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The cestodes: general considerations

General account

Cestodes represent a group of organisms which present many features of exceptional physiological interest. They are, for example, almost unique amongst parasites in that the adult worm occupies only one particular habitat, the alimentary canal, in one particular group of animals, the vertebrates. Moreover, the known exceptions to this generalisation occur in sites related to the alimentary canal – the bile duct, the gall bladder or the pancreatic ducts.

The only adult forms which occur in hosts other than vertebrates are members of the subclass Cestodaria, whose physiology is largely unknown (and is not considered here) and a few neotenic forms in oligochaetes (i.e. *Archigetes*).

The dominating morphological features of adult cestodes are: (a) an elongated tape-like body – a form elegantly adapted to the tubular habitat provided by the host gut; and (b) the absence of an alimentary canal, in either the adult or larvae. The latter feature is of major physiological importance, for it means that the external surface of the worm, which ultrastructural studies have revealed as a ‘naked’ cytoplasmic *tegument* unprotected by a resistant ‘cuticle’, has evolved as a metabolically active surface through which the transport of all nutrients into, and waste materials out of, the worm must take place. This characteristic makes the cestode tegument a superb model for membrane transport studies and, for these, several species, especially *Hymenolepis diminuta*, have been used extensively. In contrast to the adult worm, larval cestodes can occur in almost any location in the intermediate host, although many species show a predilection for a particular organ. In tissue sites, an analogy has been drawn between cysticerci and the embryos of placental mammals (796). Both theoretically and physiologically, this analogy has much to recommend it, for it must be remembered that a mammalian embryo (which is of paternal as well as maternal origin) is genetically ‘foreign’ or ‘non-self’

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tissue. Thus, it can also be considered to be 'parasitic' in the maternal uterus and essentially shares the same problems as a cestode.

Chief among these are (a) absorption of nutrients, (b) elimination of waste products, and (c) survival in an immunologically 'hostile' environment. In addition, a cestode faces a problem of access for its reproductive products (eggs or cysts) to the outside world and hence transmission to its next definitive or intermediate host.

It is self-evident that the immediate areas of contact of the cestode with its host – i.e. the *host–parasite interface* – is one of great physiological interest and its ultrastructure and biochemical activities have received much attention (459, 462, 622, 623, 624).

Problems of the life cycle

With rare exceptions (e.g. *Hymenolepis nana*), cyclophyllidean cestodes require at least one intermediate host, and pseudophyllidean cestodes require two, or more rarely, three such hosts. The physiological activities of cestodes have been studied largely in these two groups, with the result that the physiology of less well-known orders, such as the Trypanorhyncha, has been largely neglected.

In this text, the physiology of the egg, larval and adult stages of cestodes is reviewed and an attempt is made to examine those factors which may influence or determine the various development patterns encountered during the life cycles. The study of the physiology of an organism in depth involves investigations at molecular, cellular, tissue, organ, whole organism and ecological levels. Only when such wide-ranging studies are made is it possible to obtain an integrated picture of its physiology. Such studies frequently raise questions fundamental to whole areas of biology and, in this respect, cestodes can be regarded as valuable, if unusual, models for the investigation of basic biological phenomena and are so regarded in this text.

Problems of special interest are: activities at the host–parasite interface (especially the transport of substances across the tegument); the biochemistry of various species at different phases of development, in different hosts or in different habitats; the factors controlling growth and sexual differentiation of the adult strobila; the nature and formation of the egg and its protective membranes and the factors stimulating its hatching in different host habitats; the mechanism of penetration of larvae into different tissue sites; the factors which determine whether larvae differentiate in a sexual or asexual direction; and the immunological relationships of all stages of cestodes with their hosts and especially the mechanisms whereby they are able to survive in immunologically hostile environments (Chapter 11).

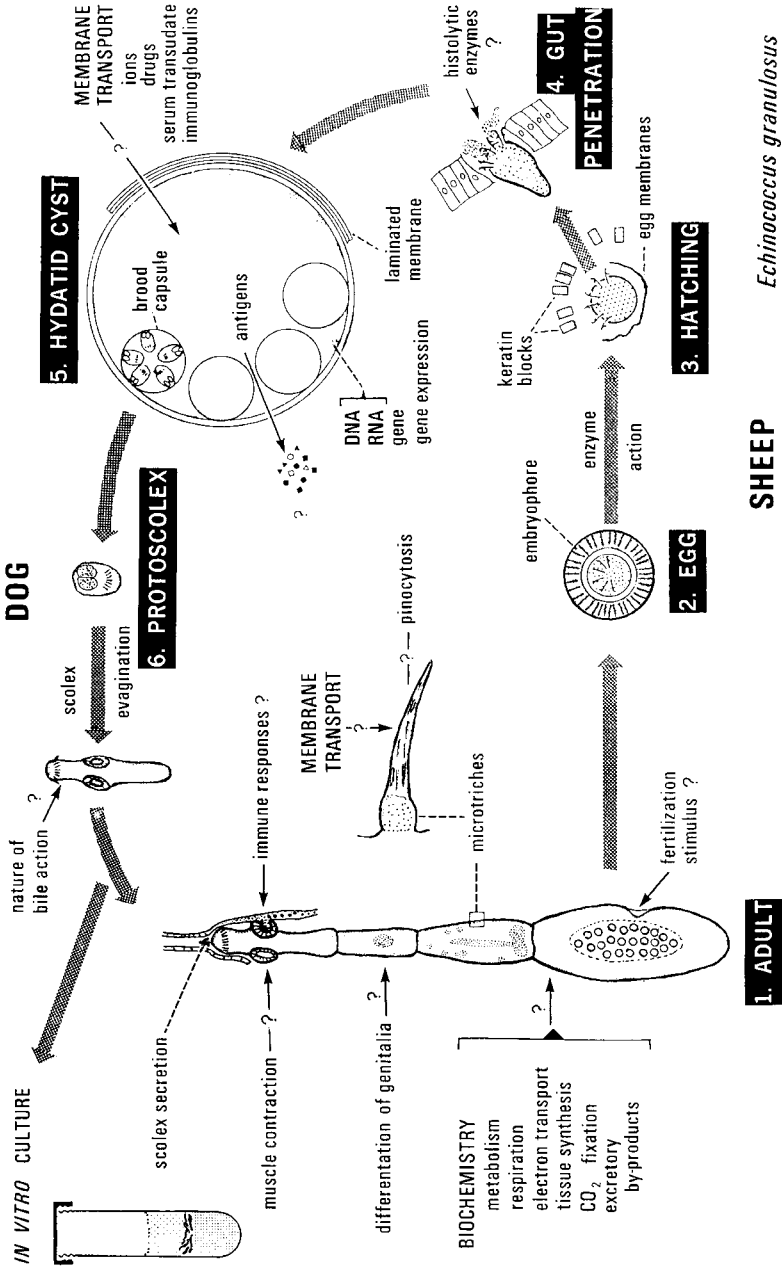


Fig. 1.1. Some physiological problems associated with the life cycle of the hydatid organism *Echinococcus granulosus*. (After Smyth, 1987a.)

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The study of many of the above problems has been greatly stimulated by the fact that cestodes of several genera (e.g. *Hymenolepis*, *Echinococcus*, *Mesocestoides*, *Spirometra*) can now be cultured through most or all of their life cycles *in vitro* (Chapter 10). In addition, the recent application of molecular techniques to the study of cestodes (Chapter 6) provides a fundamental new approach to our understanding of many aspects of their biology, and the interaction that they may have with their hosts. Some of the physiological problems which arise in the life cycle of *Echinococcus granulosus*, the causative organism of hydatid disease, are illustrated in Fig. 1.1; many of these are dealt with in this text.

A feature of the research carried out on the physiology of the group is the relatively small number of species investigated – most experiments being carried out on *Hymenolepis* spp., *Taenia* spp., *Moniezia* spp., *Echinococcus* spp. and *Mesocestoides* spp. amongst the Cyclophyllidea, and various species of Diphyllbothriidae amongst the Pseudophyllidea.

The use of these particular species has undoubtedly been due to the relative ease with which they can be maintained in the laboratory or obtained from local sources, such as abattoirs. This does not necessarily mean that the species used represent the *best* experimental material for the study of that particular problem – only the most *convenient*. Other, perhaps less readily available species, may be much better models. It cannot be stressed strongly enough, therefore, that investigation of the physiology of *any* cestode species, however rare or aberrant (and whether or not of economic or medical importance), is worthy of study.

2

The adult cestode: special structural features relevant to its physiology

General considerations

The general morphology of cestodes, including the ultrastructure, is now too well known to be reviewed at length here. It should be noted, however, that the traditional concept of the tapeworm strobila being divided into discrete 'segments' or 'proglottides' is largely illusionary, in that although the strobila is constricted at intervals between segments, the interior is filled with uninterrupted parenchymal cells and longitudinal muscles throughout the whole length of the body (519). Valuable reviews of the basic structure and/or ultrastructure are those of Arme & Pappas (27, 28) and Threadgold (878) on cestodes in general and that of Arai (19) on *Hymenolepis* spp. in particular. In this chapter therefore, with the exception of the tegument, which is discussed in some detail, only those morphological features of particular physiological interest are considered.

The tegument

General considerations

Because tapeworms lack a gut, all nutritive material must pass through the body surface and waste materials likewise be eliminated through it. The basic structure may, in fact, be compared with a gut turned inside out, with the body covering or *tegument* (Fig. 2.1) serving the absorptive functions normally associated with the intestinal mucosa (Fig. 2.2). The structure and physiology of the tegument is, therefore, of fundamental importance to the understanding of cestode physiology as a whole and has received considerable attention.

Although the tegument contains specific systems for molecular and ion transport – especially amino acids, hexose sugars, vitamins, purines, pyrimidines, nucleotides, and lipids – it probably also serves a number of other vital functions (647): (a) it is a major site of catalytic activity and

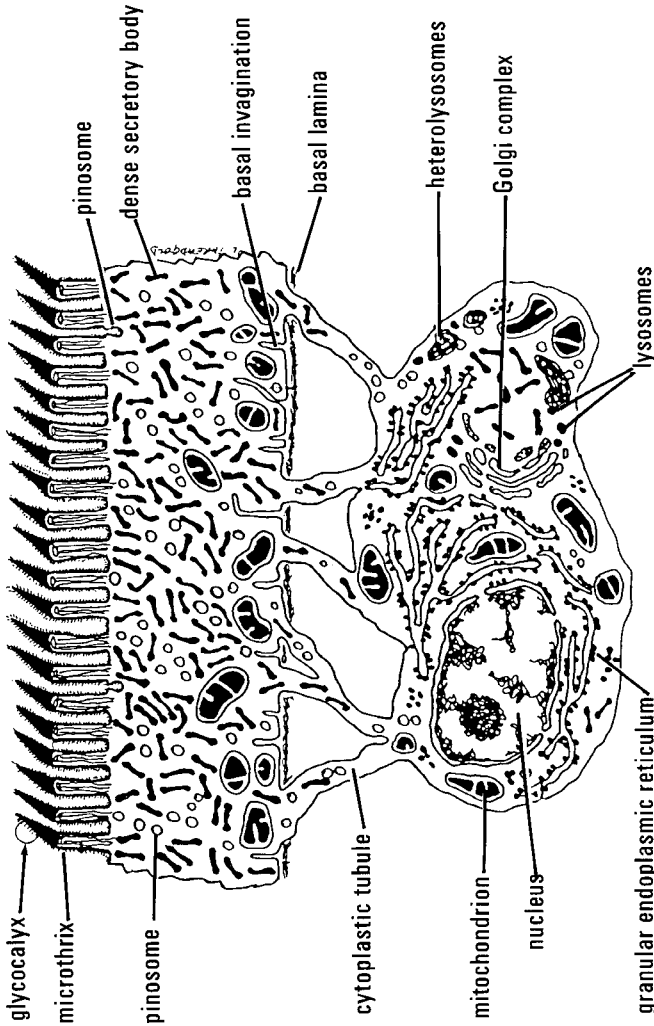


Fig. 2.1. Diagrammatic representation of the tegument of a typical adult cestode, based on several species. (After Threadgold, 1984.)

The tegument

contains enzymes of parasite and possibly of host origin (p. 10); (b) it may be a site for volume regulation; (c) it serves a protective function both against the host's digestive enzymes (see p. 11) and the host's immune reactions; (d) it may also function as a site of metabolic transfer. Valuable reviews on various aspects of the ultrastructure and physiology of the tegument are those of: Arai (19), Arme & Pappas (27, 28), Halton (289), Kuperman (419), Lumsden (456, 457), Lumsden & Murphy (459), Lumsden & Specian (462), Pappas (624), Podesta (647, 648, 649) and Threadgold (878).

Recent studies by transmission (TEM) and/or scanning (SEM) electron microscopy on the adults of species (other than *Hymenolepis*) are those on: *Multiceps endotheracicus* (342, 343), *Proteocephalus ambloplitis* (139, 369), *Bothriocephalus acheilognathi* (267), *Taenia crassiceps* (601, 410), *T. taeniaeformis* (519), *Anomotaenia constricta* (244), *Paricterotaenia porosa* (244), *Proteocephalus tidswelli* (869), *Eubothrium salvelini* (858), *Hydatigera taeniaeformis* (375), *H. krepkogarski* (742), *Diphyllobothrium dendriticum* (279), *D. latum* (974), *Tetrabothrius* spp. (14), *Triaenophorus nodulosus* (901), *Eubothrium rugosum* (901), *Echinococcus granulosus* (870), *E. multilocularis* (519), *Grillotia dollfusi* (954), and *Spirometra erinacea* (972).

Properties of absorptive surfaces

Before discussing the functioning of the cestode tegument, however, it is essential to have some understanding of the properties of absorptive surfaces in general and the intestinal mucosa in particular. Such surfaces have a number of closely identifiable morphological, physiological and biochemical characteristics. A major morphological adaptation is the amplification of the surface area exposed to the intestinal milieu. In the mammalian intestine this amplification is achieved by a 'brush border' of microvilli (Fig. 2.2) which may amplify the exposed surface by as much as 26–30 times (58, 459), there being, perhaps, 3000 microvilli per mucosal cell (877). In cestodes, the amplification of the surface is achieved by the presence of delicate cytoplasmic extensions, or microtriches (Figs. 2.1 and 2.2), reminiscent of mucosal cell microvilli. The size and numerical density of the microtriches vary both between species and in different regions of the same worm, as does the degree of amplification of the surface.

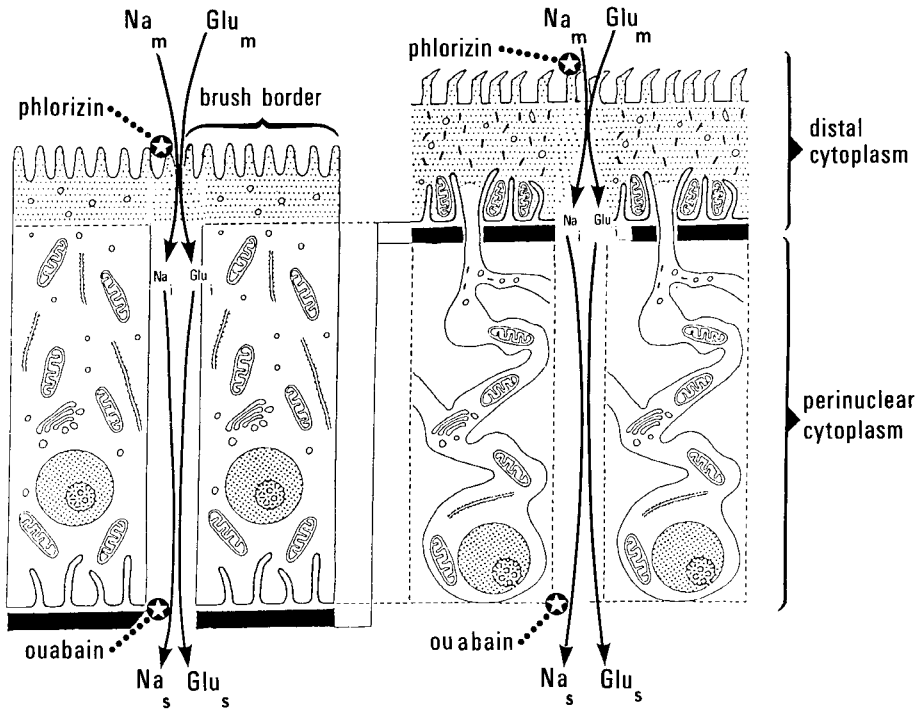
The surface amplification factor (SAF) has been comprehensively investigated in adult *Hymenolepis diminuta*, *H. nana*, *Eubothrium crassum*, *Proteocephalus pollanicoli*, *Schistocephalus solidus* (plerocercoid) and *Taenia crassiceps* (cysticercus), using a computerised image analysis system (883). The SAF ranged from 2.2 (immature proglottids of *H. diminuta* to 16.3 (mature proglottids of *P. pollanicola*). If, however, the dense distal tip

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(a) INTESTINAL MUCOSA (b) CESTODE TEGUMENT

Fig. 2.2. Structural analogy between the tegumental cells of cestodes (right) and the mammalian intestinal epithelium (left) both of which show surface amplification (see text).

Details have been omitted from the central regions of both systems to show schematically a model of a sodium-dependent glucose transport system. Phlorizin-sensitive glucose (Glu_m) is accumulative and coupled to the uptake of ambient sodium (Na_m) from the medium. In effect, sodium uptake is downhill due to a low internal concentration (Na_i) maintained by active extrusion (ouabain-sensitive) of sodium (Na_s) at the 'serosal surface'. Passage of glucose across the basolateral membrane is carried out by some mechanism, as yet unknown. (Right, based on Béguin, 1966. Left, Reprinted from *Morphological and functional aspects of the cestode surface*, by R. D. Lumsden and W. A. Murphy, in *Cellular interactions in symbiosis and parasitism*, ed. C. B. Cook, P. N. Pappas and E. D. Rudolph, 1980 by permission, © by the Ohio State University Press. All rights reserved.)

The tegument

of each microtrich is excluded – as it may not be involved in absorption and transport – the *functional* amplification factor (FAF) shows a range 1.73–11.75; this compares with a FAF value for the mouse mucosa of 26 (58). As the analogy with the intestinal mucosa is so close, this amplified border is here also referred to as a ‘brush border’.

The ultrastructure of microtriches has been extensively studied and is generally well known. For details of the modifications of the fine structure encountered, the various reviews (p. 7) should be consulted. As the microtriches of *Hymenolepis* have been described in detail (462) the account below will be confined to this species. In *H. diminuta*, microtriches have been quoted as having a maximum diameter of 0.14–0.19 μm and a maximum length of 0.9–1.08 μm , by different authors (878); these variations probably reflect differences in technique and in the region and age of the specimens examined. A microtrich has a bipartite structure, the distal point being an electron-dense tip separated from the basal shaft by what appears to be a flattened sac, which would allow for considerable flexibility of the tip. The core of each shaft contains numerous fine filaments which resemble the actin components of microvilli.

Within the interstices of the brush border is a hydrodynamic layer of ‘unstirred water’, which must act, to some extent, to modify the kinetics of the transport processes (Chapter 5). The significance of this layer as a diffusion barrier, is, however, a matter of dispute (458).

The glycocalyx

GENERAL PROPERTIES

The apical plasma membrane of the mucosal cell is further coated with a *glycocalyx* of mucopolysaccharide and glycoproteins. The membrane proper of the brush border contains pores through which molecules of amino acids, sugars etc. can pass. In cestodes, the glycocalyx, which, in common with other platyhelminths, appears to be produced by synthesis within the tegument itself, contains a preponderance of acidic groups which result in the membrane having a net electronegative fixed surface charge (459). Analysis reveals a predominance of glycoproteins, with molecular weights ranging from 12 000 to 237 000 (387) (Fig. 2.3; Table 2.1). The evidence suggests that free hexoses and amino acids absorbed by the worm are rapidly incorporated into macromolecules in the perinuclear cytoplasm and in turn are transferred to the brush border. It has been estimated that in *H. diminuta* the glycocalyx has a turnover rate of about 6 h (457). In *Echinococcus granulosus* the composition of the glycocalyx has

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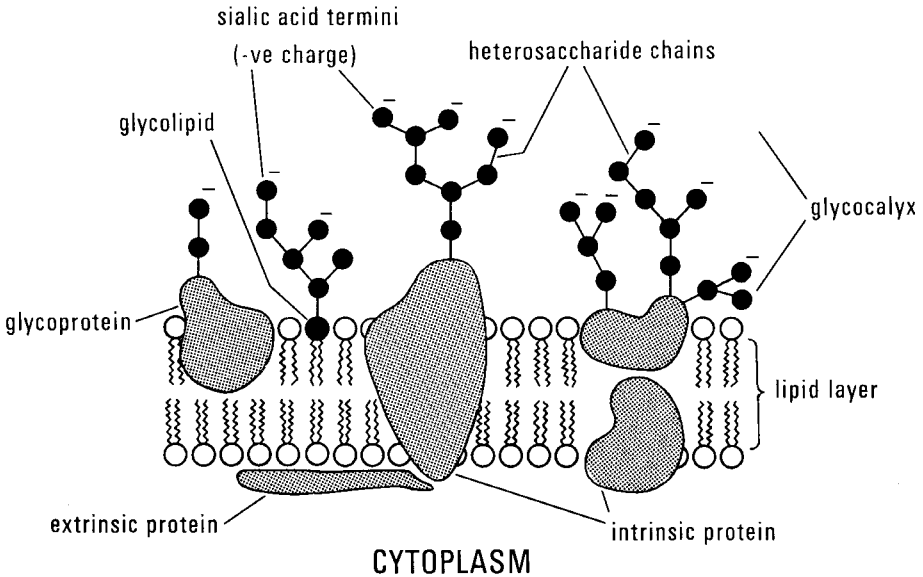
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Fig. 2.3. Diagrammatic representation of the molecular organisation of the tegument plasma membrane (based on the fluid mosaic model of membrane structure of Singer & Nicolson (1972)). The carbohydrate moieties of the membrane glycoproteins and glycolipids are exposed on the external face as the glycocalyx. (After Smyth & Halton, 1983.)

been reported to be different in protoscolexes from cysts of sheep and horse origin and this character may prove to be of taxonomic value in separating different 'strains' of this species (491).

Amongst other activities, the glycocalyx has the capacity to concentrate both inorganic and organic ions. Some of these ions may serve to activate surface (i.e. membrane-bound) enzymes, a number of which have been reported in cestodes (Chapter 6).

The glycocalyx also has the potential of binding high molecular weight substances such as *host* enzymes (e.g. amylase), which may allow 'contact digestion' (= 'membrane' digestion) to take place (674, 796). The presence of such intrinsic enzymes could confer a 'kinetic' absorption advantage on the worm (in relation to the intestinal mucosa with which it is competing for nutrients) in that the spatial relationships at the worm surface would be such that the breakdown products of enzyme activity would be immediately available for absorption by the tegument (622). This aspect is considered further in Chapter 6.