovy tsestodologii*. Vol. 4 (Ed. K.I. Skryabin). Nauka, Moscow (In Russian). (English translation, 1970, Israel Program for Scientific Translations, Jerusalem).

Agapova A.I. 1950. A new type of larval cestode structure. *Izvestiya Akademii Nauk Kazakhskoy SSR*, *Seriya Parazitologicheskaya*, 8, 242–245 (In Russian).

Alvarez F., Iglesias R., Bos J., Tojo M., Sanmartín M.L. 1990. New findings of the helminth fauna of the common European genet (*Genetta genetta* L.): first record of *Toxocara genettae* Warren, 1972 (Ascarididae) in Europe. *Annales de Parasitologie Humaine et Comparée*, 65, 244–248.

Baer J.G. 1926. Contributions to the helminth fauna of South Africa. 11 & 12 Reports on Veterinary Research. Union of South Africa, Pretoria, 61–136.

Baron P.J. 1968. On the histology and ultrastructure of *Cysticercus longicollis*, the cysticercus of *Taenia crassiceps* Zeder, 1800 (Cestoda, Cyclophyllidea). *Parasitology*, 58, 497–513.

Baron P.J. 1971. On the histology, histochemistry and ultrastructure of the cysticercoid of *Raillietina cesticillus* (Molin, 1858) Fuhrmann, 1920 (Cestoda, Cyclophyllidea). *Parasitology*, 62, 233–245.

Bernard J. 1961. Quelques espèces d'helminthes de micromammifères récoltés en France et en Espagne. *Vie et Milieu*, 12, 125–149.

Bernard J. 1963. Cysticerques polycéphales chez le mulot. *Archives de l'Institut Pasteur*, *Tunis*, 40, 269–277.

Beveridge I. 2001. The use of life-cycle characters in studies of the evolution of cestodes. In: *Interrelationships of the Platyhelminthes* (Eds. D.T.J. Littlewood and R.A. Bray). Taylor and Francis, London, 250–256.

Beveridge I., Richard M.D., Gregory G.G., Munday B.L. 1975. Studies on *Anoplotaenia dasyuri* Beddard, 1911 (Cestoda: Taeniidae), a parasite of Tasmanian devil. Observations on the egg and metacestode. *International Journal for Parasitology,* 5, 257–267.

Bilqees F.M., Freeman R.S. 1969. Histogenesis of the rostellum of *Taenia crassiceps* (Zeder, 1800) (Cestoda), with special reference to hook development. *Canadian Journal of Zoology*, 47, 251–261.

Burt M.D.B. 1987. Early morphogenesis in the Platyhelminthes with special reference to egg development and development of cestode larvae. *International Journal for Parasitology*, 17, 241–253.

Burt M.D.B., Jarecka L. 1984. Studies on the life cycle of *Hymenolepis ductilis* Linton, 1927 and on the ultrastructure of its

cysticercoid tegument. *Acta Parasitologica Polonica*, 39, 35–42.
Caley J. 1974. The functional significance of scolex retraction and subsequent cyst formation in the cysticercoid larva of *Hymenolepis microstoma*. *Parasitology*, 68, 207–227.
Caley J. 1976. Ultrastructural studies of the cysticercoid of *Moniezia expansa* (Anoplocephalidae) with special reference to the development of the cyst. *Zeitschrift für Parasitenkunde*, 48, 251–262.
Campana-Rouget Y. 1950. Un cysticerque polycéphale chez le mulot, *Apodemus sylvaticus* L. *Vie et Milieu*, 1, 202–206.
Casanova J.C., Feliu C., Torres J., Miquel J., Špakulová M. 2000. Faunistic and ecological trends on the helminthic community of *Genetta genetta* Linnaeus, 1758 (Carnivora: Viverridae) in the Iberian Peninsula. *Helminthologia*, 37, 223–228.
Chervy L. 2002. The terminology of larval cestodes or metacestodes. *Systematic Parasitology*, 52, 1–33.
Chung Y., Kong Y., Cho S., Yang H. 2003. Purification and localization of a 10 kDa calcareous corpuscle binding protein of *Spirometra mansoni* plerocercoid. *Parasitology Research*, 89, 235–237.
Conn D.B. 1986. Comparative fine structure of *Mesocestoides* spp. tetrathyridia. In: *Handbook of the 6th International Congress of Parasitology* (Ed. M.J. Howell). Australian Academy of Science, Canberra, 114.
Conn D.B. 1988a. Fine structure of the tegument of *Mesocestoides lineatus* tetrathyridia (Cestoda: Cyclophyllidea). *International Journal for Parasitology*, 18, 133–135.
Conn D.B. 1988b. The role of cellular parenchyma and extracellular matrix in the histogenesis of the paruterine organ of *Mesocestoides lineatus* (Platyhelminthes: Cestoda). *Journal of Morphology*, 197, 303–314.
Conn D.B. 1990. The rarity of asexual reproduction among *Mesocestoides* tetrathyridia (Cestoda). *Journal of Parasitology*, 76, 453–455.
Conn D.B. 1993. The biology of flatworms (Platyhelminthes): Parenchyma cells and extracellular matrices. *Transactions of the American Microscopical Society*, 112, 241–261.
Conn D.B. 2000. Atlas of Invertebrate Reproduction and Development. John Wiley & Sons, Inc., New York.
Conn D.B. 2005. Comparative aspects of postembryonic development of cestodes (Platyhelminthes) and other animal taxa. In: *Multidisciplinarity for Parasites, Vectors and Parasitic Diseases*. *Proceedings of the 9th European Multicolloquium of Parasitology*. Vol. *1*. *Articles of Keynote Speakers* (Ed. S. Mas-Coma). Monduzzi Editore, Bologna, 319–325.
Conn D.B., Etges F.J. 1984. Fine structure and histochemistry of the parenchyma and uterine egg capsules of *Oochoristica anolis* (Cestoda: Linstowiidae). *Zeitschrift für Parasitenkunde*, 70, 769–779.
Conn D.B., Galán-Puchades M.T., Fuentes M. 2002. Ultrastructure of cells and extracellular matrices in the hindbody of non-proliferative tetrathyridia of *Mesocestoides lineatus* (Cestoda: Cyclophyllidea). In: *Proceedings of the 10th International Congress of Parasitology*. Monduzzi Editore, Bologna, 535–538.
Conn D.B., Rocco L.J. 1989. Fine structure of the cellular parenchyma and extracellular matrix of *Ophiotaenia loennbergii* (Cestoda: Proteocephalidea). *Acta Zoologica* (*Stockholm*), 70, 105–110.
Crowe D.G., Burt M.D.B., Scott J.S. 1974. On the ultrastructure of the polycercus larvae of *Paricterotaenia paradoxa* (Cestoda: Cyclophyllidea). *Canadian Journal of Zoology*, 52, 1397–1411.
Crusz H. 1947. The early development of the rostellum of *Cysticercus fasciolaris* Rud., and the chemical nature of its hooks. *Journal of Parasitology*, 33, 87–98.
Crusz H. 1948. Further studies on the development of *Cysticercus fasciolaris* and *Cysticercus pisiformis*, with special reference to the growth and sclerotization of the rostellar hooks. *Journal of Helminthology*, 22, 179–198.
Dollfus R.-P., Saint Girons M.C. 1958. Modification du comportement d'un *Apodemus* parasité par de cystiques polycéphales, en relation avec la croissance de ceux-ci. *Vie et Milieu*, 9, 116–123.
Dubinina M.N. 1966. Ligulids (Cestoda: Ligulidae) of the fauna of the USSR. Nauka, Moscow (In Russian).
Eckert J., Von Brand T., Voge M. 1969. Asexual multiplication of *Mesocestoides corti* (Cestoda) in the intestine of dogs. *Journal of Parasitology*, 55, 241–249.
Eckert J., Gemmell M.A., Meslin F.-X., Pawłowski Z.S. (Eds.). 2002. WHO/OIE Manual on Echinococcosis in Humans and Animals: a Public Health Problem of Global Concern. World Organisation for Animal Health (Office International des Epizooties) and World Health Organization, Paris.
Etges F.J., Marinakis V. 1991. Formation and excretion of calcareous bodies by the metacestode (tetrathyridium) of *Mesocestoides vogae*. *Journal of Parasitology*, 77, 595–602.
Feliu C. 1980. Contribución al conocimento de la helmintofauna de micromammíferos ibéricos. Helmintos de Gliridae y Muridae (Rodentia). PhD Thesis, University of Barcelona.
Freeman R.S. 1956. Life history studies on *Taenia mustelae* Gmelin, 1790 and the taxonomy of certain taenioid cestodes from Mustelidae. *Canadian Journal of Zoology*, 34, 219–242.
Freeman R.S. 1962. Studies on the biology of *Taenia crassiceps* (Zeder, 1800) Rudolphi, 1810 (Cestoda). *Canadian Journal of Zoology*, 40, 969–990.
Freeman R.S. 1973. Ontogeny of cestodes and its bearing on their phylogeny and systematics. *Advances in Parasitology*, 11, 481–556.
Galán-Puchades M.T., Fuentes M., Conn D.B. 2002. A new type of endogenous asexual proliferation in cyclophyllidean metacestodes. *Acta Parasitologica*, 47, 288–293.
Georgiev B.B., Bray R.A., Littlewood D.T.J. 2006. Cestodes of small mammals: taxonomy and life cycles. In: *Micromammals and macroparasites*. *From evolutionary ecology to management* (Eds. S. Morand, B.R. Krasnov, R. Poulin). Springer Verlag, Tokyo, 29–62.
Georgiev B.B., Sánchez M.I., Green A.J., Nikolov P.N., Vasileva G.P. Mavrodieva R.S. 2005. Cestodes from *Artemia parthenogenetica* (Crustacea, Branchiopoda) in the Odiel Marshes, Spain: a systematic survey of cysticercoids. *Acta Parasitologica*, 50, 105–117.
Gulyaev V.D. 2000. On gemmation of *Polycercus paradoxa* (Cestoda, Cyclophyllidea) metacestode generations. *Zoologicheskiy Zhurnal*, 79, 1103–1110 (In Russian).
Gvozdev E.V., Agapova A.I. 1963. Life cycle of *Multiceps endothoracicus* Kirschenblatt, 1948. *Trudy Instituta Zoologii*, *Alma-Ata*, 19, 46–48 (In Russian).
Halton D.W., Fairweather I., Shaw C., Johnston C.F. 1990. Regulatory peptides in parasitic platyhelminths. *Parasitology Today*, 6, 284–290.
Halton D.W., Gustafsson M.K.S. 1996. Functional morphology of the platyhelminth nervous system. *Parasitology*, 113, S47–S72.
Halton D.W., Maule A.G., Marks N.J., Followes R.A., Shaw C. 1999. FMRF amide-related peptides (FaRPs) in helminth parasites. *Acta Parasitologica*, 44, 11–18.
Halton D.W., Shaw C., Maule A.G., Smart D. 1994. Regulatory peptides in helminth parasites. *Advances in Parasitology*, 34, 163–227.
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. *Systematic Parasitology*, 42, 51–73.

Hoberg E.P., Jones A., Rausch R.L., Eom K.S., Gardner S.L. 2000. A phylogenetic hypothesis for species of the genus *Taenia*. *Journal of Parasitology*, 86, 89–98.

Hoberg E.P., Mariaux J., Brooks D.R. 2001. Phylogeny among the orders of the Eucestoda (Cercomeromorphae): integrating morphology, molecules and total evidence. In: *Interrelationships of the Platyhelminthes* (Eds. D.T.J. Littlewood and R.A. Bray). Taylor and Francis, London, 112–126.

Jarecka L. 1970a. Phylogeny and evolution of life cycles of Cestoda from fresh water and terrestrial vertebrates. *Journal of Parasitology*, 56 (sect. II, pt. 1), 169–170.

Jarecka L. 1970b. Life cycle of *Valipora campylancristrota* (Wedl, 1855) Baer and Bona 1958–1960 (Cestoda – Dilepididae) and the description of cercoscolex – a new type of cestode larva. *Bulletin de l'Academie Polonaise des Sciences*, *Classe II*, *Series des Sciences Biologiques*, 18, 99–102.

Jarecka L. 1975. Ontogeny and evolution of cestodes. *Acta Parasitologica Polonica*, 23, 93–114.

Jarecka L., Bance G.N., Burt M.D.B. 1984. On the life cycle of *Anomotaenia micracantha dominicana* (Railliet et Henry, 1912), with ultrastructural evidence supporting the definition of cercoscolex for dilepidid larvae (Cestoda, Dilepididae). *Acta Parasitologica Polonica*, 29, 27–34.

Jarecka L., Burt M.D.B. 1984. The cercoid larvae of *Pseudanthobothrium hanseni* Baer, 1956 and *Pseudanthobothrium* sp. (Cestoda, Tetraphyllidea) from experimentally infected harpacticoid copepods. *Acta Parasitologica Polonica*, 29, 23–26.

Jarecka L., Michajlow W., Burt M.D.B. 1981. Comparative ultrastructure of cestode larvae and Janicki's cercomer theory. *Acta Parasitologica Polonica*, 28, 65–72.

Joyeux C. 1922. Recherches sur l'*Urocystis prolifer* Villot. Note preliminaire. *Bulletin de Société Zoologique de France*, 47, 53–58.

Joyeux C., Baer J.G. 1936. Quelques helminthes nouveaux et peu connus de la musaraigne, *Crocidura rusula* Herm. *Revue Suisse de Zoologie*, 43, 25–50.

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

Kisielewska K. 1960. Life cycle of the tapeworm *Pseudodiorchis prolifer* (Villot, 1890) comb. nova (= *Pseudodiorchis multispinosa* Zarnowski, 1955). *Acta Parasitologica Polonica*, 8, 199–203.

Kornakova E.E. 1994. Ultrastructure of parenchyma and the extracellular matrix of *Passerilepis crenata* (Cestoda: Cyclophyllidea). *Parazitologiya*, 28, 119–123 (In Russian).

Krasnoshchekov G.P., Pluzhnikov L.T. 1984. Ultrastructure of the cysticercoid of *Fimbraria fasciolaris* (Hymenolepididae). *Parazitologiya*, 18, 47–52 (In Russian).

Loos-Frank B. 2000. An up-date of Verster's (1969) 'Taxonomic revision of the genus *Taenia* Linnaeus' (Cestoda) in table format. *Systematic Parasitology*, 45, 155–183.

Lumsden R.D. 1965. Macromolecular structure of glycogen in some cyclophyllidean and trypanorhynch cestodes. *Journal of Parasitology*, 51, 501–515.

Lumsden R.D. 1966. Fine structure of the medullary parenchymal cells of a trypanorhynch cestode, *Lacistorhynchus tenuis* (Van Beneden, 1858), with emphasis on specializations for glycogen metabolism. *Journal of Parasitology*, 52, 417–427.

Lumsden R.D. 1975. Surface ultrastructure and cytochemistry of parasitic helminths. *Experimental Parasitology*, 37, 267–339.

Lumsden R.D., Byram J.E. III 1967. The ultrastructure of cestode muscle. *Journal of Parasitology*, 53, 326–342.

Lumsden R.D., Hildreth M.B. 1983. The fine structure of adult tapeworms. In: *Biology of the Eucestoda*. Vol. 1 (Eds. C. Arme and P.W. Pappas). Academic Press, London, 177–233.

Lumsden R.D., Specian R.D. 1980. The morphology, histology and fine structure of the adult stage of the cyclophyllidean tapeworm *Hymenolepis diminuta*. In: *Biology of the tapeworm Hymenolepis diminuta* (Ed. H.P. Arai). Academic Press, New York and London, 157–280.

Mariaux J. 1998. A molecular phylogeny of the Eucestoda. *Journal of Parasitology*, 84, 114–124.

Mas-Coma S., Feliu C. 1977. Contribución al conocimento de la helmintofauna de micromamíferos ibéricos. IV. Parásitos de *Apodemus sylvaticus* Linnaeus, 1758 (Rodentia: Muridae). *Revista Ibérica de Parasitología*, 37, 301–317.

Mehlhorn H., Eckert J., Thompson R.C.A. 1983. Proliferation and metastases formation of larval *Echinococcus multilocularis*. II. Ultrastructural investigations. *Zeitschrift für Parasitenkunde*, 69, 749–763.

Metchnikov E. 1869. Entwicklungsgeschichtliche Beiträge. *Bulletin de l'Académie Impériale de Saint-Pétersburg*, 13, 284–300.

Miquel J., Eira C., Świderski Z., Conn D.B. 2007. *Mesocestoides lineatus* (Goeze, 1782) (Mesocestoididae): new data on sperm ultrastructure. *Journal of Parasitology*, 93, in press.

Miquel J., Feliu C., Marchand B. 1999. Ultrastructure of spermiogenesis and the spermatozoon of *Mesocestoides litteratus* (Cestoda, Mesocestoididae). *International Journal for Parasitology*, 29, 499–510.

Młocicki D., Eira C., Żebrowska J., Miquel J., Świderski Z. 2004. Ultrastructure of the tegument of the anoplocephalid cestode *Mosgovoyia ctenoides* (Railliet, 1890) Beveridge, 1978. *Wiadomości Parazytologiczne*, 50, 579–585.

Młocicki D., Świderski Z., Miquel J., Eira C., Conn DB. 2006. Cellular organisation of the oncosphere of *Mosgovoyia ctenoides* (Cestoda, Anoplocephalidae). *Journal of Parasitology*, 92, 953–961.

Moore J., Brooks D.R. 1987. Asexual reproduction in cestodes (Cyclophyllidea: Taeniidae): ecological and phylogenetic influences. *Evolution*, 41, 882–891.

Morseth D.J. 1967. Fine structure of the hydatid cyst and protoscolex of *Echinococcus granulosus*. *Journal of Parasitology*, 53, 312–325.

Mount P. 1970. Histogenesis of the rostellar hooks of *Taenia crassiceps* (Zeder, 1800) (Cestoda). *Journal of Parasitology*, 56, 947–961.

Murai E., Tenora F., Stanek M. 1989. Atypical strobilocercus (Cestoda: Taeniidae) – a parasite in experimental stocks of *Ondatra zibethicus* (Rodentia). *Miscellanea Zoologica Hungarica*, 5, 21–27.

Nieland M.L., Von Brand T. 1969. Electron microscopy of cestode calcareous corpuscle formation. *Experimental Parasitology*, 24, 279–289.

Nieland M.L., Weinbach E.C. 1968. The bladder of *Cysticercus fasciolaris*: electron microscopy and carbohydrate content. *Parasitology*, 58, 489–496.

Nobrega-Lee M., Hubbard G., Gardiner C.H., LoVerde P., Carvalho-Queiroz C., Conn D.B., Rohde K., Dick Jr. E.J., Nathanielsz P., Martin D., Siler-Khodr T., Schlabritz-Loutsevitch N. 2007. Sparganosis in wild-caught baboons (*Papio cynocephalus anubis*). *Journal of Medical Primatology*, 36, 47–54.

Pojmanska T. 1986. Points in question: terminology in parasitology. *International Journal for Parasitology*, 16, 433–434.

Race G.J., Larsh J.E. Jr., Esch G.W., Martin J.H. 1965. A study of the larval stage of *Multiceps serialis* by electron microscopy. *Journal of Parasitology*, 51, 364–369.

Rausch R. 1952. Studies on the helminthofauna of Alaska. XI. Helminth parasites of microtine rodents – taxonomic considerations. *Journal of Parasitology*, 38, 415–444.

Rausch R. 1959. Studies on the helminthofauna of Alaska. XXXVI. Parasites of the wolverine, *Gulo gulo* L., with observations on the biology of *Taenia twitchelli* Schwartz 1924. *Journal of Parasitology*, 45, 465–484.

Rausch R. 1977. The specific distinction of *Taenia twitchelli* Schwartz 1924 from *T. martis* (Zeder, 1803) (Cestoda: Taeniidae). *Excerta Parasitológica en Memoria del Doctor Eduardo Caballero y Caballero*. *Instituto de Biología*, *Publicaciones Especiales*, 4, 357–366.

Rees G. 1951. The anatomy of cysticercus of *Taenia taeniaeformis* (Batsch, 1786) (*Cysticercus fasciolaris* Rud., 1808) from the liver of *Rattus norvegicus* (Erx.), including an account of spiral torsion in the species and some minor abnormalities in structure. *Parasitology*, 41, 46–59.

Ryzhikov K.M, Gvozdev E.V., Tokobaev M.M., Shaldybin L.S., Matsaberidze G.V., Merkusheva I.V., Nadtochiy E.V., Khokhlova I.G., Sharpilo L.D. 1978. Key to the helminth parasites of rodents from the fauna of the USSR. Cestodes and trematodes. Nauka, Moscow (In Russian).

Ryzhikov K.M., Tolkacheva L.M. 1981. Acoleata – tapeworms of birds. In: *Osnovy tsestodologii*. Vol. 10 (Ed. V.I. Freze.). Nauka, Moscow (In Russian).

Sakamoto T., Sigimura M. 1969. Studies on echinococcosis. XXI. Electron microscopical observations on general structure of larval tissue of multilocular echinococcosis. *Japanese Journal of Veterinary Research*, 17, 67–80.

Sakamoto T., Sigimura M. 1970. Studies on echinococcosis. XXIII. Electron microscopical observations on histogenesis of larval *Echinococcus multilocularis*. *Japanese Journal of Veterinary Research*, 18, 131–144.

Scott J.S. 1965. The development and morphology of *Polycercus lumbrici* (Cestoda: Cyclophyllidea). *Parasitology*, 55, 127–143.

Šlais J. 1973. Functional morphology of cestode larvae. *Advances in Parasitology*, 11, 395–480.

Šlais J., Serbus C., Schramlová J. 1972. The fine structure of the contractile elements in the bladder wall of *Cysticercus bovis*. *Folia Parasitologica*, 19, 165–168.

Smyth J.D. 1964. The biology of the hydatid organisms. *Advances in Parasitology*, 2, 169–219.

Smyth J.D., McManus D.P. 1989. The physiology and biochemistry of cestodes. Cambridge University Press, Cambridge.

Specian R.D., Lumsden R.D., Ubelaker J.E., Allison V.E. 1979. A unicellular endocrine gland in cestodes. *Journal of Parasitology*, 65, 569–578.

Stoitsova S.R., Georgiev B.B., Vasileva G.P., Jordanova M. 2001. Rostellar apparatus of *Fernandezia spinosissima* (von Linstow, 1894) (Cestoda, Cyclophyllidea, Davaineidae): microanatomy and fine structure. *Acta Zoologica* (*Stockholm*), 82, 241–250.

Stunkard H.W. 1962. The organization, ontogeny, and orientation of the Cestoda. *Quarterly Review of Biology*, 37, 23–34.

Świderski Z. 1972. La structure fine de l'oncosphère du cestode *Catenotaenia pusilla* (Goeze, 1782) (Cyclophyllidea, Catenotaeniidae). *La Cellule*, 69, 205–237.

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. 1983. *Echinococcus granulosus*: hook-muscle system and cellular organisation of the infective oncospheres. *International Journal for Parasitology*, 13, 289–299.

Świderski Z. 1997. Ultrastructure of the oncospheral nerve cells in *Echinococcus granulosus* and *E. multilocularis*. In: *Archivos Internacionales de la Hidatidosis*. Vol. 32. *XVIII International Congress of Hydatidology*, *Lisboa*, *Portugal*, 126–128.

Świderski Z., Chomicz L., Grytner-Zięcina B., Sereda M.J. 2002b. Ultrastructural characteristic of the oncospheral germinative cells in *Echinococcus multilocularis* and *E. granulosus*. In: *Proceedings of the 10th International Congress of Parasitology – ICOPA X*: *Symposia*, *Workshops and Contributed Papers*, *Vancouver*, *Canada*, *August 4–9*, *2002*, 551–554.

Świderski Z., Euzet L., Schönenberger N. 1973. Ultrastructures du système nephridien des cestodes cyclophyllides *Inermicapsifer madagascariensis*, *Catenotaenia pusilla* et *Hymenolepis microstoma*. *La Cellule*, 71, 7–18.

Świderski Z., Huggel H., Schönenberger N. 1970. Electron microscopy of calcareous corpuscle formation and their ultrastructure in the cestode *Inermicapsifer madagascariensis*. In: *Proceedings of the 7th International Congress of Electron Microscopy* (Ed. J. André), *6–12 September*, *1970*, *Grenoble*, *France*, 821–822.

Świderski Z., Mackiewicz J.S. 2004. Ultrastructural studies on the cellular organisation of the coracidium of the cestode *Bothriocephalus clavibothrium* Ariola, 1899 (Pseudophyllidea, Bothriocephalidae). *Acta Parasitologica*, 49, 116–139.

Świderski Z., Sereda M.J., Vakarenko E., Kornyushin V.V., Salamatin R.V. 2002a. Fine structure of the cysticercoid of the cestode *Sobolevitaenia verulamii* (Cyclophyllidea, Dilepididae). In: *Proceedings of the 15th International Congress on Electron Microscopy*, *1–6 September*, *2002*, *Durban*, *South Africa*. Vol. 2. *Biology and Medicine* (Ed. T. Sewell), 489–490.

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.

Thompson R.C.A. (Ed.). 1986. The biology of *Echinococcus* and hydatid disease. George Allen & Unwin Publishers Ltd., London, Boston & Sidney.

Threadgold L. 1962. An electron microscope study of the tegument and associated structures of *Dipylidium caninum*. *Quarterly Journal of Microscopical Sciences*, 103, 135–140.

Trouvé S., Morand S., Gabrion C. 2003. Asexual multiplication of larval parasitic worms: a predictor of adult life-history traits in Taeniidae? *Parasitology Research*, 89, 81–88.

Ubelaker J.E. 1980. Structure and ultrastructure of the larvae and metacestodes of *Hymenolepis diminuta*. In: *Biology of the tapeworm* Hymenolepis diminuta (Ed. H.P. Arai). Academic Press, New York and London, 59–156.

Ubelaker J.E. 1983. Metacestodes: morphology and development. In: *Biology of the Eucestoda*. Vol. 1 (Eds. C. Arme and P.W. Pappas). Academic Press, London & New York, 139–175.

Verster A. 1969. A taxonomic revision of the genus *Taenia* Linnaeus 1758. *Onderstepoort Journal of Veterinary Research*, 36, 3–58.

Villot F.C.A. 1877. Migrations et métamorphoses des ténias des musaraignes. *Annales des Sciences Naturelles*, *Zoologie*, 6ème Série, 8, 1–19.

Voge M. 1967. The post-embryonic developmental stages of cestodes. *Advances in Parasitology*, 11, 707–730.

Von Brand T., Nylen M.U., Martin G.N., Churchwell F.K., Sites E. 1969. Cestode calcareous corpuscles: phosphate relationships, crystalization patterns, and variations in size and shape. *Experimental Parasitology*, 25, 291–310.

Wardle R.A., McLeod J.A. 1952. The zoology of tapewoms. The University of Minnesota Press, Minneapolis.

Xylander W.E.R. 1987. Ultrastructure of the lycophora larvae of *Gyrocotyle urna* (Cestoda, Gyrocotylidea). II. The protonephridial system. *Zoomorphology*, 107, 88–95.

Xylander W.E.R. 1992. Investigations of the protonephridial system of postlarval *Gyrocotyle urna* and *Amphilina foliacea* (Cestoda). *International Journal for Parasitology*, 22, 287–300.

(Accepted January 3, 2007)