A METHODOLOGY FOR THE MORPHOANATOMIC AND SYSTEMATIC STUDY OF THE SPECIES OF THE FAMILY HYMENOLEPIDIDAE RAILLIET ET HENRY, 1909 (CESTODA: CYCLOPHYLLIDEA)

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ABSTRACT: The hymenolepidid heterogeneity concerning adult stage morphoanatomy, specifity and biogeography is discussed. Dismemberment attempts of the hymenolepidid cestode group are reviewed. The problems of the «satellite» genera of the type genus *Hymenolepis* and the origin of the recent confusion in hymenolepidid classification are analyzed. The systematic value of the morphoanatomic characteristics of the adult stage of hymenolepidids is reviewed at the level of scolex, rostellum, rostellar hooks, suckers, strobila, neck, strobilar type, proglottid type, excretory system, sexually mature segments, male genital organs, female genital organs, posterior segments and eggs. The need for a standardized method for hymenolepidid studies is pointed out. A concrete methodological standardization proposal is presented and described. This standardization proposal concerns material collection and preparation, fixation and conservation, staining and mounting, as well as the whole microscopic study, including measurements, description material, specimens, scolex, strobila, excretory system, genital system, male genital organs, female genital organs and eggs. The main characteristics of a correct description of hymenolepidid cestodes are: availability of appropriate material, complete description, detailed description, intraspecific variability analysis and need of drawings. Time and space consumption appear to be the only disadvantages of the methodological standardization proposal presented. These disadvantages become however insignificant when taking into account that the actual availability of data makes it impossible to attempt an appropriate classification of the hymenolepidids reflecting the natural evolution and phylogeny of this complicated group comprising a large number of species. The only correct way to arrange such a situation is the appropriate study of old, recent and new materials and the corresponding adequate and complete (re)description of each species. Unfortunately, this will need a very long time, but for the time being there is no other way to attempt a correct rearrangement of the systematics and taxonomy of the Hymenolepididae.

KEY WORDS: Cestoda, Hymenolepididae, adult stage, morphology, anatomy, systematics, taxonomy, study methodology, standardization proposal.

INTRODUCTION

The hymenolepidid group

The family Hymenolepididae Fuhrmann, 1907 comprises a large number of cestode species exclusively parasitising mammals and birds, a few of these hymenolepidid species being of veterinary and even medical interest. The type genus of the family, *Hymenolepis* Weinland, 1858 *sensu lato*, is worth mentioning, because it is the cestode genus which includes the largest number of species.

SPASSKY (1951) included the family among the superfamily Hymenolepidoidea Spassky, 1949, in turn comprised among the suborder Anoplocephalata Skrjabin, 1933, always included in the order Cyclophyllidea Beneden in Braun, 1900. JOYEUX & BAER (1961) included the Hymenolepididae, as well as the family Anoplocephalidae Cholodkowsky, 1902, among others, in the same order, without particularizing intermediate taxonomic levels. MATHEVOSSIAN (1963) considered the Hymenolepididae among the suborder Hymenolepidata Skrjabin, 1940. More recently, WARDLE, MC LEOD & RADINOVSKY (1974) decided to raise the family directly to ordinal rank, thus creating the order Hymenolepididea Wardle, Mc Leod et Radinovsky, 1974. Finally, SCHMIDT (1986), in the most recent review of Cestode systematics, reestablished hymenolepidids at the family rank among the order Cyclophyllidea, as already done by WARDLE & MC LEOD (1952). Summing up, since WEINLAND (1858) created the genus *Hymenolepis*, it was observed that there was a great number of species parasitising mammals and birds showing a similar morphology. Systematicists began then to give progressively higher taxa to this relatively homogeneous group of Cyclophyllidids. Thus, from tribu to order there are all kinds of intermediate stages: tribu Hymenolepae Skrjabin et Mathevossian, 1941; subfamily Hymenolepidinae Perrier, 1897; family Hymenolepididae Fuhrmann, 1907; superfamily Hymenolepidoidea Spassky, 1949; suborder Hymenolepidata Skrjabin, 1940; and finally order Hymenolepididea Wardle, Mc Leod et Radinovsky, 1974 (see SPASSKY, 1951; WARDLE & MC LEOD, 1952; YAMAGUTI, 1959; JOYEUX & BAER, 1961; MATHEVOSSIAN, 1963, 1969; SCHMIDT, 1970; BURT, 1980; WARDLE, MC LEOD & RADINOVSKY, 1974; SCHMIDT, 1986). The sustaining of the group at superfamily level, Hymenolepidoidea, within the suborder Anoplocephalata Skrjabin, 1933, among the Cyclophyllidea, agrees with the ontogenic conclusions reached by FREEMAN (1973).

Hymenolepidid heterogeneity and dismemberment attempts

In spite of the generally accepted monophyletism of this cestode group suggested by its morphological constants (Czaplinsky, 1973; Baer, 1973), its heterogeneity has been recognized for a long time. Thus, several attempts to dismember the subgroup of mammal parasites, as well as that of bird parasites, have been made (see summary by Spassky & Spasskaya, 1978).

The Hymenolepididae, and above all the type genus *Hymenolepis* Weinland, 1958 *sensu lato* (Weinland, 1858), characterized by including species with three testes per sexually mature segment, have been the subject of numerous papers and classification attempts, among which the following most important monographic papers must be listed: Blanchard (1891), Cohn (1901, 1904), Clerc (1903), Fuhrmann (1906), Mayhew (1925), Fuhrmann (1932), Hübscher (1937), Hughes (1940, 1941), Lopez-Neyra (1942 a, b), Skrjabin & Mathevossian (1948), Spassky (1950 a, 1954 a), Spassky & Spasskaya (1954), Czaplinsky (1956), Yamaguti (1959), Rybycka (1959), Baer (1961), Spassky (1961, 1963), Spassky (1962, in Burt, 1980), Spasskaya (1966), Voge (1969), Schmidt (1970), Baer & Tenora (1970), Vaucher (1971), Baer (1973), Hunkeler (1974), Ryzhikov *et al.* (1978), Spassky & Spasskaya (1978), Mas-Coma, Tenora & Gallego (1980), Mas-Coma (1982) and Schmidt (1986). The species *Hymenolepis diminuta* (Rudolphi, 1819), established as type species for the genus by Stiles (1903), and generally accepted as such (see Burt, 1980), has become one of the most important cestode species, if not the most important, above all because of its availability for experimental purposes (see Arai, 1980).

The common denominator of all these studies resides in the difficulties posed by the realization of a systematic ordering which portrays the natural evolutionary lines of this cestode group. As a result several authors use different ones of the numerous proposed genera, and other authors do not agree with the dismemberment of the large genus *Hymenolepis* into various different genera, consequently prefering to continue the ascription of the different species to the genus *Hymenolepis sensu lato*. This fact is patent in the species parasitising mammals (above all insectivores, rodents and bats), although specialists working on the hymenolepidid species parasitising birds seem to accept such a dismemberment. Important papers justifying the use of *Hymenolepis sensu lato* for the time being are those of Vaucher (1971) and Hunkeler (1974) in parasites of insectivorous mammals, Baer & Tenora (1970), Hunkeler (1974) and Mas-Coma, Tenora & Gallego (1980) in rodents, and Vaucher (1986 a) in bats, among others.

Morphoanatomy, specifity and biogeography

Clearly, the cestode group in question is far from being homogenous from the point of view of morphoanatomy as well as specificity and biogeography point of views.

From the morphoanatomic point of view, there are monocephalic and polycephalic cysticercoid larval stages (Skrjabin & Mathevossian, 1942 a), cysticercoids developing an external scolex and others developing the scolex within the cyst (Rothman, 1957), aquatic and terrestrial life cycles (Jarecka, 1961; Jourdane, 1975), arostellar unarmed and rostellar unarmed or armed adult stages (Vaucher, 1971; Mas-Coma, Tenora & Gallego, 1980; Mas-Coma, 1982; Schmidt, 1986; Schmidt, Bauerle & Wertheim, 1988; Schmidt & Dailey, 1992), short (with only a few segments) and long (with a large number of segments) strobila (e.g. Vaucher, 1971; Hunkeler, 1974), very different internal genital anatomies (Schmidt, 1986) and eggs with very different morphologies (very thin or thick external wall, different egg shell and embryophore shapes, with and without embryophoral filaments, etc.) (Schmelz, 1941; Jarecka, 1961; Hunkeler, 1974; Mas-Coma, 1982; Mas-Coma *et al.*, 1986 b; Sawada, 1987, 1988, 1989; Sawada & Molan, 1988; Sawada & Mohammad, 1989), only to mention a few very evident important distinguishing characters.

From the point of view of specificity, the adult stage seems to present a marked host selection capacity. Thus, birds do not share any hymenolepidid species with mammals (see Fuhrmann, 1906, 1932; Mayhew, 1925; Spassky & Spasskaya, 1954; Czaplinsky, 1956; Yamaguti, 1959; Spasskaya, 1966; Schmidt, 1986), and at an inferior level, among mammals, for instance, insectivores, rodents, lagomorphs, bats, carnivores, marsupials, pigs and wild primates do not share any parasite species. In many cases the adult stage specificity even reaches the oioxenic level (strict specificity for only one host species) (see for instance Vaucher, 1971, 1982 a, and Hunkeler, 1974).

The biogeographic endemicity of the hymenolepidids in general is also worth mentioning. Thus, for instance, species parasitising European shrews (see Vaucher, 1971; Mas-Coma *et al.*, 1984, 1986 b; etc.) are completely different from species parasitising African shrews (see Hunkeler, 1974) or American shrews (Voge & Rausch, 1955; Vaucher & Durette-Desset, 1978). Similarly, species parasitising European bats (see Hübscher, 1937; Murai, 1976; etc.) are completely different from species parasitising Asian bats (see Sawada, 1990) or American bats (Rausch, 1975; Zdzitowiecki & Rutkowska, 1980; Vaucher, 1986 a; etc.). Only a few hymenolepidid species have been described in lagomorphs (Gvosdev *et al.*, 1970), carnivores (Meggitt, 1927 a; the finding of *Hymenolepis diminuta* in dogs by Santos, Fenerich & Amaral, 1972, if true, must be estimated as accidental for the time being), marsupials (Beveridge & Barker, 1975), pigs (Spassky, 1980, 1981) and wild primates (Baer & Tenora, 1970; Mas-Coma, Tenora & Gallego, 1980).

DESCRIPTION OF PROBLEMS

The problem of the satellite genera of *Hymenolepis*

There is a clear lack of consensus not only concerning the question of the highest taxonomic rank which should be applied to this cestode group, but also concerning the internal systematic-taxonomic organization of the group, at subfamily as well as at generic level. The confusion is above all remarkable at generic level in the tritesticular forms, as the consequence of applying different levels of systematic importance to several morphoanatomic characteristics of the adult stage by different authors. VAUCHER (1971: 84) referred specifically to this question: «Comme plusieurs auteurs l'ont déjà remarqué, les diagnoses de ces genres récents ne tiennent pas toujours compte des mêmes caractères: tantôt l'importance est donnée au scolex, tantôt à la forme des crochets, tantôt à l'anatomie des proglottis ou à l'hôte définitif. Il en résulte une très grande difficulté à placer les espèces de manière certaine dans le genre adéquat et par conséquent de longues listes de synonymes.»

Worth mentioning is the sentence of BAER (1961) in his review of volume II of Yamaguti's series *Systema Helminthum*, when referring to the question of the satellite genera of *Hymenolepis*: «The 20 genera introduced by Yamaguti to the family Hymenolepididae confound the confusion that has already been created by the Russian authors and in no way further a clear understanding of this difficult group.» Posteriorly, SPASSKY (1962, in BURT, 1980) introduces modifications in the system of YAMAGUTI (1959), accepting 26 different genera of tritesticular cestodes. In the most recent review by SCHMIDT (1986), a total of 56 genera of tritesticular hymenolepidids are included. The latter (SCHMIDT, 1986: 267) clearly defined the problem: «Until recent years most species with three testes have been placed in the genus *Hymenolepis*, which became so large as to be nearly impossible to work with». The large number of monospecific genera can be interpreted as a clear illustration of the artificiality of the classification by SCHMIDT (loc. cit.)

The problem of the satellite genera of *Hymenolepis* even increases owing to pure taxonomic questions. A good illustrative example is the problem posed by SCHMIDT (1986) in his last review concerning the genus *Staphylocystis* Villot, 1877. SCHMIDT (1986) accepted this genus as valid, including the species *S. pistillum* (Dujardin, 1845) Spassky, 1950 as type species, together with a series of 24 additional species. However, and as already demonstrated by MAS-COMA & JOURDANE (1977) after clarifying the confusion created by VILLOT (1877) in proposing a new genus based only on the polycephalic morphology of a larval stage, the type species of this genus is *Hymenolepis biliarius* (Villot, 1877) (=*H. dodecacantha* Baer, 1925 *sensu* Vaucher, 1971; =*Hymenolepis* sp. *sensu* Jourdane, 1972). Taking into account that a genus is defined mainly by its type species, the taxonomic problem is evident: how to ascribe hymenolepidid species to this genus without knowing whether they present a polycephalic larval stage. But this is only one example of the confusion. VAUCHER (1971) listed other cases which clearly illustrate the problem.

In the last review by SCHMIDT (1986) several satellite genera which have already been demonstrated to be invalid by different authors are accepted. Thus, the subfamily Ditestolepidinae Yamaguti, 1959 includes only one genus, *Ditestolepis* Soltys, 1952 for a sole species *D. diaphana* (Cholodkowsky, 1906) from shrews, based on two characteristics (suckers almost completey fused in pairs, two testes) which already VAUCHER (1971) had already verified as erroneous. Or the genus *Pseudoparadilepis* Brendow, 1969 erected for the sole species *P. ankeli* Brendow, 1969 from shrews based on the distribution of rostellar hooks in two crowns, a characteristic which VAUCHER (1971), when reviewing the original materials of BRENDOW (1969) and consequently synonymizing this species with *Hymenolepis jacutensis* (Spassky et Morosov, 1959), demonstrated to be incorrect, hooks being of different sizes and inserted not following two crowns but in an irregular line, that is, inserted at different levels. The confusion becomes evident when observing that *H. jacutensis* was included in the genus *Skrjabinacanthus* Spassky et Morosov, 1959 (a genus characterized by presenting two circles of hooks) by SCHMIDT (1986) in the same review. Or the shrew parasite genus *Vigisolepis* Mathevossian, 1945, characterized by SCHMIDT (1986) as presenting a well developed rostellum, with a single wavy circle of hooks and numerous smaller hooks posterior to it. VAUCHER (1971) had occasion to review the type species of this genus, *V. spinulosa* (Cholodkowsky, 1906), demonstrating that no posterior smaller hooks were present in the rostellum, thus invalidating the most important diagnosis characteristic of this genus.

The genus *Hymenolepis sensu lato* was created originally to include the species of the family presenting 3 testes per strobilar segment. However, studies carried out on the gonads by several authors (PALAIS, 1933; VOGE, 1952 a, b; SCHILLER, 1952; ZARNOWSKI, 1955; JOHRI, 1959; RYBYCKA, 1959; SPASSKY, 1959, 1962; COLLINS, 1972; CZAPLINSKI & VAUCHER, 1986; etc.) have demonstrated that this character is extremely variable, even in segments of the same strobila (from 1 to even sometimes 6 testes per segment). This fact suggests that the cestode group in question is perhaps a polyphyletic group (BAER, 1973), the mentioned testicular variability being no more than the reflection of a character in evolution. Effectively, several authors have already attempted to subdivide the group in question (LOPEZ-NEYRA, 1942 a, b; SKRJABIN & MATHEVOSSIAN, 1942 c, d, 1948; SPASSKY, 1954 a; YAMAGUTI, 1959; etc.), but all the resulting classifications up to the present are very arbitrary and far from portraying a natural system. Thus, it is not surprising that opinions concerning the subdivisions of this large cestode group have been traditionally far from unanimous (CZAPLINSKI, 1973; MATHEVOSSIAN, 1973; BAER, 1973).

It should be added, moreover, that in all these cases the creation of numerous new genera have always been based almost exclusively on merely bibliographic data. This has caused the inevitable introduction of errors, above all in those cases of species insufficiently described, unfortunately very numerous in the literature. Rybycka (1959), Vaucher (1971) and Baer (1973) have already adequately discussed this question. Thus, for instance, Baer (1973: 152) pointed out the following: «The absence of correlative, specific characters makes it practically impossible to define natural groups unequivocally and even less so, to give generic names to such groups for which not even sub-generic rank is assured. We must concentrate on collecting fresh materials under the conditions proposed above; on studying the variability of the species and their evolution and relationships within a given host group.» The «conditions proposed above» by Baer (loc. cit.) referred to adequate conditions of collecting, fixation, staining, mounting and study detailed by him in the same paper.

Curiously, despite the non-sharing of parasite species among the above-mentioned host groups, there are hymenolepidid genera proposed and accepted in the last review by Schmidt (1986), which include parasite species from these different host groups in a single cestode genus. The following examples can be listed: *Triodontolepis* Yamaguti, 1959 includes parasites of rodents, insectivores and bats according to Schmidt (1986), although he afterwards listed only species from soricid insectivores and one from a bat, and recently this genus has been restricted to shrews by Tkach (1991); the genus *Staphylocystis* Villot, 1877 comprises, after Schmidt (1986), a large number of species from insectivores and bats, with *S. pistillum* (Dujardin, 1845) Spassky, 1950 as type species, which is erroneous according to Mas-Coma & Jourdane (1977) who have described the species *S. biliarius* Villot, 1877 and have demonstrated that it is an independent valid species and which consequently becomes the correct type species of this genus; the genus *Vampirolepis* Spassky, 1954 includes, after Schmidt (1986), an enormous number of species from bats, insectivores, primates, rodents, marsupials and even birds (!), becoming the odds and ends of the most usual armed tritesticular hymenolepidids; and all this without forgetting the long appendices to Hymenolepidinae from mammals and from birds including a very large number of species which remained unclassified in the book by Schmidt (1986) [and where *Hymenolepis biliarius* (Villot, 1877) Mas-Coma et Jourdane, 1977 can be found].

Origin of the hymenolepidid classification problem

It is evident that a large classification problem exists among hymenolepidids and that the opinion is unanimous that the origin of the problem is above all the insufficiency of morphoanatomic descriptions of the adult stages of the known species. However, this problem is not restricted to hymenolepidid species described long ago. Unfortunately, several years have already elapsed after the

positive critical papers of Vaucher (1971) and Baer (1973) and it seems that their suggestions have not had the desired impact. Since then, numerous new species and genera have been described, repeating the same errors, that is, descriptions lacking references and concrete details on several morphoanatomic characters of an undoubted systematic value at adult stage level. This problem is exacerbated by the lack of sufficient figures and morphoanatomic details, because usually only drawings of the scolex, of the rostellar hooks (if any) and of a sexually mature segment (sometimes a gravid segment is included too), are given, so that several details cannot be appropriately interpreted from the text, if they are described.

Additional problems are posed sometimes by the biological material available, above all concerning first an inappropriate fixation of the parasites and second a very limited number of parasite individuals making a minimum study of intraspecific variability impossible. At any rate, if a good fixation is achieved, a minimum analysis of the morphoanatomic variability of segments along a single strobila can be carried out, at least in relatively long cestode adults comprising a non-scarce number of strobilar segments. Papers written long ago, such as those by Schiller (1952, 1959), Voge (1952 b) and Read & Voge (1954), have already demonstrated the importance of intraspecific variability studies in hymenolepidids, in specimens from naturally infected hosts as well as from experimentally infected hosts. And it has to be taken into account that the intraspecific variability sometimes allows the distinction of very similar species, as in the case of unarmed species of the genus *Hymenolepis sensu stricto* as demonstrated by Voge (1952 a).

Recent descriptions concerning new species and even genera including unarmed hymenolepidids clearly illustrate the problem in question. As is well known, in armed hymenolepidids the description and distinguishing of species is mainly based on the characteristics of the rostellar hooks, owing to the high systematic value of these scolex structures, so that usually even very short descriptions of new species have been accepted for publication in well known journals if a sufficient description of hooks was included to assure species differentiation. However, in unarmed tapeworms of this family the absence of such hooks introduces a high risk of insufficiency if the descriptions are made following a short pattern similar to the one used for armed species. The very recent paper of Schmidt & Dailey (1992) is a good example of this problem and undoubtedly demonstrates that specialists have not found the right way to allow for a future resolution of the question, and that the problem is even growing.

Systematic value of morphoanatomic characters of the adult stage

As already pointed out, there is an evident lack of unanimity concerning the the systematic importance of

the different morphoanatomic characteristics. A critical review of the morphoanatomic details of the hymenolepidid adult stage is presented here. The aim of the following considerations is not to carry out a complete review of the morphoanatomy of the adult stage of hymenolepidids, but only an analysis of the different characteristics of the tapeworms of this group to demonstrate, first, the extent of heterogeneity of these cestodes and, second, which morphoanatomic elements have been shown to be useful to classification and to which taxonomic level they may be ascribed in order to portray a natural phylogenetical system following acceptable evolutionary patterns. In cases of morphoanatomic exceptions to general rules in this cyclophyllidean group, examples of species or genera are listed to illustrate the characteristic in question, but in no way is it intended that the listings of examples be complete (that is, including all the hymenolepidid species or genera so far known presenting the characteristic under discussion). The majority of examples listed come from the field of hymenolepidid cestodes from mammals, owing to the personal experience of the authors, but in no way does this mean that bird hymenolepidids are more uniform. In the following, the systematic ascription of given species to one or another genus follows exactly the authors of the respective references used and thus does not necessarily portray the opinion of the authors of the present paper.

The following concerns only the typical hymenolepidids, that is, the forms included in the subfamily Hymenolepidinae Perrier, 1897 by SCHMIDT (1986). The other four subfamilies accepted by SCHMIDT (1986), Fimbriariinae Wohlffhügel, 1899 (with reticulate uterus and pseudoscolex), Pseudhymenolepidinae Joyeux et Baer, 1935 (uterus replaced with egg capsules), Echinorhynchotaeniinae Spassky et Spasskaya, 1975 (with an evaginable, spiny rostellum) and Ditestolepidinae Yamaguti, 1959 (with the uterus continuous between proglottids, each pair of suckers almost completely fused), will not be taken into consideration in this paper. It should be mentioned here, however, that Ditestolepidinae cannot be differentiated from Hymenolepidinae, since this subfamily was based on the genus *Ditestolepis* Soltys, 1952 with the sole species *D. diaphana* (Cholodkowsky, 1906). This species was erected because it presents two testes per proglottid, a fact which was demonstrated by VAUCHER (1971) to be erroneous, as was the characteristic of each pair of suckers almost completely fused, so that the uterus element remains as only difference.

Scolex

The nature of the scolex has traditionally been a basic characteristic in the division of Cestodes at levels of higher taxa (orders) and sometimes also of intermediate ones (families). Thus, for instance, Anoplocephalidae tapeworms show, among their marked heterogeneity, the presence of a scolex always lacking rostellum and hooks as sole common distinctive (see VOGE, 1969). The on-

togenic interest, as portrayer of phylogenetical relationships, of the scolex and its structures among hymenolepidids is doubtless evident (see RYBYCKA, 1959), since if there are rostellum and hooks in the scolex of the adult, they are already present at metacestode level.

Rostellum: Three possibilities are included among the hymenolepidids: species lacking rostellum, species with unarmed rostellum, and species with rostellum bearing hooks. The presence or absence of a rostellum is a character which can be interpreted, *a priori*, as an indicator of a differentiation of both types for a long time. Nevertheless, the question is difficult to solve if one takes into consideration the scolex alone, since there are species in which the scolex shows a vestigial rostellum detected in both adults and in metacestodes. Moreover, most authors describe such rostellum with the term «rudimentary», which usually give rise to confusion, because of the relativity of this objective assumption (a rudimentary rostellum for one author can sometimes be interpreted simply as an unarmed but patent rostellum by another author). Regarding the forms with rostellum, it should be noted moreover that probably some of the species described only from adult material, and whose metacestodes remain unknown, are in reality armed forms, original specimens having lost their rostellar hooks for different reasons (bad fixation; species with easily caducous hooks; etc.).

These brief considerations indicate the importance of the absence or presence of a rostellum, armed or unarmed, in the phylogenetical reconstruction of the different lines among hymenolepidoids. But at the same time they imply the possible errors to which the exclusive consideration of scolex can lead. Nor should we forget the possibility of increasing these errors bibliographically through the consideration of inappropriate descriptions of species. For instance, the case of *Hymenolepis macyi* Locker et Rausch, 1952 can be noted. This species was originally described without rostellum by LOCKER & RAUSCH (1952), but was demonstrated to present a vestigial rostellum after VOGE (1955 a), SENGER (1955) and DAVIS & VOGE (1957), a character we have also observed in the materials obtained for review study. There is also the opposite case, as that of *Hymenolepis alpestris* Baer, 1931, originally described with rostellum by BAER (1931, 1932), but redescribed as lacking rostellum by JOURDANE (1971), although the revision of Pyrenean material carried out by the authors of the present paper has demonstrated the presence of a rudimentary rostellum. A similar case is that of *Hymenolepis anthocephalus* Van Gundy, 1935, described by the majority of authors as a rostellar species following VAN GUNDY (1935), but that lacks a rostellum, as verified by the authors of the present paper. FASBENDER (1956) has demonstrated the absence of this structure with serial sections of scolices, writing: «That *H. anthocephalus* has no true rostellum is apparent since the only indication of one is the triangular area of darkly-staining cells at the apex of the scolex .... VAN GUNDY

may be justified in refering to the triangular-shaped area as a vestigial rostellum.» RAUSCH & KUNS (1950) also placed *H. antocephalus* with the cestodes characterized as lacking a rostellum.

These observations suggest the need to apply simultaneously the consideration of other characteristics of systematic value which show an undeniable parallelism with the absence of rostellum on the scolex and allow the pursuit of the line without errors. A good example is the proposal of grouping the arostellar hymenolepidoids parasitising insectivores, rodents and lagomorphs under a single taxon Arostrilepididae by MAS-COMA & TENORA (in MAS-COMA, 1982), who demonstrated a parallelism between the absence of rostellum and special egg characteristics. Similarly, MAS-COMA, TENORA & GALLEGO (1980) distinguished between hymenolepidids presenting and lacking a rostellum among species parasitising rodents. In birds, species lacking rostellum also belong to five given genera: *Amphipetrovia* Spassky et Spasskaya, 1954; *Arhynchotaeniella* Saakova, 1958; *Woodlandia* Yamaguti, 1959; *Cloacotaeniella* Schmidt, Bauerle et Wertheim, 1988 and *Amazilolepis* Schmidt et Dailey, 1992 (SCHMIDT, 1986; SCHMIDT, BAUERLE & WERTHEIM, 1988; SCHMIDT & DAILEY, 1992). In bats, up to 19 unarmed, arostellar and rostellar species have been described so far (2 from Europe and 17 from Asia, after the paper by SAWADA & MOHAMMAD, 1989), in different genera, depending on authors (ESTEBAN, pers. comm.). Of these 19 hymenolepidid unarmed species, only *Hymenolepis moniezi* Parona, 1893, *H. parvus* Sawada, 1967, *Insectivorolepis yosidai* Sawada, 1967 and *H. nishidai* Sawada, 1982 lack a rostellum or present a rudimentary rostellum (see PARONA, 1893; SAWADA, 1967 a, b, 1982), the remaining 15 species presenting a well-developed unarmed rostellum. But the confusion in bat hymenolepidids concerning this question seems evident. In the very old description of *H. moniezi* by PARONA (1893) it is not clear whether this species lacks a rostellum or has a rudimentary one, according to the description of this author (PARONA, 1893: 205): «rostrello nullo, però vi si osserva un piccolissimo rilievo circolare, al tutto inerme.» In *H. parvus*, SAWADA (1967 a) described a rudimentary rostellum of only 14-18 μm of diameter. In *I. yosidai*, SAWADA (1967 b) described a rudimentary rostellum without giving size measures. In *H. nishidai* SAWADA (1982) referred to the presence of a rudimentary rostellum or the absence of a rostellum (?!). Even more complicated seem the cases of *I. okamotoi* Sawada, 1970, originally described as bearing a rostellum in SAWADA (1970) although the same author later included in this species materials lacking a rostellum (SAWADA, 1975), and *H. rashomonensis* Sawada, 1972, originally described as bearing a well-measurable rostellum in SAWADA (1972) although the same author later included in this species materials presenting a rudimentary rostellum or lacking a rostellum (SAWADA, 1978).

Rostellum and rostellar sheet, when present, are usually of a given size, showing only a scarce intraspecific variability. The rostellar sheet shows, however, more variation depending on the invagined or protruded situation of the rostellum (see for instance MAS-COMA et al., 1984, 1986 a, b) and the fixation, but its relationship of length and maximum width is clear. Thus, the dimensions of both rostellum and rostellar sheet can be of great systematic value.

The shape of the rostellum is most often oval or conoid, not very long, but there are species in which the base of the very long cylindrical rostellum may even reach the first proglottids, as in the bird parasite species *Sobolevicanthus dlouhyi* Czaplinski et Vaucher, 1981 (CZAPLINSKI & VAUCHER, 1981 b). Some rare special forms of the rostellum have sometimes been used for taxonomic differentiation, as in the bird parasite *Hymenolepis lobulata* Mayhew, 1925, which bears a long, slender rostellum with knob-like enlargement and deep marginal lobes in its tip, each conspicuous lobe carrying a hook on the lateral margin, which induced YAMAGUTI (1959) to erect the genus *Lobatolepis* Yamaguti, 1959, or the huge hemispherical rostellum of the shrew hymenolepidids included in the genus *Hilmylepis* Skrjabin et Mathevossian, 1942 (HUNKELER, 1974).

Hooks: These chitinized rostellar structures have been traditionally used as the most important systematic characteristic in armed hymenolepidid species. It is evident that hook shape, size, number and distribution are very important classifying elements owing to their very scarce intraspecific variability. Consequently it is considered that no more space is needed here to discuss this question. There are, however, several aspects which require some interesting thoughts.

One important issue is the technique of hook preparation for study. There are several techniques described and used, among which probably the technique of hook preparation by means of the Berlese's medium is the most appropriate because of its results and duration of the definitive preparations obtained (see for instance PRITCHARD & KRUSE, 1982). At any rate, in many cases hook morphology and measures are described and taken directly from whole scolex or specimen mounts, thus usually inducing errors, above all in descriptions of small hooks, in measuring inclined instead of completely flattened (perpendicular respecting the microscope axis) hooks or in counting hooks when numerous. Another usual problem is the absence of the description or the drawing of a hook in a completely apical view in order to observe the width and shape of the guard, which in many cases becomes very important, i.e., to distinguish generic groupings, as in the case of *Triodontolepis* Yamaguti, 1959 (see TKACH, 1991).

Another question is the method for appropriately measuring the hooks. Once a hook is completely flattened in the preparation, there are different measures possible in order to describe it as accurately as possible if needed. See for instance the standard measures used by MEGGIT (1927 b) and VAUCHER (1986 a) or the more

numerous measures proposed and used by TKACH (1991). MACKO (1991) has recently applied to the hymenolepidids the proportions of the hooks proposed by BONA (1983) for Dilepididae (I_1 = blade length/handle length; I_2 = blade length/hook length). It has been most usual, however, to measure only the length of the hook, the distance between the base of the handle and the distal pointed extremity of the blade, and the base of the hook, the distance between the base of the handle and the distal rounded extremity of the guard. All measures are useful if the distance measured is clearly specified, but at least the length of the hook must be noted.

Worth mentioning is the possibility of distinguishing different species groupings according to hook patterns, hook types and different hook fixation mechanisms. Thus, there are:

A) species with a rostellum bearing hooks of a different size and inserted at different levels in the same individual *Hymenolepis spinulosa* Cholodkowsky, 1906; *H. jacutensis* (Spassky et Morosov, 1959); *H. multihami* Hunkeler, 1972], whereas in the majority of hymenolepidid species the hooks of a single crown are almost identical and inserted at the same level; the presence of a rostellum with two circles of hooks in the shrew parasite *S. diplocoronatus* Spassky et Morosov, 1959 gave rise to *Skrjabinacanthus* Spassky et Morosov, 1959 (HUNKELER, 1974, analyzes the figure of SPASSKY & MOROSOV on *S. diplocoronatus* reaching the conclusion that, similarly as in *H. jacutensis*, the rostellar hooks are arranged irregularly and not in two crowns, thus invalidating the genus *Skrjabinacanthus* Spassky et Morosov, 1959); the presence of a conoid rostellum, armed with very numerous tiny hooks apparently not arranged in regular circles, in the African rodent hymenolepidid *Hymenolepis petteri* Quentin, 1964 (QUENTIN, 1964; HUNKELER, 1974) led SPASSKY (1973) to propose *Lophurolepis* Skassky, 1973;

B) species with rostellum bearing a crown of numerous very small hooks opposed to species with a crown of fewer and larger hooks;

C) different types of hook shape (with long handle or with very short handle; with long guard or with very short guard; with thin guard or with wide, flat or bifurcate guard; with blade and guard extremities closing or opening; etc.); see SKRJABIN & MATHEVOSSIAN (1942 b) and SPASSKY (1963: 63, fig. 4) concerning the different hook morphological types existing among hymenolepidids; different names have even been given to several shapes: aploparaxoid hooks (handle reduced, guard and blade well-developed and about parallel, as for instance in the numerous bird parasites of the genus *Dicranotaenia* Railliet, 1892); fraternoid hooks (handle well-developed, sometimes curved ventrad, guard and blade well-developed and about parallel, as in the numerous bird parasites of the genus *Variolepis* Spassky et Spasskaya, 1954); arcuatioid and nitidoid hooks (long handle and blade, guard much

reduced or absent, as in bird parasites of the genera *Octacanthus* Spassky et Spasskaya, 1954 and *Microsomacanthus* Lopez-Neyra, 1942); skrjabinoid hooks (the blade constitutes the greatest part of the hook with a much-reduced guard, as in the bird hymenolepidid *Sobolevicanthus dlouhyi* Czaplinski et Vaucher, 1981 (CZAPLINSKI & VAUCHER, 1981 b); etc.; the rostellar hooks in the rodent parasite species *H. petteri* are not only of a different size, but moreover acquire a peculiar shape by the loss of the guard (HUNKELER, 1974); the contrary is found in the bat parasite species *Hymenolepis phyllostomi* Vaucher 1982 in which the guard is three times longer than the blade (VAUCHER, 1982 b); in *Hymenolepis uncinispinosa* Joyeux et Baer, 1930 the rostellar hooks present a peculiar shape in the form of thorns of a rose-bush (HUNKELER, 1974); see SPASSKY (1963: 64) concerning the names and a key to the different hook types among hymenolepidids;

D) species in which the hooks appear regrouped in a central depression of the rostellum when retracted (in these species hooks assure the fixation of the worm to the host's intestine by their own) opposed to species in which the hooks appear inserted in the periphery of a rostellum lacking a central depression (in these species, the intestinal fixation is assured by the grasping of the host's intestinal epithelium between the rostellum and the rostellar sheet) (VAUCHER, 1971, 1982).

Different associations of several of these characteristics could be observed, allowing the distinguishing of some species groupings by VAUCHER (1971, 1982) and HUNKELER (1974), although they apparently could not confirm the possibility of distinguishing natural groups which could be systematically translated into generic taxa, despite the existence of clear relationships between several of such associations and testes distribution patterns and even the specificity towards given host groups. These authors (VAUCHER, loc. cit.; HUNKELER, loc. cit.), however, pointed out that following this way there was undoubtedly the possibility of distinguishing satisfactory natural groupings and evolutionary lines.

Finally, the existence of different species bearing undifferentiable hook crowns and, on the contrary, the existence of different populations of a single species presenting different size, shape and number of rostellar hooks is worth emphasizing. Concerning the first, the case of *Hymenolepis chrysochloridis* Janicki, 1906, which cannot be distinguished from *H. maclaudi* Joyeux et Baer, 1928 at rostellar hook level, can be noted (HUNKELER, 1974). Concerning the second, the study carried out by VAUCHER (1971) demonstrated the possibility of the existence of a large intraspecific variability (even including significant differences) in hook size among different geographic populations of the species *Hymenolepis singularis* Cholodkowsky, 1912. The cases of *Hymenolepis straminea* (Goeze, 1782) and *H. tiara* (Dujardin, 1845) are good examples concerning a large intraspecific variation

of hook shape and hook number, respectively (see Baer & Tenora, 1970 and Vaucher, 1971 respectively).

Suckers: In hymenolepidid cestodes, suckers usually appear to be very prominent, sometimes more or less forwardly directed, although in a few cases suckers are with respect to small respecting the size of the scolex.

As exceptions to the general pattern, the following can be listed: several species presenting vestigial suckers have been described in the bird parasite large genus *Aploparaksis* Clerc, 1903; there is even one species, *Hymenolepis anacetabula* Soltys, 1952 from shrews, which was originally described as lacking suckers (!?), thus inducing the creation of the genus *Acotylolepis* Yamaguti, 1959 accepted by Schmidt (1986); among hymenolepidids from birds, several species presenting armed suckers have been described, such as those included in the monorchid genus *Skrjabinoparaxis* Krotov, 1949 (entire sucker cavity with minute hooks), in the diorchid *Schillerius* Yamaguti, 1959 (suckers armed with small spines), and the triorchid monospecific genera *Echinolepis* Spassky et Spasskaya, 1954 (suckers armed with minute hooks) and *Gonoscolex* Saakova, 1958 (suckers armed with four to six circles of about 40 spines)

Worth mentioning is the generally lower intraspecific variability shown by the size of the suckers, not in absolute terms but in relation to the size of the scolex, thus becoming an element of important systematic value. Vaucher (1971) detected, however, large intraspecific variations in the size of the suckers, related to a similar large variability in scolex dimensions. Worth noting too are the rare cases in which the suckers show a different orientation linked to a transformation of the scolex shape. Thus, in several specialised species [*Hymenolepis integra* (Hamann, 1891), *H. omissa* Baer et Joyeux, 1943] parasitising aquatic shrews, the scolex has a flower-like appearance, so that the suckers have been displaced to the inner side of the «petals», the whole anterior part of the scolex functionning as a large «sucker» (Vaucher, 1971, 1982).

In relation to suckers, the general type of scolex, in a few specialised forms, has been sometimes considered within hymenolepidoids for classification attempts. Spassky (1954 a), for instance, gives to the «hypertrophic» tissue among the suckers in the case of *Hymenolepis anthocephalus* Van Gundy, 1935 enough value to create the genus *Cryptocotylepis* Spassky, 1954 for it. A similar phenomenon of flower-like appearance is adopted by the scolex of other species such as *H. globosoides* (Soltys, 1954) and *H. fodientis* Vaucher, 1971 after fixation, a fact which considered together with other characteristics led Mas-Coma (1982) to include these last two species in the same genus.

Strobila

From the systematic point of view, the following comments lead us to the conclusion that length of strobila

and number and shape of segments are generally useful only at species level. But there are sometimes many cases in which it is possible to distinguish natural groupings of species or enough important morphological or developmental exceptions in isolated species to use these features as a basis for supraspecific, generic classification.

Neck: Strobilation starting from the neck region is a feature not to be forgotten. The presence of a neck (non-segmented zone of the strobila situated after the scolex) and its length are typical characteristics of a species, but showing a variability also related to contraction and fixation method. Hymenolepidid tapeworms do not show great differences in this sense, the neck region ranging generally between relatively common limits. At any rate, there are a completely abnormal species, such as *Gvosdevilepis fragmentata* (Gvosdev, 1948) Spassky, 1953, in which strobilation appears only very far from the scolex, thus showing a long body without segmentation (Gvosdev, 1948; Gvosdev et al., 1970). This fact is related to hyperapolysis, a peculiar development type of segments by which proglottids do not develop united to the strobila till the last gravid stage, but detach precociously to continue development independently in the host's intestine (see Joyeux & Baer, 1961: 348). The presence of hyperapolytic segments has sometimes been used to erect new supraspecific taxa among Hymenolepidoidea, as, for instance, in the genus *Pseudhymenolepis* Joyeux et Baer, 1935, for which the subfamily Pseudhymenolepidinae Joyeux et Baer, 1935 was erected taking into consideration the characteristic uterus breaking up into egg capsules (Joyeux & Baer, 1936). Hunkeler (1974) gave enough importance to the hyperapolytic character of proglottids of the *Pseudhymenolepis* species, to question the inclusion of the species *Pseudhymenolepis eisenbergi* Crusz et Sanmugasunderam, 1971 in this genus because of the lack of hyperapolytic development in the latter. Vaucher (1984) is of the same opinion. However, Schmidt (1986) continues to include this species in the genus *Pseudhymenolepis*.

Strobilar type: The size of the strobila is a variable feature, depending on different factors (host diet, immunological response, age of host and of parasite, crowding effect, hypothermia, etc.) as shown by experimental research with hymenolepidids (Read & Rothman, 1957; Roberts, 1961, 1966; Roberts & Mong, 1968; Dunkley & Mettrick, 1969; Turton, 1971; Ford, 1972; Hopkins, Subramanian & Stallard, 1972; Hopkins & Stallard, 1974; Befus & Featherson, 1974; Befus, 1975; Komuniecki & Roberts, 1975; Hesselberg & Andreassen, 1975; Roberts, 1980; etc.). But, as already pointed out by Rybicka (1959), it is necessary to remember that these authors were doing experimental work and that in natural conditions a considerable variability of these characters is also observed, but to a limited extent.

Czaplinski (1956) based on the examination of

hymenolepidids from birds and considered the length of the strobila and the number of segments to be «plastic features». We agree with RYBICKA (1959) on the impossibility of generalizing this fact. In small mammals there are hymenolepidid species of minute size and scarce number of segments that show only limited variability of the features in question, so that the smaller the number of segments the smaller the variability. VOGE & RAUSCH (1955: 568) wrote: «The shape of the strobila is distinctive and even diagnostic for some of the very small hymenolepidids». RAUSCH (1976) used strobila type for grouping the species in an anoplocephalid genus (*Anoplocephaloides* Baer, 1923 *emend.* Rausch, 1976), showing that length and general shape of strobila allows us to distinguish a determined phyletic line composed of cestode species occurring only in a specific group of hosts.

Length of strobila and number of segments are obviously related to the development of internal organs. Two species parasitising European shrews, *Hymenolepis diaphana* Cholodkowsky, 1906 and *Hymenolepis tripartita* (Zarnowski, 1955), present adult stages in which this correlation is markedly exteriorized (see VAUCHER, 1971: 36, fig. 31).

Peculiar strobila are found among shrew hymenolepidids such as *Hymenolepis diaphana* Cholodkowsky, 1906 and *Hymenolepis tripartita* (Zarnowski, 1955). In these two species the strobila is clearly distinguished in three parts, according to the degree of development (VAUCHER, 1971).

Finally, the very rare exception of a hymenolepidid species parasitising birds must be noted here. *Parafimbriaria websteri* Voge et Read, 1954 is peculiarized by the lack of external segmentation, despite the presence of an evident internal metamerism (VOGE & READ, 1954).

Proglottid type: As RYBICKA (1959: 515) wrote, «the shape of segments, the ratio of length to the width is usually considered as a variable feature (particularly as in the examination of preparations, there may appear some differences depending on the method of fixation used)». Nevertheless, it is evident that they will range within given limits in a particular species. Species differences are generally reduced to distinct dimensions, always considering the level within strobila and the influences due to contraction or fixation method.

As in Anoplocephaloidea, in hymenolepidids the most frequent shape of proglottids is symmetrical, acraspedote or craspedote (sometimes contraction can induce the appearance of the craspedote configuration in acraspedote segments), generally wider than long, with width and length increasing posteriad. Exceptions can however be found in last gravid segments, for instance in parasites of insectivorous mammals, where they are sometimes longer than wide. Thus, proglottid shape has not been traditionally used as a taxonomically useful element to distinguish between species groups, but only sometimes to classify at species level.

There are, however, a very few rare cases showing a very

peculiar proglottid development in which segments detach precociously to continue development independently in the host's intestine: individual segments in *Mathevolepis petrotschenkoi* Spassky, 1948 (SPASSKY, 1948, 1954 a); groups of segments in *Gvosdevilepis fragmentata* Gvosdev, 1948 (GVOSDEV, 1948; GVOSDEV *et al.*, 1970). In these last cases, such proglottid peculiarities have been used to distinguish at a suprapecific level. In the case of *G. fragmentata*, the lost of symmetry in the proglottids is also worth mentioning (GVOSDEV, 1948; GVOSDEV *et al.*, 1970).

A more extreme case of proglottid asymmetry is that of the bird hymenolepidids of the genus *Hispaniolepis* Lopez- Neyra, 1942, in which the antiporal margin of segments is strongly fimbriated, giving rise to an elongate appendage which becomes longer as the segments mature, whereas the poral margin appears normal (LOPEZ-NEYRA, 1942 a, b; SCHMIDT, 1986). Another curious hymenolepidid morphology is found in the bird parasite species included in the genus *Pararetinometra* Stock et Holmes, 1982, in which the posterolateral margins of the velum of each segment bears a row of spines (STOCK & HOLMES, 1982). Patent small «spines» are found on the surface of the posterior margins of the proglottides in the bird hymenolepidid *Sobolevicanthus dlouhyi* Czaplinski et Vaucher, 1981 (CZAPLINSKI & VAUCHER, 1981 b).

It has been shown that the pattern and relative development of muscle bundles are highly variable in Cestodes, but constant within a species, and that therefore they are often valuable taxonomic characters. Worth mentioning in this sense is the study carried out by HUNKELER (1974) on the muscle fibers (mainly the longitudinal muscles) of proglottids in hymenolepidid species from African insectivores and rodents. He could distinguish clear musculature differences between species and even groupings of species bearing similar muscle patterns, although he did not try to analyze the possible taxonomic usefulness of these characteristics in hymenolepidids. Unfortunately, hymenolepidid species in which the proglottid muscle pattern is known are too few to produce valid conclusions on this question for the time being. Several authors, however, have included the musculature characteristics in the diagnosis of hymenolepidid genera, as for instance CZAPLINSKI & VAUCHER (1986).

Excretory system

In hymenolepidids, the excretory system is always simple, with two bilateral excretory canals, a ventral one of greater diameter and a dorsal one of reduced width, the ventral canals presenting transversal anastomoses at the posterior level of the proglottids. Rare exceptions exist, such as the presence of only one pair (instead of the common two pairs) of excretory canals per segment flowing into a posterior excretory pore, in members of the genus *Pseudhymenolepis* of the subfamily Pseudhymenolepidinae (HUNKELER, 1974). An extreme case of five pairs of osmoregulatory canals (= ten osmoregulatory canals

present) has been described in the bird parasite *Hymenofimbria merganseri* Skrjabin, 1914, the only species of the genus *Hymenofimbria* Skrjabin, 1914 (SCHMIDT, 1986). Another case of an unusual excretory system is that of the rodent parasite species *Hymenolepis pearsei* Joyeux et Baer, 1930, in which the ventral excretory canal gives rise to numerous anastomosing ramifications forming a network, whereas the dorsal excretory canal remains normal. HUNKELER (1974) interpreted this last rarity as an adaptation to the long length of the strobila of this species.

At scolex level, differences can be observed depending on the absence or presence of a rostellum. In species lacking a rostellum, a common origin for all four canals at anterior level can be observed. On the contrary, when a rostellum is present, the excretory system seems to be related to it or to the rostellar sac in some species (see, for instance, SCHULTZ, 1939; MAS-COMA & JOURDANE, 1977; LUMSDEN & SPECIAN, 1980; MAS-COMA et al., 1984, 1986 a, b), whereas in other species it shows no communication to them, but each pair of lateral excretory canals has its own common origin or sole anterior connection (see, for instance, DEBLOCK & ROSE, 1964).

Opinions of authors concerning the systematic value of the excretory system among Cyclophyllidea seem, however, to differ markedly. Concerning Catenotaeniata, QUENTIN (1971 a, b) gave systematic value to the nature (structure) of the excretory system at generic level, whereas GENOV & TENORA (1979) sustained the opposite. Recent papers on anoplocephaloidean cestodes also seem to give no systematic importance to the type of excretory system (see BEVERIDGE, 1976; TENORA & MURAI, 1978). But, what must be considered of great interest is the unanimity shown by recent papers concerning the value of the relative location and extent of sexual organs (genital ducts, cirrus pouch, testes, uterus, etc.) with respect to excretory canals in all types of proglottids, from mature to last gravid segments. In both Anoplocephalata and Catenotaeniata, this fact has been considered not only at specific level (see, for instance, RAUSCH, 1976; TENORA & MURAI, 1980), but also at the generic (TENORA & MAS-COMA, 1978; TENORA & MURAI, 1978; TENORA et al., 1980; TENORA, VAUCHER & MURAI, 1981-1982; TENORA, MURAI & VAUCHER, 1984, 1985, 1986).

In hymenolepidids, the consideration of the relative location and extent of sexual organs, especially testes and uterus, with respect to the excretory system furnishes a solid basis for supraspecific differentiation. Thus, the arrangement of the three testes external to the excretory canals in the species *Hymenolepis phalacrocorax* Woodland, 1929, a parasite of cormorants, allowed YAMAGUTI (1959) to erect the genus *Woodlandia* Yamaguti, 1959, whose validity has recently been accepted by SCHMIDT (1986). MAS-COMA (1982) has shown that the extent of the uterus with respect to the excretory canals even allows the understanding of natural evolutionary lines of species, at least among the group of hymenolepidid species lacking a rostellum.

Sexually mature segments

All hymenolepidids present a single set of reproductive organs per segment, genital pores always unilateral and genital ducts passing dorsal to excretory canals. There are however some few rare forms, as for instance the presence of two sets of reproductive organs in each proglottid in the bird parasite genus *Diplogynia* Baer, 1925, the irregularly alternating genital pores in the bird parasite *Neoligorchis alternatus* Johri, 1960, a species with 5-6 testes per proglottid and the only member of the genus (SCHMIDT, 1986), and in the Passeriform parasite species of the genus *Allohymenolepis* Yamaguti, 1956 (included in Pseudhymenolepidinae by SCHMIDT, 1986 despite the absence of hyperapolysis), or the irregularly alternating genital pores in a Swiss form of *Hymenolepis sulcata* (Linstow, 1879) described by FAIVRE & VAUCHER (1978). An extreme case of absence of genital pores, male and female ducts joining together near lateral margin, on the same side throughout strobila, has been described in the bird parasite species *Aporodiorchis occlusus* (Linstow, 1906) Yamaguti, 1959 and accepted by SCHMIDT (1986).

Peculiar genital atria can be found in bird hymenolepidids. Thus, there are species presenting a genital atrium with accessory sacs: A) with one accessory sac in *Hymenofimbria* Skrjabin, 1914, *Sobolevicanthus* Spassky et Spasskaya, 1954, *Phoenicolepis* Jones et Khalil, 1980, *Nadejdolepis* Spassky et Spasskaya, 1954, *Debloria* Spassky, 1975, and *Anatinella* Spassky et Spasskaya, 1954; B) with two accessory sacs in *Bisaccanthes* Spassky et Spasskaya, 1954, *Parabiglandatrium* Gvosdev et Maksimova, 1968, *Parabisaccanthes* Maksimova, 1963, and *Biglandatrium* Spasskaya, 1961 (SCHMIDT, 1986). Moreover, sometimes the accessory sac is armed with spines, as in *Debloria*, *Anatinella*, *Parabisaccanthes* and *Biglandatrium*. Another exception is the very deep genital atrium, lined with spines at its bottom, in *Echinatrium* Spassky et Yurpalova, 1965. An extreme case is the very large, complex, genital atrium, with two or three complete circles of unequal spines lying in its depth and a huge accesory sac found in the dorsal wall of the atrium and lined with many small spines and ten large hooks (this organ, called «gonoscolex» in the original description, can be evaginated and does look quite like a rostellum) in *Gonoscolex paradoxus* Saakova, 1958, the only member of the genus *Gonoscolex* Saakova, 1958 (SCHMIDT, 1986).

Male genital organs: The male genital organs develop in general more or less parallel to the female ones, except in species in which the phenomenon of protandrya is very pronounced (maturation and beginning of degeneration of testes largely before the ovary reaches its maturity), such as for instance in the mammal parasites *Hymenolepis mathevossianae* Akhumjan, 1946 (EGOROVA & NADTOCHY, 1975; RYZHIKOV et al., 1978), *Hymenolepis khalili* Hilmy, 1936, *Hymenolepis uranomidis* Hunkeler, 1972 (HUNKELER, 1974) or *H. cerberensis* Mas-Coma,

Fons, Galán-Puchades et Valero, 1986 (MAS-COMA *et al.*, 1986 b).

Hymenolepididae are characterized by the tendency to few testes. Most species have 3 testes, but species with 1 to up to 12 testes may be found. Testes are undoubtedly one of the structures of greater systematic usefulness among hymenolepidoids. Their number and distribution have traditionally been the basis for all dismemberment attempts at generic level. Nevertheless, the results of studies on testicular intraspecific variability (FUHRMANN, 1932; PALAIS, 1933; VOGE, 1952 a, b; SCHILLER, 1952; ZARNOWSKI, 1955; JOHRI, 1959; RYBYCKA, 1959; SPASSKY, 1959, 1962; VAUCHER, 1971; COLLINS, 1972; CZAPLINSKI & VAUCHER, 1986; etc.) introduce a logical doubt about their systematic value at supraspecific level. Consequently, synonymizations of a great number of genera have sometimes been made (see, for instance, JOYEUX & BAER, 1961: 552).

An extreme case of synonymyzation was that made by YAMAGUTI (1959), who established the synonymy of *Hymenolepis horrida* (Linstow, 1901) and *Oligorchis nonarmatus* Neiland, 1952, based on the suppositions of SPASSKY (1954 b). SPASSKY (loc. cit.) thought that, in hymenolepidids, adaptation to an unusual host can imply an increase of the number of testes. At any rate, MAS-COMA, TENORA & GALLEGO (1980) have already referred to the implausibility of this synonymization, because it disregards other specific characters, such as the armature of the cirrus (spinose in *Hymenolepis horrida*; unarmed in *Oligorchis nonarmatus*) and receptaculum seminis (present in *Hymenolepis horrida*; absent in *Oligorchis nonarmatus*). Moreover, the acceptance of this mentioned synonymy would depreciate the conclusions of VOGE (1952 a, b) on intraspecific variability, including the testicular one. VOGE (loc. cit.) demonstrated that the intraspecific variability, including the frequency of some types of structural abnormalities, of a species must also be considered a typical, specific characteristic of the species in question. VOGE (loc. cit.) showed that variability, incidence in testes position and number, types of abnormalities and other characters did not differ between naturally and experimentally infested specimens and that this constancy was independent of the host species. According to VOGE (1952 a), there are 2-4 testes, average 3 and only in 0,03 % of segments 5 testes, in *Hymenolepis horrida*. In *Oligorchis nonarmatus* there are, after NEILAND (1952), 4-6 testes, average 5 and only one proglottid with 3 testes.

The suppositions of SPASSKY (1954 b) about the increase in testes number implied by the adaptation to an unusual host were also discussed by DEBLOCK & ROSE (1964). These French authors found two armed hymenolepidid forms in the same species of Charadriiform bird (*Charadrius laticula* L.) in France, which they described as subspecies: *Oligorchis paucitesticulatus paucitesticulatus* Deblock et Rosé, 1964 and *Oligorchis paucitesticulatus hymenolepidoideus* Deblock et Rosé, 1964. The two forms differ almost ex-

clusively in the number of testes per segment: 5-8 testes (only very few proglottids with 1, 4, 9, 10 or 11 testes) in *Oligorchis paucitesticulatus paucitesticulatus*; 2-4 testes (with a clear majority with 3 testes and only few with 1 or 5 testes) in *Oligorchis paucitesticulatus hymenolepidoideus*. DEBLOCK & ROSE (1964) provisionally justified their description as subspecies by the absence of forms having a predominant number of 4-5 testes between both groups of strobilae. As they duly pointed out in their paper, these findings clearly hinder the hypothesis of SPASSKY (1954 b). Later, SPASSKY (1975) synonymized both subspecies. We are not going to discuss here whether we agree or not with the systematic classification of these two forms done by DEBLOCK & ROSE (1964). It is evident, however, that if we accept the conclusions also reached by VOGE (1952 a, b) for hymenolepidids from Avian hosts, we shall refer undoubtedly to them as different species and not only as subspecies. The question that rises immediately is at what point can we distinguis between variability and abnormality in this armed hymenolepidid group from birds.

Intraspecific variability in the number of testes per segment should not be taken merely as an indicator of static morphological variability through time, but also as a remainder of a character in evolution to simpler forms. As SPASSKY (1962) pointed out himself, a high number of testes represents an archaic character. The presence of several *vasa efferentia* per testis, perfectly illustrated in the case of *Hymenolepis horrida* by VOGE (1952 a: plate 7), suggests a testicular reduction as a secondary condition derived originally from pluritesticular forms (BAER, 1973). Consequently, if we accept *a priori* one line derived from archaic multitesticular forms of Cestodes, older forms would be the ones having more testes, while forms of more recent origin would show fewer testes. Therefore, the fewer testes they have, the more recent their appearance. According to SCHMIDT (1986), hymenolepidid genera with more than 3 testes per proglottid are: *Pentorchis* Meggitt, 1927 (5 testes, in carnivores: *Ursus*), *Paraoligorchis* Wason et Johnson, 1977 (4-7 testes, in rodents), *Chitinolepis* Baylis, 1926 (9-12 testes, in rodents), *Hymenandrya* Smith, 1954 (7-15 testes, in rodents), *Pseudoligorchis* Johri, 1934 (8-12 testes, in bats), *Oligorchis* Fuhrmann, 1906 (3-7 testes, in birds, rodents, insectivores, bats), and *Neoligorchis* Johri, 1960 (5-6 testes, in birds). *Pseudanoplocephala* Baylis, 1927 (around 20 testes, in pigs) (included in Anoplocephalidae Anoplocephalinae by SCHMIDT, 1986) must be added to this list according to SPASSKY (1980, 1981). *Fuhrmanacanthus* Spassky, 1966 (more than 10 testes, in birds) (included in Dilepididae Dilepidinae by SCHMIDT, 1986), *Polytestilepis* Oschmarin, 1960 (in birds) (not mentioned by SCHMIDT, 1986) and *Diploposthe* Jacobi, 1896 (3-17 testes, in birds) (included in Acoleidae by SCHMIDT, 1986) must be added to this list according to CZAPLINSKI & VAUCHER (1986).

Regarding spatial distribution of testes in sexually mature segments, among tritesticular hymenolepidids

there is a marked tendency to a more or less triangular or linear arrangement, with one poral and two aporal testes. There are, however, several exceptions to this general pattern found in bird parasites, such as the presence of all the 3 aporal to ovary testes in *Amphipetrovia* Spassky et Spasskaya, 1954 (a similar pattern is found in the diorchid genus *Gopalaia* Dixit, Capoor et Rengaragu, 1980 including one species in bats) or the 3 aporal to ovary testes in *Drepanidotaenia* Railliet, 1892. The three testes located porally are also found in the mammal parasite species *Gvosdevilepis fragmentata*. A curious case is that of the bird parasite species *Oshmarinolepis microcephala* (Rudolphi, 1819) Spassky et Spasskaya, 1954, the only species of the genus in which the poral and most aporal testes are located outside the osmoregulatory canals. Intermediate forms with one poral, one median and one aporal testes can also be found, as in the mammal species *Hymenolepis soricis* Baer, 1925 and *Hymenolepis skrjabiniana* Akhumjan, 1947. As can be expected, these arrangements of testes in the different species show, in general and more or less pronounced, the common variability of this character proper to all hymenolepidids (see, for instance, VOGE, 1952 a, b, and others).

Types of distributional testes patterns have been accepted in hymenolepidids as one of the basic criteria for classification at generic level (SKRJABIN & MATHEVOSSIAN, 1942 c, 1948; SPASSKY, 1954 a; SPASSKY & SPASSKAYA, 1954; YAMAGUTI, 1959; SPASSKY, 1963; etc.). This criterion has often been questioned and the criticism appears to be justified (see discussion in RYBICKA, 1959). ZARNOWSKI (1955), however, pointed out that some types of testes patterns have a certain stability.

Concerning the shape of the testes, little taxonomic significance has usually been given to this characteristic, owing to the fact that in hymenolepidids testes shape is usually from regularly spherical or ovoid to scarcely lobated, without forgetting the effects of the fixation method used. There is, however, the species parasitising grebes *Pararetinometra lateralacantha* Stock et Holmes, 1982, the only species of the genus, in which the 3 testes are markedly lobated (STOCK & HOLMES, 1982).

An analysis of the general literature on hymenolepidids allows us to conclude that the presence or absence of internal and external seminal vesicles are of importance only at species level. Nevertheless, we think that in view of the almost monotonous presence of both seminal vesicles (see BAER, 1973: 149), more care should be given to those species lacking one or both of them. CZAPLINSKI & VAUCHER (1986), when discussing the systematic location of the multitesticular genus *Fuhrmanacanthus*, considered the presence of internal and external seminal vesicles very important to accept its inclusion in the family Hymenolepididae. The absence of the external seminal vesicle has been described in the diorchid monospecific bird parasite genus *Jonesius* Yamaguti, 1959. The absence of both vesicles has been mentioned, for instance, in the bird parasites *Cladogynia* Baer, 1937 (placed in Dilepididae by some authors) and *Dilepidoides* Spassky

et Spasskaya, 1954 (SCHMIDT, 1986), as well as in the mammal parasite species *Hymenolepis palmarum* Johri, 1956 (JOHRI, 1956). Worth mentioning is the rodent hymenolepidid species *Hymenolepis uranomidis* Hunkeler, 1972 in which evident glandular cells are found around the external seminal vesicle (HUNKELER, 1974).

Regarding the systematic value of the cirrus being armed with spines or unarmed, RYBICKA (1959: 513) wrote: «it seems that this character has no particular phylogenetic importance, while in practice, in the course of species classification it may be considered as an important taxonomical feature». It is evidently an organ which exhibits considerable stability of structure within a given species. And this peculiarity of the cirrus leads MAS-COMA, TENORA & GALLEGO (1980) to suggest the convenience of reviewing the North-American material of *Hymenolepis horrida* studied by SCHILLER (1952), in which this author found forms with spinose cirrus and other forms with unarmed one. JOHRI (1956: 275) also discussed the paper of SCHILLER (loc. cit.) writing the following about the specimens analysed by this North-American author: «some of these originally belong to totally different species». The presence of a spined cirrus has also been demonstrated to be a useful taxonomic element in anoplocephalids, as in the lagomorph parasite genus *Leporidotaenia* Genov, Murai, Georgiev et Harris, 1990 (GENOV *et al.*, 1990). In the majority of hymenolepidids presenting an armed cirrus, the spines are distributed in the distal part of the cirrus, but species are known in which only its proximal part is covered with small spines, as in the bird hymenolepidid *Hymenolepis cervotestis* Ahern et Schmidt, 1976 (AHERN & SCHMIDT, 1976). In the shrew parasite species *Hymenolepis virilis* Voge, 1955, the cirrus is of interest because it is very large in relation to the size of the proglottid and it is armed with relatively few, long spines (VOGE, 1955 a).

The presence of a cirrus with a long stylet has also been described in bird hymenolepidids, as in *Sobolevicanthus* Spassky et Spasskaya, 1954 (SCHMIDT, 1986). A cirrus pouch containing a long narrow stylet is known in *Pararetinometra lateralacantha* Stock et Holmes, 1982 (STOCK & HOLMES, 1982). Usually the stylet is long, even becoming coiled within the cirrus pouch, whereas there are species in which this stylet appears short. Thus, the length of the cirrus stylet appears to be of specific importance.

The cirrus pouch is an organ to which an important systematic value usually is given, above all to its size and extent regarding the poral excretory canals. In hymenolepidids, as well as in anoplocephalids, the dimensions of the cirrus pouch have often been used for differentiation at least at species level. However, although the size of the cirrus pouch used to be an important characteristic of a species, VAUCHER (1971) observed large intraspecific variabilities in its dimensions in shrew cestodes. Concerning its relative extent, in hymenolepidids from birds, there are species in which the cirrus pouch appears enormous, exceeding the midline of the segment

[as in *Retinometra deblocki* (Schmidt et Neiland, 1968) or *Armadoskrjabinia medici* (Stossich, 1890)] and other species in which it even surpasses the aporal excretory canals [as in *Echinocotyle longirostris* (Rudolphi, 1819) and *Debloria capetownensis* (Deblock et Rosé, 1962)] (MAYHEW, 1925; DEBLOCK, 1964; DEBLOCK & ROSE, 1962; SCHMIDT, 1986). *Hymenolepis stefanskii* (Zarnowski, 1954) is an example of mammal hymenolepidid in which the cirrus pouch is also very large, even surpassing the aporal excretory canals (VAUCHER, 1971).

Female genital organs: The ovary generally has a tendency to be from plurilobed to compact and oval, usually more or less median in segment. It shows, in most species, a tendency to be slightly porally displaced. In general the ovary extends through the anterior half part of the segment, although species exist in which it extends throughout the whole length of the proglottid, as for instance in several species parasitising insectivores Soricidae Soricinae.

The vitelline gland is often irregular, somewhat lobed, or compact and oval, and is situated directly behind the ovary in those species in which the female gonad is anterior, and contiguous to it when the gonad occupies the whole length of the segment.

The vagina opens posterior or ventral to the orifice of the male duct. In some species the female duct enlarges and constitutes a distal, more or less pronounced receptaculum seminis, while in other species, such as for instance *Oligorchis nonarmatus*, *Hymenolepis palmarum*, *Hymenolepis globosoides* or *Hymenolepis anthocephalus*, a differentiation of this structure has not been observed (see respectively NEILAND, 1952; JOHRI, 1956; VAUCHER, 1971; VAN GUNDY, 1935).

From the systematic point of view, it should be stressed, as already pointed out by RYBICKA (1959), that the general structure of the female reproductive organs (ovary, vitelline gland) is usually stable within a species and that they also show a constant position. VAUCHER (1971: 80-81) remarked, however, that sometimes a variability in the ventral/dorsal situation of the vitelline gland with respect to the ovary can be found. The variability of the shape of ovary and vitelline gland within a single strobila is connected with the degree of development of the respective segments. In spite of the constancy of the characteristics from ovary and vitelline gland, these female organs have never been the basis for differentiation at supraspecific level (with the sole exception of the presence of a persistent reticular ovary in the type and sole species of the brd parasite genus *Avocettolepis* Spassky et Kornyushin, 1971 —see SPASSKY & KORNYUSHIN, 1971). Only their situation with respect to other organs (testes; beginning of uterus; etc.) seems to have been considered. The importance which has been given to the relative position of testes and ovary has been already mentioned. Concerning the vitellarium, an interesting study of the large intraspecific variability of the shape of this organ along a strobila in the bird parasite species *Sobolevicanthus stolli*

(Brock, 1941) has been carried out by CZAPLINSKI & AESCHLIMANN, 1984). The aporal location of the vitellarium with respect to the ovary is in the base of the erection of the bird parasite genus *Skrjabinoparaxis* Krotov, 1949 (see SCHMIDT, 1986), whereas a similar location in shrew hymenolepidid species such as *Hymenolepis schaldybini* (Spassky, 1947), *Hymenolepis singularis* (Spassky, 1947), *Hymenolepis hamanni* (Mrazek, 1891) and *Hymenolepis integra* (Hamann 1891) has received no special taxonomic use (VAUCHER, 1971).

According to the literature, the systematic value of the receptaculum seminis seems to be only at species level. Concerning the female genital ducts, they do not seem to have been taken into consideration for supraspecific classification purposes among hymenolepidids in general. RAUSCH (1976) includes, however, the situation of the opening of the vagina with respect to the orifice of the male duct as one of the generic features in Anplocephalidae. Very recently, SCHMIDT & DAILEY (1992) have given enough importance to the situation of the vagina anterior to the cirrus sac to allow a generic differentiation for the bird hymenolepidid genus *Amazilolepis* Schmidt et Dailey, 1992. At any rate, the vagina sometimes presents peculiarities which have been demonstrated to be useful from the taxonomic point of view, Thus, the following examples can be listed (see SCHMIDT, 1986): a vagina forming an eversible, spinose terminal organ followed by a funnel-shaped portion is found in the shrew parasite species *Lockerrauschia intricata* (Locker et Rausch, 1952) Yamaguti, 1959, sole species of the genus (LOCKER & RAUSCH, 1952); a funnel-like copulatory part of the vagina surrounded by thin circular muscles is found in the bird hymenolepidid *Retinometra serrata* (Fuhrmann, 1906) (CZAPLINSKI & VAUCHER, 1981 a); a vagina with a distal, sclerotized clamp is found in the bird parasite monospecific genus *Arhynchotaeniella* Schmidt, 1986 (=*Arhynchotaenia* Saakova, 1958, preoccupied); a powerful vaginal sphincter is present in the bird parasite genus *Debloria* Spassky, 1975.

Posterior segments

The morphological evolution of the uterus constitutes a character with systematic value of general acceptance at levels of high intermediate taxa (families, subfamilies, genera) among Cyclophyllidea, specially in Anoplocephaloidea (see SPASSKY, 1950 b, 1951; SCHMIDT, 1970; TENORA, 1976; RAUSCH, 1976; TENORA, VAUCHER & MURAI, 1981-1982; etc.), but also in Hymenolepidoidea (see JOYEUX & BAER, 1961; SCHMIDT, 1970). As a rule the only consideration that can be noted is that typical hymenolepidids (subfamily Hymenolepidinae) show a final sacciform uterus at the level of gravid segments. SCHMIDT (1986) has contributed to this fact when arranging all the species presenting a final reticulate uterus in the subfamily Fimbriariinae and those with a uterus breaking up into egg capsules in the subfamily

Pseudhymenolepidinae. There are however several variations within this typical final uterine morphology and, above all, different types of origin and posterior development of uterine structure until the ulterior saccular form is reached. The following examples duly illustrate this point.

Concerning the origin of the uterus, different patterns can be distinguished, for instance, in mammal hymenolepidids: uterus appearing unawares, directly from origin as irregularly lobed median sac [in *Hymenolepis infirma* (Zarnowski, 1955), *H. globosa* Baer, 1931, *H. kenki* Locker et Rausch, 1952, *Gvosdevilepis fragmentata* (Gvosdev, 1948)] (Mas-Coma, unpublished data; Gvosdev, 1948; Gvosdev *et al.*, 1970]; uterus appearing unawares, directly with the aspect of elongated longitudinal sac from its origin (*Mathevolepis petrotschenkoi* Spassky, 1948) (Spassky, 1948); origin of the uterus as a transverse lobed double sac (in species of rather long segments) or tube-sac (in species of short and wide segments) [*H. globosoides* (Soltys, 1954), *H. fodientis* Vaucher, 1971] (Mas-Coma, unpublished data); uterus appearing as an inverse U or horseshoe-shaped [in *Hymenolepis scutigera* (Dujardin, 1845)] (Vaucher, 1971); uterus appearing as bilobed (in *Hymenolepis spinulosa* Cholodkowsky, 1906) (Vaucher, 1971).

Concerning the intermediate development of the uterus, the following examples of mammal hymenolepidids clearly demonstrate that there are numerous types of uterus development. A patent reticular evolution before becoming saccate is found in *Hymenandrya thomomyis* Smith, 1954, *Hymenolepis horrida* (Linstow, 1901), *H. neurotrichi* Rausch, 1962 (Mas-Coma, unpublished data), *Hymenolepis pearsei* Joyeux et Baer, 1930 and *Hymenolepis uncinispinosa* Joyeux et Baer, 1930 (Hunkeler, 1974). Worth mentioning here is the high taxonomic importance that has been given to the reticulate development of the uterus in anoplocephalids (see for instance Spassky, 1950 b and Tenora, 1976). In *Hymenolepis cerberensis* a curious appearance and disappearance of trabecules inside the uterus has been described (Mas-Coma *et al.*, 1986 b). In the majority of hymenolepidids, however, the uterine development up to the last sacciform stage has no sign of reticulation and the final enlarged uterine sac completely or almost completely fills gravid segments. In several species, the uterus develops quickly up to the final gravid stage, that is, the uterine maturation takes place in a very scarce number of proglottids (*Hymenandrya thomomyis, Hymenolepis horrida, H. neurotrichi* —Mas-Coma, unpublished data), whereas in other species the uterus develops slowly, over a large number of segments. Thus, in *H. globosoides* and *H. fodientis*, for instance, the uterus extends porally and aporally and enlarges gradually and slowly through a high number of segments up to the final gravid stage (Mas-Coma, unpublished data). Also of interest is whether the uterus surpasses or not the excretory canals bilaterally. Such a characteristic has been demonstrated to be taxonomically useful in anoplocephalids (Tenora,

Vaucher & Murai, 1981-1982; etc.), in catenotaeniids (Tenora *et al.*, 1980) and also in hymenolepidids lacking a rostellum (Mas-Coma, 1982). Species in which the uterus bilaterally surpasses the excretory canals directly after its beginning or during its development (in these cases final uterus also bilaterally surpasses excretory canals) are, among many others, *Hymenolepis diminuta, H. horrida, H. claudevaucheri* Mas-Coma, Fons, Galán-Puchades et Valero, 1984, and *H. cerberensis* Mas-Coma, Fons, Galán-Puchades et Valero, 1986 (Mas-Coma, 1982; Mas-Coma *et al.*, 1984, 1986 b). On the contrary, species like for instance *Hymenolepis biliarius* (Villot, 1877), *H. neurotrichi, H. globosoides, H. fodientis, H. kenki, H. infirma* and *H. banyulsensis* Mas-Coma, Fons, Galán-Puchades et Valero, 1986 present a uterus not bilaterally surpassing the excretory canals during its development (in these cases final uterus does or does not surpass excretory canals bilaterally) (Mas-Coma & Jourdane, 1977; Mas-Coma, 1982; Mas-Coma *et al.*, 1986 a). Also of interest is the more or less pronounced lobated appearance of the development of the uterus. Thus, in *Hymenolepis furcata* (Stieda, 1862) and *Hymenolepis uranomidis* Hunkeler, 1972, the uterus appears as markedly lobated during its development (Vaucher, 1971; Hunkeler, 1974), whereas it appears as only scarcely lobated in *Hymenolepis gilloni* Hunkeler, 1972 (Hunkeler, 1974). In *Hymenolepis schaldybini* (Spassky, 1947) and *Hymenolepis singularis* (Spassky, 1947), the uterus develops as a transversal lobated tube (Vaucher, 1971). In *Hymenolepis pistillum* (Dujardin, 1843), the initial bilobed uterine sac develops as an inverse U or horseshoe (Joyeux & Baer, 1936). Very curious are the species in which the uterus develops till final gravid stage only in free segments precociously detached from strobila in the host's intestine. In *Gvosdevilepis fragmentata*, for instance, the uterus appears as an irregularly lobed median sac that develops slowly in freely, precociously detached groups of segments in the host's intestine, enlarging very scarcely (Gvosdev, 1948; Gvosdev *et al.*, 1970).

Concerning the final stage of the uterus, different morphologies can also be found. A peculiar mammal hymenolepidid is *Hymenandrya thomomyis* Smith, 1954, in which the uterus, in spite of clearly showing its terminal sacciform tendency, does not completely break down and become saccate, but retains some of its previous reticulate nature, restricting distribution of eggs in proglottid (Smith, 1954). The reticulation of the uterus is also known in bird hymenolepidids of the genus *Flamingolepis* Spassky et Spasskaya, 1954 (Schmidt, 1986). As a rule, in hymenolepidids the final saccular uterus usually occupies all or almost all of the inner space of the proglottid. There are, however, species such as the shrew cestode *Hymenolepis multihami* Hunkeler, 1972 in which the final uterus is small, divised in several large lobes, occupying only half of the width of the proglottid (Hunkeler, 1974). On the contrary species such as *H. infirma, H. globosa* or *H. kenki* are found, in which the final sacciform uterus presents thin

walls which distend irregularly up to the external walls of the gravid segment, whose outline can even be deformed due to the growth of a typically very reduced number of some relatively large eggs. There are species like *Hymenolepis hamanni* (Mrazek, 1891) and *Hymenolepis multihami* Hunkeler, 1972, both from shrews, in which the final uterus includes only a few eggs (VAUCHER, 1971; HUNKELER, 1974), whereas there are species with a very large number of eggs in the final gravid segments, such as the well known rodent hymenolepidid *H. diminuta* or the shrew cestodes *Hymenolepis furcata* (Stieda, 1862), *H. spinulosa* Cholodkowsky, 1906, *H. globosoides* and *H. fodientis* (see VAUCHER, 1971). Whether with few or with a large number of eggs, there are species in which the final sacciform uterus surpasses the excretory canals bilaterally (*Hymenolepis diminuta*, *H. horrida*, *H. claudevaucheri* and *H. cerberensis*) and others in which it does not (*H. neurotrichi*, *H. globosoides*, *H. fodientis*, *H. kenki*, *H. infirma* and *H. banyulsensis*) (MAS-COMA, 1982; MAS-COMA *et al.*, 1984, 1986 a, b; MAS-COMA, unpublished data). As already stressed, this last characteristic of the uterus surpassing/non-surpassing excretory canals bilaterally has received a large taxonomic usefulness in recent years, in hymenolepidids as well as in other cyclophyllidean cestode groups.

The final stage of the uterus sometimes shows given morphological types, always within the general saccular pattern. Thus, a gravid uterus forming two sacs, which may be joined by a narrow isthmus, is found in the bird parasite genera *Armadoskrjabinia* Spassky et Spasskaya, 1954 and *Passerilepis* Spassky et Spasskaya, 1954. A similar uterus terminal shape made up of two non-lobated sacs united by a thin canal is also present in mammal hymenolepidids, such as in the shrew cestode *Hymenolepis khalili* Hilmy, 1936 (HUNKELER, 1974). Another peculiar terminal uterus shape is known in shrew hymenolepidids, such as in *Hymenolepis integra* (Hamann 1891), *H. omissa* Baer et Joyeux, 1943, *H. bifurca* (Hamann 1891) and *Triodontolepis rysavyi* Prokopic, 1972, in which the uterus develops a very thick, capsule-like wall (VAUCHER, 1971; PROKOPIC, 1972). VOGE (1955 b) and JOURDANE (1971) described the uterus development of the shrew hymenolepidids *Hymenolepis pulchra* Voge, 1955 and *H. alpestris* Baer, 1931, respectively, which also gives rise to an oval capsule-like sac not surpassing the excretory canals billaterally. DAVIS & VOGE (1957) described in detail the uterus of the shrew hymenolepidid *Hymenolepis macyi* Locker et Rausch, 1952, in which an abrupt development gives rise to a capsule-like uterus, the surface of the uterine wall presenting numerous encircling tubules and cellular processes which give the uterine surface a hairy appearance. In *Hymenolepis hamanni* (Mrazek, 1891), another shrew cestode, JOYEUX & BAER (1952) described a special terminal uterus development by which the uterus wall undergoes a pronounced thickening giving rise to a regular elipsoidal sac which detaches from the proglottid chain thus becoming free in the lumen of the host's intestine, whereas the cortical proglottid

parenchyma remains as a sort of empty frame which afterwards withers. Also characteristic are the cases of the shrew cestode species *Hymenolepis tiara* (Dujardin, 1845) (MAS-COMA *et al.*, 1986 a), *Hymenolepis nagatyi* Hilmy, 1936 and *Hymenolepis vaucheri* Hunkeler, 1972 (HUNKELER, 1974) and *H. banyulsensis* Mas-Coma, Fons, Galán-Puchades et Valero, 1986 (MAS-COMA *et al.*, 1986 a), in which eggs are expelled even before the detachment of the gravid segment, so that the uterus of the last strobilar proglottids either appears empty or including only a very few eggs. Even more curious is the uterine morphology described in *Mathevolepis petrotschenkoi*, a shrew hymenolepidid in which the final sacciform uterus presents a uterine canal in the posterior extremity of the segment (SPASSKY, 1948).

There are also species in which the whole uterus development appears to be very special, as in the following two shrew hymenolepidids. In *Hymenolepis tripartita* (Zarnowski, 1955) the uterus first appears as an inverse U or an irregular ring, afterwards becomes sacciform, and then the gravid segments become oval and detach individually from the strobila to continue isolated development in the host's intestinal lumen, the terminal uterus becoming a thick-walled capsule (VAUCHER, 1971). Even more special is the case of *Hymenolepis diaphana* Cholodkowsky, 1906, in which the uterus first appears as an inverse U, to quickly become sacciform, filling the whole segment; then the external uterus wall undergoes a thickening, the uterine interproglottidean walls afterwards disappear, and thus finally the eggs of 2-18 segments are reunited in the common multisegmental muscular cover (VAUCHER, 1971).

These different variations, uterine types of development and morphological patterns allow us to distinguish the existence of different groups of species and even evolutionary lines among these groups. Such applications have already been carried out in anoplocephalids (SPASSKY, 1950 b; TENORA, 1976; TENORA, VAUCHER & MURAI, 1981-1982) and catenotaeniids (TENORA *et al.*, 1980) some time ago and also more recently in hymenolepidis (MAS-COMA, 1982).

But in posterior proglottids not only the uterus development is there. As with the appearance of sexual structures in premature segments, the progressive degeneration and disappearance of the different sexual structures parallel to the uterus development have been shown to follow at least specific patterns. Thus, a detailed description of these degeneration and disappearance processes along the strobila becomes of great classificatory interest for the differentiation of species. In the shrew species *Hymenolepis claudevaucheri*, *H. banyulsensis* and *H. cerberensis* different orders of degeneration and disappearance of the sexual structures along the posterior strobilar proglottids were described by MAS-COMA *et al.* (1984, 1986 a, b).

Eggs

The systematic interest of eggs in Cestodes has long

been accepted and applied at levels of higher taxa (orders). Based on his own studies, OGREN (1957) established seven general types of eggs among Cyclophyllidea, thus opening the possibility of their application at intermediate taxonomic levels to the subdivision of this order. Nevertheless RYBICKA (1966) has called in question the suggestions of OGREN (loc. cit.) about the phylogenetical significance of the structure of eggs, making reference to the studies of JARECKA (1961). The work of this authoress indicates that the variety of forms in the embryonic covers of Cestodes could be the result more of morphological adaptations to the environment and nutrition of intermediate hosts than to the exteriorization of phylogenetical relationships. At any rate, it should be noted that the studies of JARECKA (loc. cit.) concern hymenolepidids exclusively of aquatic life cycle (eggs disseminated by the definitive host in water; intermediate hosts being aquatic invertebrates) and that a relationship between egg morphology and the nature of intermediate hosts was observed in them, thus concluding in the consequent marked specificity. But if it can be accepted that this adaptation can affect on the external aspect of the egg (size, shape and ornamentation used for the atraction of the specific intermediate host), it is not easy to understand how it can influence other structures (nature of the embryophore, oncospheral hooks, etc.).

Moreover, this is not the case with terrestrial hymenolepidids, in which there does not seem to be any close relationship between egg morphology and nature of intermediate hosts, that is, in which a scarce specificity at larval level can be detected; the well known case of *Hymenolepis diminuta* is a good illustrative example in this sense. In hymenolepidids of terrestrial life cycle, some remarkable biogeographical variations of intermediate hosts in the different species have been observed. Eggs of the same species adapt to very distinct invertebrates, depending on the possibilities offered by the place, as evidently suggest, for instance, several papers about hymenolepidids from shrews as those of VAUCHER (1971), JOURDANE (1975) and GABRION (1977). Consequently it could be presupposed that in hymenolepidids of terrestrial life cycle using terrestrial intermediate hosts, eggs would better reflect their affinities and origin for not having to adapt to one or another intermediate hosts according to physiology, geography, ethology and ecology.

FREEMAN (1973) once again reviewed the question of the systematic significance of eggs and referred to the papers of OGREN (1968) and STUNKARD (1962). OGREN (1968) wrote: «Thus, it is clear that oncosphere morphogenesis results from a developmental system programmed to produce an invasive oncosphere and a few stem germinative cells capable of multiplying to provide embryonic mesenchyme of the early cysticercoid [metacestode].» STUNKARD (1962) wrote: «Organs formed during the course of the life history of the individual are related to stages in the life cycle of the species and probably were functional in progenitors, so the life cycle portrays a succesion of forms adapted to the life of the animal

at corresponding previous stages.» The above, added to a great number of other related considerations, lets FREEMAN (1973) conclude that: «The oncosphere, and structures associated with it, apparently are among the most conservative cestode features. Next are those associated with development of the metacestode.»

Unfortunately, the detailed morphology and size of the different egg envelopes and structures are often not given or figured in published descriptions of hymenolepidid species. And, if given, the descriptions of eggs usually concern the preserved material where, if visible, the oncosphere and the shape of egg membranes inevitably appear deformed, mainly by dehydration, sometimes also, but less often, by fixation, in the eggs crowded in the uterus. Moreover, in such a situation, the descriptions could concern immature eggs, that is, eggs without well-developed membranes. There is even the problem of confusion, so that in eggs measured directly in the uterus of mounted specimens, the different structures (external egg shell, embryophore, oncosphere) are usually confounded and thus it becomes impossible to know exactly what the authors were measuring in reality. Papers like those by JARECKA (1961), JOURDANE (1971), MAS-COMA & JOURDANE (1977) and MAS-COMA *et el.* (1984, 1986 a, b) have demonstrated the importance of the microscopic study of eggs, isolated from the uterus and the gravid proglottid, without passing through the dehydration process and being mounted in non-permanent preparations. That means that despite the large number of hymenolepidid species known, the eggs of only a relatively small number of species have so far been appropriately studied and described following such a method. At any rate, that is enough to know that several different morphological types of egg outer shells, embryophores and oncospheral hooks are present among hymenolepidids.

Concerning the external egg shell, the following main variations may be noted concerning thickness, shape, size and external ornamentation.

Concerning thickness, the outer shell of the majority of hymenolepidids is a transparent, fine, outlined film which is crushed in the eggs crowded in the uterus, but when under natural conditions it assumes a definite shape and size characteristic for the particular species (JARECKA, 1961). The outer shell is a very thin membrane, which is even invisible under low magnification in the bird hymenolepidid *Hymenolepis furcifera* (Krabbe, 1869) (JARECKA, 1961). It is also thin, but a little more consistent, in the bird parasite species *Hymenolepis compressa* (Linton, 1892) and *H. spiralibursata* Czaplinski, 1956, as well as in the eggs of the shrew hymenolepidid species *H. fodientis* Vaucher, 1971, *H. diaphana* Cholodkowski, 1906, *H. furcata* (Stieda, 1862), *H. schaldybini* (Spassky, 1947), *H. stefanskii* (Zarnowski, 1954), *H. biliarius* (Villot, 1877), *H. claudevaucheri* Mas-Coma, Fons, Galán-Puchades et Valero, 1984, *H. banyulsensis* Mas-Coma, Fons, Galán-Puchades et Valero, 1986 and *H. cerberensis* Mas-Coma, Fons, Galán-Puchades et Valero, 1986 (JOURDANE, 1971; MAS-COMA & JOURDANE, 1977; MAS-

COMA *et al.*, 1984, 1986 a, b). Among a subsequent category of eggs presenting a slightly thicker outer shell, the bird parasites *H. megalops* (Creplin, 1829) and *H. sacciperium* Mayhew, 1925, as well as the rodent parasite *H. diminuta*, can be included (JARECKA, 1961; OGREN, 1957; etc.). The outer envelope of the bat parasites *Vampirolepis brevihamata* Sawada, 1988 and *H. scotophili* Sawada et Harada, 1988 is a little thicker (SAWADA, 1988; SAWADA & HARADA, 1988). An extreme category of eggs presenting a very thick outer shell is found among bat hymenolepidids, such as *Hymenolepis temminki* Vaucher, 1986, *H. dasipteri* Vaucher, 1985 and *H. mazanensis* Vaucher, 1986 (VAUCHER, 1986 a, b), *Vampirolepis rikuchuensis* Sawada, 1987, *V. kaguyae* Sawada, 1987, *V. ikezakii* Sawada, 1988, *V. toohokuensis* Sawada, 1988, *V. urawaensis* Sawada, 1989 (SAWADA, 1987, 1988, 1989), and also in the bird hymenolepidids included in the genus *Schmelzia* Yamaguti, 1959 (SCHMIDT, 1986).

Concerning shape, the variations are not numerous, but include very rare extreme forms. The outer egg shell is spherical in the bird hymenolepidids *Hymenolepis compressa* and *H. spiralibursata* (Bloch, 1782) (JARECKA, 1961), as well as in the shrew parasite *Hymenolepis stefanskii* (JOURDANE, 1971), the rodent parasite species *H. diminuta* (OGREN, 1957; etc.) or the bat hymenolepidids *Vampirolepis kaguyae* Sawada, 1987 and *Hymenolepis rhinopomae* Sawada et Mohammad, 1989 (SAWADA, 1987; SAWADA & MOHAMMAD 1989). The external egg shell is oval, more or less elongate according to species, in the bird parasites *Diorchis stefanskii* Czaplinski, 1956, *D. parvogenitalis* Skrjabin et Mathevossian,1945 and *Hymenolepis aequabilis* (Rudolphi, 1810) (JARECKA, 1961), as well as in the mammal hymenolepidids *Hymenolepis fodientis*, *H. magnirostellata* Baer, 1931, *H. diaphana*, *H. furcata* and *H. schaldybini* (JOURDANE, 1971; MAS-COMA, unpublished data), *H. biliarius* (MAS-COMA & JOURDANE, 1977), *H. claudevaucheri*, *H. banyulsensis* and *H. cerberensis* (MAS-COMA *et al.*, 1984, 1986 a, b), *H. olsoni* Neiland et Senger, 1952 (NEILAND & SENGER, 1952), *H. sulcata* (MAS-COMA, unpublished data) or *Vampirolepis rikuchuensis* Sawada, 1987, *V. kaguyae* Sawada, 1987, *V. ikezakii* Sawada, 1988, *V. toohokuensis* Sawada, 1988, *V. urawaensis* Sawada, 1989 (SAWADA, 1987, 1988, 1989), as in the well-known species *H. nana* (von Siebold, 1852) from Man and *H. fraterna* (Stiles, 1906) from rodents. MAS-COMA (1982) observed that the external shell of eggs from all mammal hymenolepidids lacking a rostellum, in which eggs are known, is thin and always more or less oval, but never spherical. In the mammal hymenolepidid *H. oregonensis* Neiland et Senger, 1952, the outer egg shell is markedly elongate, with the ends separated from the middle part by slight constrictions (NEILAND & SENGER, 1952).

Very rare shapes can also be found. The eggs of *Diorchis nyrocae* Yamaguti, 1935, *D. ransomi* Schultz, 1940 and *D. inflata* (Rudolphi, 1819) are filiform-shaped (JARECKA, 1961). Those of *Diorchis* sp. *sensu* Jarecka, 1961 are ramified (JARECKA, 1961). Finally, the outer egg

shells of some species are glued together, thus forming permanent packet-like connections of eggs which vary in shape. The packet of *Hymenolepis abortiva* (Linstow, 1904) eggs is horseshoe-shaped and the external rectangular egg shells are glued at their edges (JARECKA, 1961). In *Aploparaksis furcigera* (Rudolphi, 1819) the eggs are joined by a common membrane in irregular little lumps, the common membrane probably being not an external egg shell but an additional membrane of the packet which is also glued together (JARECKA, 1961).

Although in the majority of hymenolepidid species the outer surface of the external egg shell is smooth, there are species in which an ornamentation of the egg surface has been described, as in the rodent parasite species *Hymenolepis diminuta* (VOGE, 1952 a) and *H. uranomidis* Hunkeler, 1972 (HUNKELER, 1974) and the bat hymenolepidids *Hymenolepis temminki* Vaucher, 1986, *H. dasipteri* Vaucher, 1985 and *H. mazanensis* Vaucher, 1986 (VAUCHER, 1986 a, b). The outer egg shell is ornated with numerous bumps, in the species *Hymenolepis petteri* Quentin, 1964 from African rodents (QUENTIN, 1964), for which SPASSKY (1973) proposed the genus *Lophurolepis* Skassky, 1973.

Whereas egg shape appears to be characteristic to species, there is an intraspecific variability concerning egg size. However, this variability appears to be restricted to a given specific rank whose limits are within a narrow range when eggs are measured appropriately (that is, separately under natural conditions and not in uterus after dehydration) (see for instance MAS-COMA & JOURDANE, 1977 and MAS-COMA *et al.*, 1984, 1986 a, b). Among hymenolepidids, the egg size is usually under 100 μm. Worth mentioning is the relatively large size of the eggs in several small hymenolepidids which are characterized by presenting only a small number or even a few eggs in the terminal uterus, as for instance in the shrew parasite species *Hymenolepis schaldybini* (Spassky, 1947), *H. stefanskii* (Zarnowski, 1954), *H. infirma* (Zarnowski, 1955) or *H. magnirostellata* Baer, 1931 (VAUCHER, 1971; JOURDANE, 1971).

The embryophore, or inner egg shell enveloping the oncosphere, also presents different morphological patterns among hymenolepidids. First, a large variation in relative size of the embryophore is found. Thus, there are shrew hymenolepidids in which the embryophore appears to be very small in relation to the size of the outer egg shell, such as the shrew parasites *Hymenolepis alpestris* Baer, 1971, *H. stefanskii* and *H. schaldybini*, whereas in *H. fodientis*, *H. diaphana*, *H. furcata* (JOURDANE, 1971), *H. claudevaucheri*, *H. cerberensis* (MAS-COMA *et al.*, 1984, 1986 b) or the bat hymenolepidids *Vampirolepis rikuchuensis* Sawada, 1987, *V. kaguyae* Sawada, 1987 and *V. brevihamata* Sawada, 1988 (SAWADA, 1987, 1988), the embryophore occupies the greatest part of the internal volumetric space of the egg. There are also intermediate cases such as in *H. banyulsensis* (MAS-COMA *et al.*, 1986 a) or *Vampirolepis iraqensis* Sawada et Molan, 1988 (SAWADA & MOLAN, 1988).

Different morphological types of embryophores can be distinguished. Sometimes the embryophore is spherical or spheroidal, as in the mammal parasites *Hymenolepis furcata* (Stieda, 1862), *H. stefanskii* (Jourdane, 1971), *H. biliarius* (Mas-Coma & Jourdane, 1971) and *H. scotophili* (Sawada & Harada, 1988). A pentagonal tendency can be laterally observed in the embryophore of given species, as in *Hymenolepis diminuta*. A similar asymmetric tendency is observed in *H. banyulsensis* (Mas-Coma *et al.*, 1986 a). In other cases it is clearly oval and more or less elongate according to species, as in *H. fodientis*, *H. schaldybini* (Jourdane, 1971) and *Vampirolepis iraqensis* (Sawada & Molan, 1988). In *Hymenolepis olsoni* Neiland et Senger, 1952, the embryophore is lemon-shaped (Neiland & Senger, 1952).

Worth noting is the presence of polar protuberances in the embryophores of many species. These protuberances are very small in several species, as in *H. diaphana* and *H. schaldybini* (Jourdane, 1971). In *H. magnirostellata* the polar protuberances are well-developed and thick, thus giving to the embryophore a markedly elongate lemon shape, with the ends separated from the middle part by slight constrictions (Jourdane, 1971). In many bird parasite species the embryophore shows two polar, more or less long, progressively thin protuberances, as in *H. spiralibursata*, *H. compressa*, *H. vistulae* and *H. paracompressa* (Jarecka, 1961). In *Hymenolepis aequabilis* it is spindle-shaped, with the ends twisted in opposite directions (Jarecka, 1961). Similarly, in given mammal hymenolepidids lacking a rostellum, the embryophore acquires a typical form, presenting two polar, more or less thin prolongations: of filamentous tendency such as in *Hymenandrya thomomyis* (Smith, 1954); of stronger aspect and more or less reduced length in species such as *Hymenolepis horrida* (Voge, 1952 a), *Hymenolepis neurotrichi* (Rausch, 1962), *Hymenolepis infirma*, *Hymenolepis globosoides*, *Hymenolepis fodientis* (Mas-Coma, 1982; Mas-Coma, unpublished data) and *Gvosdevilepis fragmentata* (Gvosdev, 1948). The absence of these prolongations in the embryophore of *Hymenandrya aegyptica* Mikhail et Fahmy, 1968, besides the consideration of host pictures in the only two species of the genus *Hymenandrya*, are enough for Hunkeler (1974) to suggest the inappropriate adjudication of species *aegyptica* to *Hymenandrya*.

Peculiar embryophore shapes are also known, as in the bird hymenolepidids *Diorchis nyrocae* and *D. stefanskii* in which it is cylindrical, or in *Hymenolepis megalops* in which it ressembles an epithelium (Jarecka, 1961).

Concerning the thickness of the embryophore wall, there are species in which it is thin (at any rate usually thicker than the outer egg shell) such as in *H. fodientis*, *H. furcata*, *H. schaldybini* (Jourdane, 1971), *H. biliarius*, *H. claudevaucheri*, *H. banyulsensis*, *H. cerberensis* (Mas-Coma *et al.*, 1986 b), whereas in other hymenolepidids the wall is thick, as in *Vampirolepis brevihamata* (Sawada, 1988), or even markedly thick as in *H. magnirostellata* and *H. diaphana* (Jourdane, 1971).

Worth mentioning is the presence of filaments emerging from polar protuberances of the embryophore, such as in the well-known species *Hymenolepis nana* and *H. fraterna*. These filaments are usually numerous and long, as in the shrew hymenolepidids *Hymenolepis vaucheri* Hunkeler, 1972 (Hunkeler, 1974), *H. claudevaucheri*, *H. banyulsensis* and *H. cerberensis* (in *H. claudevaucheri* and *H. cerberensis* although the filaments are of a polar origin, no polar protuberances are present) (Mas-Coma *et al.*, 1984, 1986 a, b) or in the bat parasites *Vampirolepis yakusimaensis* Sawada, 1987, *V. iraqensis* Sawada et Molan, 1988 and *V. mesopotamiana* Sawada et Mohammad, 1989 (Sawada, 1987; Sawada & Molan, 1988; Sawada & Mohammad, 1989). However, in the mammal hymenolepidid *H. oregonensis* Neiland et Senger, 1952 only a long recurved filament at each end is found (Neiland & Senger, 1952).

The most important and useful oncosphere structures are the six embryonic hooks, although Jarecka (1961) was also able to distinguish significant differences of oncosphere size among species.

The length of the oncospheral hooks of hymenolepidids usually ranges from 9 to 16 μm. At least three general different patterns of oncospheres can be distinguished, according to the nature of their embryonic hooks:

—Oncospheres with six equal hooks of anoplocephaline type (according to Ogren, 1957): in the species *Hymenolepis horrida* (Linstow, 1901) the six hooks are of the same type, very thin and of anoplocephaline form (Mas-Coma, unpublished); such characteristic of embryonic hooks can also be clearly observed in *Hymenolepis neurotrichi* Rausch, 1962 (according to Rausch, 1962: 814, plate I, fig. 3);

—Oncospheres with six slightly different hooks as in the hymenolepidine type (according to Ogren, 1957): in the species *Hymenolepis infirma*, *H. globosoides* and *H. fodientis* the two internal hooks of both external hook pairs are slightly differentiated, becoming somewhat stronger and showing the beginning of a change of form as in the hymenolepidine type (Mas-Coma, unpublished data), but yet being different from typical hymenolepidid embryonic hooks as well known, for instance, in *Hymenolepis diminuta* and proximal species (see Ogren, 1957);

—Oncospheres with six clearly different hooks as in the hymenolepidine type (according to Ogren, 1957): in the species *Hymenolepis diminuta* and proximal species (Ogren, 1957), *H. claudevaucheri*, *H. banyulsensis* and *H. cerberensis* (Mas-Coma *et al.*, 1984, 1986 a, b), as well as in several bird hymenolepidids (Jarecka, 1961), the two hooks of the middle pair present a particular thin shape and are longer than the other four hooks, and in each lateral pair the internal hooks are characteristic, thicker and longer than the external hooks of the same pair; the latter appear to be of a similar shape but smaller than the hooks of the middle pair.

The size of the oncospheral hooks usually presents a

marked constancy within a given hymenolepidid species. In this sense, however, it is worth mentioning the study carried out by VAUCHER (1971) demonstrating the possibility of the existence of a large intraspecific variability (even including significant differences) in the size of the oncospheral hooks among different geographic populations of a same shrew hymenolepidid species (*Hymenolepis singularis* Cholodkowsky, 1912).

PRESENTATION OF THE PROPOSAL

Need for a standardized method for hymenolepidid studies

There are four reasons supporting the standardization proposal presented in this paper: A) the apparent lack of knowledge or consciousness of many authors concerning the classification problem of hymenolepidids here described; B) the continuous appearance of insufficient descriptions of the morphoanatomy of new species, despite the clear points of attention marked by BAER (1973); C) the need to help in the upcoming phase of species redescriptions; D) the need to supply the necessary methodological basis for the studies of non- specialist authors in this cestode group. This proposal does not aim to achieve a new or original methodology, but only a complete method of traditional morphoanatomic study of the adult stage for hymenolepidid descriptions in order to establish the basis of knowledge necessary for later systematic-taxonomic assays. In order to be considered as a standardization proposal acceptable for as many authors as possible (the only way by which a standardization proposal can be successful), the method described in the present paper has been thought to have the indispensable qualities of being simple, cheap and easy to carry out in all situations (even in centres with only a basic infrastructure) (see for instance MAS-COMA, MONTOLIU & VALERO, 1984 concerning the qualities needed by a standardized methodology).

The method described in the present paper only addresses studies of the adult stage, above all of the tritesticular hymenolepidid forms, which have hitherto posed the greatest classification problems. Of course this method can be applied to adult stages of species belonging to other hymenolepidid subgroups. The whole method is based on the considerable experience of the authors with hymenolepidid cestodes parasitising mammals of the orders Insectivora, Rodentia and Chiroptera. Bibliographically obtained knowledge on hymenolepidids from other host groups (mainly birds), as well as personal experience and information on other proximal cestode groups, such as similarly problematic groups mainly of Anoplocephalidae (RAUSCH, 1976; BEVERIDGE, 1976; TENORA, 1976; TENORA & MURAI, 1980; TENORA, VAUCHER & MURAI, 1981-1982; TENORA, MURAI & VAUCHER, 1984, 1985, 1986; GENOV & GEORGIEV, 1988; GENOV *et al.*, 1990) but also Catenotaeniidae (TENORA *et al.*, 1980), have been also taken into consideration.

A short analysis of the incidence of the methodological question in the systematic confusion existing in hymenolepidids parasitising shrews has already been published (GALAN-PUCHADES & MAS-COMA, 1987). In fact, the present proposal of methodology for the appropriate study of hymenolepidids has already been applied in the published descriptions of three species from the Pigmy white-toothed shrew *Suncus etruscus* (Savi, 1822) (Insectivora: Soricidae: Crocidurinae) (MAS-COMA *et al.*, 1984, 1986 a, b). These descriptions may be consulted for examples (see Fig. 1 and 2).

Description of the methodological standardization proposal

In the detailed presentation of the proposal of standardization which follows, only reference to the aspects intended to be standardized are made. Well-known questions are avoided. It is in this sense that the short review above on the morphoanatomy of the adult stage of the hymenolepidids becomes important, in order to pay attention to the structures and their different aspects which have demonstrated to be useful in classification and must consequently be accurately studied and described.

Material collection and preparation

Concerning the different techniques demonstrated to be most appropriate for cestodes (collection, fixation, staining, dehydration, clearing, mounting, conservation, storage) the recent specialized papers of PRITCHARD & KRUSE (1982), BERLAND (1984), BURT (1984), LICHTENFELS (1984) and BRAY (1984) may be consulted.

Specifically concerning hymenolepidid cestodes, BAER (1973) is worth mentioning. This author stressed the need to standardize the methods of collecting and preparing hymenolepidids.

Among hymenolepidids there are no species presenting a large thick-bodied strobila. The dimensions of the hymenolepidid species range from minute to middle size, so that techniques for tegument removal to expose the internal organs are not usually needed. At any rate, if needed (as for instance in old specimens not allowing appropriate staining), HEYNEMAN (1959), HSU (1968), BONA (1974) or JONES (1990) may be followed. If histological sections for a more detailed study of small internal structures are needed, COOPER (1988) can be consulted.

Referring specifically to hymenolepidids, some comments arising from personal experience and related to the present standardization proposal are needed.

Fixation and conservation: The need to collect fresh material from recently killed hosts is evident, as already noted by BAER (1973). BAER (1973) and HUNKELER (1974) used hot or boiling, 10 % neutral buffered formalin for fixation, because of its capacity to stretch the tapeworms (ordinary formalin is acid and contracts the tapeworms). HUNKELER (loc. cit.) conserved the cestodes in 70° alcohol until the moment of microscopic preparation. Our personal experience has demonstrated that formalin,
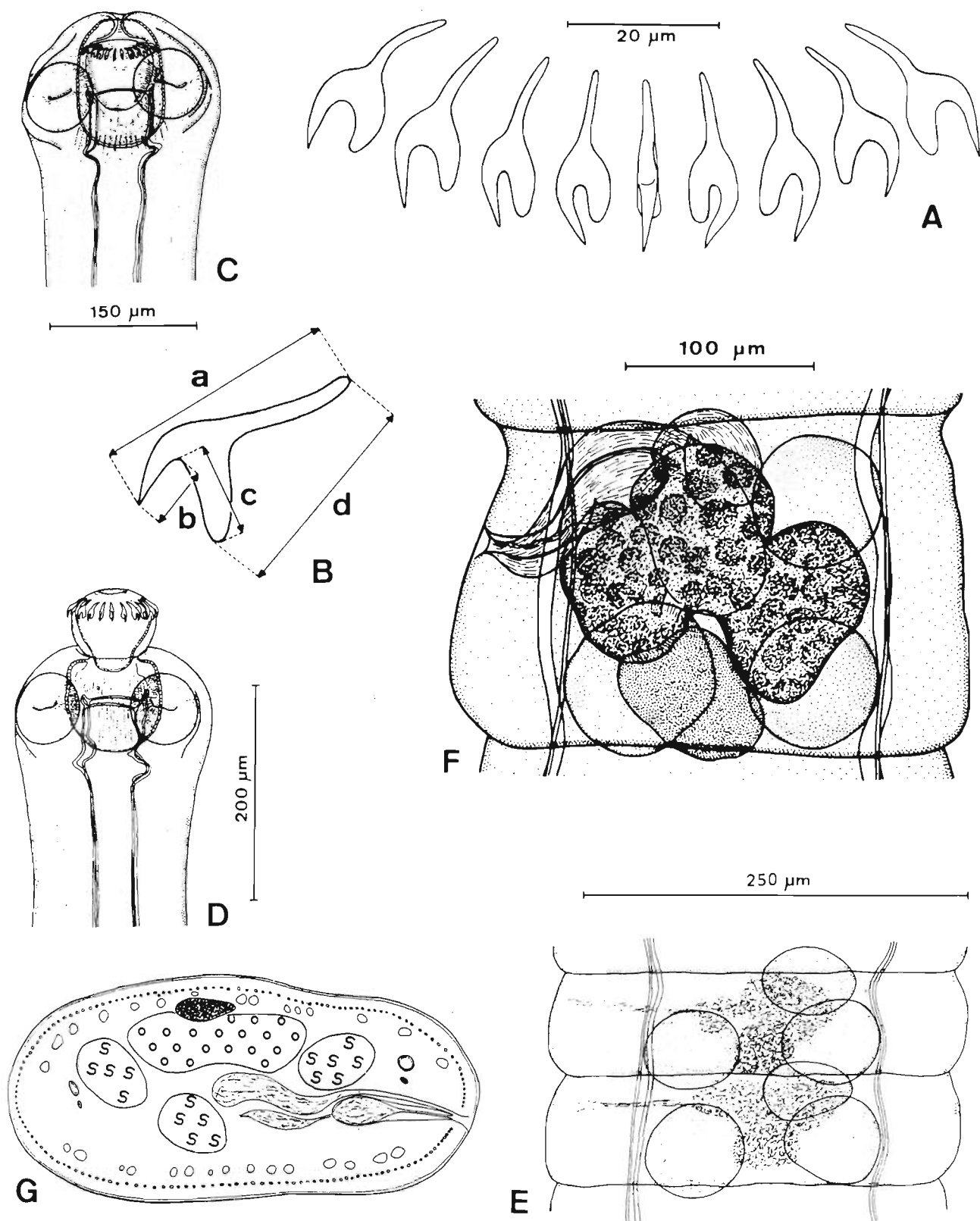
Fig. 1.—Illustration examples of hymenolepidid adult aspects: A) rostellar hooks; B) hook measures (a: hook length; b: blade length; c: guard length; d: base length); C, D) scolex with invaginated and protruded rostellum; E) premature proglottids showing protandry; F) Mature proglottid in ventral view; G) Transversal section of mature proglottid in apical view. A, C, D) *Hymenolepis banyulsensis* (after Mas-Coma *et al.*, 1986 a); B a, b, c) schematic measures used by Vaucher (1986 a); B d) present paper; E) *H. cerberensis* (after Mas-Coma *et al.*, 1986 b); F) *H. claudevaucheri* (after Mas-Coma *et al.*, 1984); G) *H. tiara* (after Vaucher, 1971).
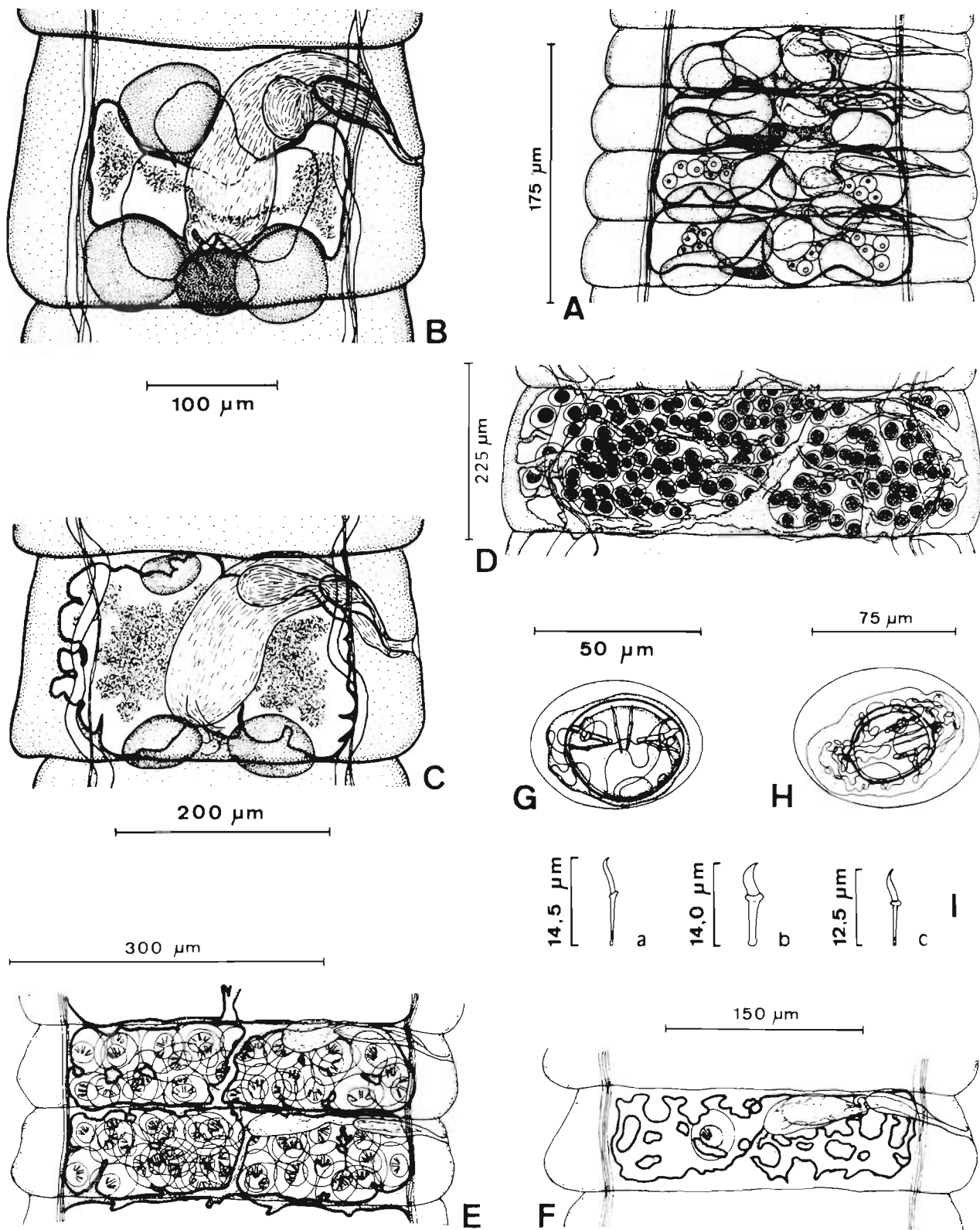
Fig. 2.—Illustration examples of hymenolepidid adult aspects (cont.): A) first postmature proglottids; B, C) postmature proglottids; D) pregravid proglottid; E) gravid proglottid; F) postgravid proglottid; G, H) eggs; I) oncospheral hooks (a: central hook; b: inner lateral hook; c: outer lateral hook). A, E, F, H) *Hymenolepis banyulsensis* (after Mas-Coma *et al.*, 1986 a); B, C, G, I) *H. claudevaucheri* (after Mas-Coma *et al.*, 1984); D) *H. cerberensis* (after Mas-Coma *et al.*, 1986 b).

despite the important advantage of being cheap and easily available, presents a characteristic which sometimes causes problems in the preparation. This excellent fixative fluid hardens the materials, and although this hardening is not excessive, it is enough to break strobila on dehydration and mounting, above all in small delicate specimens or larger specimens which have been fixed incurved, so that a straightening is necessary in the final mounting process between slide and cover-glass.

We therefore propose the use of hot-boiling 70 % alcohol for fixation, together with short vigorous shaking (hand shaking for a few seconds is enough) in the first moments of the fixation until the appropriate stretching of the strobila and proglottids is obtained, a process which can be perfectly followed when fixing in transparent cristal tubes. In this way excellent materials are easily obtained and their staining capacity is always superior to that obtained in formalin fixed specimens. Moreover, taking into account the conservative attribute of 70 % alcohol, a later change to a different new conservative medium is not necessary, so that specimens can be conserved in the same liquid and tube used in fixation until preparation. Alcohol is evidently more expensive than formalin, but when using the latter you also need alcohol for conservation, so that the use of a single medium becomes more economic.

Only two precautions must be taken when using this method. First, boiling alcohol can easily burn if fire comes in contact with the liquid, so that simple but opportune measures must be taken to avoid this possibility (only a small amount of alcohol should be heated). Second, shaking while hot can break the specimens if carried out too vigourously. Thus, each specimen must be fixed separately in an individual tube whenever possible, so that if the strobila breaks down, the certainty that the different parts belong to the same specimen is always there. Moreover, it must not be forgotten that shaking several long specimens in the same tube can give rise to knots which can be difficult or even impossible to disentangle afterwards without beaking up the different strobila.

Summing up, both methods are appropriate and allow us to obtain excellent materials, above all concerning the important question of avoiding contraction.

Staining: Different stains can be used for hymenolepidid studies (for stains used in cestodes see PRITCHARD & KRUSE, 1982), but the classical chlorhydric carmine is enough. However, although the stain selected is not important, this is not the case for differentiation, which must be made with the maximum accuracy under direct observation by means of a binocular microscope to decide precisely when the internal structures show the best contrast.

Worth mentioning is the staining method for cestodes with iron acetocarmine recently described by GEORGIEV, BISERKOV & GENOV (1986) which, despite being time-consuming, is very useful, above all in old conserved materials or *in situ* fixed specimens (that is, cestodes fixed directly in the host's intestine).

Mounting: The mounting process is decisive in the preparation of hymenolepidids. It must not be forgotten that the steps described hereafter must always be followed.

A) *Hook preparations*: If an armed rostellum is present and enough specimens are available, at least 2-3 scolex must be separated from their respective strobila even before staining to carry out special preparations for hook study. Rostellar hooks must be prepared and mounted separately. The best mounting technique of rostellar hooks is with Berlese's medium (see PRITCHARD & KRUSE, 1982 concerning its composition and preparation). This medium possesses a refraction-index which brings out all the details of the hooks, making it easy to draw and to measure them accurately. By pressing on the coverslip before the medium has dried, it is possible to spread the hooks and to separate them from one another, so that they can then be counted accurately and also drawn from different angles. The advantages of this technique are that such mounts are permanent and that the shape and the size of the hooks is in no way altered (BAER, 1973). To assure permanency, these preparations must be ringed when dry (HUNKELER, 1974) or made after the double cover glass mount technique (PRITCHARD & KRUSE, 1982). It is also possible to study the hooks by means of non-permanent preparations using a clearing agent such as lactophenol, following a similar mounting process as described above. It is a rapid technique, but care must be taken that lactophenol is only a temporary medium; and although it does not cause swelling of hooks as glycerine does, the study of the hooks must be carried out immediately after mounting and finished in a reatively short time to avoid possible hook deformation problems. There is an additional problem of inevitable material loss with lactophenol, so that it is only recommended when enough specimens are available.

B) *Egg preparations*: At least 2-3 gravid proglottids from the terminal part of one strobila must be isolated by hand sectioning, even before staining and always before dehydration, and conserved in 70 % alcohol until microscopic study. For egg study, a gravid proglottid is deposited on a slide and broken up with two needles to allow the exit of the eggs. A cover glass is placed and the study can be made. This process can be made in the alcohol or in water, but a clearing agent such as lactophenol makes the observation of the different small egg structures easier. Of course, the same precautions already specified above when working with lactophenol must here be applied. It would evidently be best to study not previously fixed eggs in water, but this offers the methodological problem of material conservation. As no permanent egg preparations can be obtained, the necessity of conserving gravid proglottids in 70 % alcohol must always be taken into account (a label including the number of the specimen to which the proglottids belong must not be forgotten). Finally, worth stressing is the need to study, measure and draw eggs in a perfect lateral view to avoid shape and size errors.

C) *Transversal proglottid preparations*: The mounting

of isolated sexually mature already stained proglottids is recommended for the study of the relative ventral/dorsal positions of the different structures and organs (if there are difficulties in the lateral study of specimens mounted *in toto* or there appear to be rare situations for given organs —see for instance VAUCHER, 1971), as well as for the study of the musculature (see for instance VAUCHER, 1971 and HUNKELER, 1974). To obtain isolated sexually mature segments, hand sectioning under the binocular microscope is enough. Specimens in which the scolex has already been separated for rostellar hook study are specially recommended since they are still incomplete specimens. The isolated proglottids are mounted flat to allow apical view.

D) *In toto preparations*: See PRITCHARD & KRUSE (1982) for cestode microscopic preparation methods including dehydration and mounting in Canada balsam. Concerning hymenolepidids, there are no problems in the mounting of small or middle-sized specimens, but in long specimens the strobila must be hand cut and the parts mounted in order in parallel rows. In longer specimens even more than one slide will be needed. In these cases care must be taken to appropriately label the preparations, so that in each label not only the number of the specimen is noted, but also the number of order of the parts included in the preparation in relation to the whole preparation series covering the hymenolepidid specimen in question.

E) *Histological sections*: Sometimes the observations made in the lateral view of specimens mounted *in toto* need a more detailed study to verify the morphoanatomy. A good example is the histological demonstration of the very peculiar uterus development of the shrew parasite *Hymenolepis diaphana* carried out by VAUCHER (1971). COOPER (1988) can be consulted for histological methods applied to cestodes. Of course material originally fixed with 70 % alcohol would be not useful for such a purpose. Hot formalin, or better, hot Bouin's fluid (also with hand shaking as described above) are recommended for platyhelminth histological studies with the aim of ascertaining the worm morphoanatomy.

Microscopical study

Measurements: The paper on a methodology standardization proposal by MAS-COMA, MONTOLIU & VALERO (1984) may be consulted concerning how to take the measurements of structures and organs and present the results in publications. In structures and organs where the length and the maximum width are clear, such as in rostellum, rostellar sheet, whole specimens, whole proglottids, cirrus sac, protruded cirrus, cirrus stylet, etc., no problems usually appear. In irregularly oval structures and organs, such as suckers and testes, the maximum diameter and the opposed diameter (following the perpendicular axis) must be measured (measurements of only one diameter must be rejected). This makes it possible to calculate the surface by applying the ellipse formula, which appears to be the most approximative (see MAS-COMA, MONTOLIU & VALERO, 1984). In usually completely irregular bodies, such as ovary and vitellarium, the measures must be taken always trying to select the most representative axis (at least two measures of each ovary or vitellarium must be taken) in order to better portray the visible surface of the structure or organ. There are, however, structures which offer difficulties for measurements which must necessarily be made, such as the lengths of the scolex, neck, receptaculum seminis, seminal vesicles, etc. In these cases it is suggested to define exactly how the measurement is taken. Concerning rostellar hooks, only completely flattened hooks must be used for measurement. At least hook length (distance between the base of the handle and the distal pointed extremity of the blade) must be noted. Hook base (distance between the base of the handle and the distal rounded extremity of the guard), as well as hook maximum width (usually corresponding to the guard in peculiarly shaped hooks) may be added if appropriate according to hook shape. Other measures can be added but only if a clear schematic drawing illustrating the measurements carried out is given.

Extreme values and mean must always be noted for each measure. To obtain better information on intraspecific variability, a given measurement of a structure must not only refer to the different proglottids of a strobila but also to different strobila whenever possible. Care must be taken never to mix the measures of specimens coming from different host species and from different geographic localities. When an important variability study can be carried out, the number of measurements (n), as well as ΣX^2 and s^2 shall also be noted (see MAS-COMA, MONTOLIU & VALERO, 1984).

Description material: At least definitive host species (adding order and family to which it pertains), microhabitat of parasitation (location in the host; if possible the intestine part or level must be noted), locality (geographical origin of the specimens; the *terra typica* must be pointed out in descriptions of new species besides other localities of findings, if any), and description specimens (including: number of individuals; fixation, staining and mounting techniques used; collection in which specimens are deposited with collection number, if any).

Specimens: Only totally gravid individuals must be measured to express the total length and maximum width of the worms. Concerning the maximum width, care must be taken that it is not necessarily always found at the level of the last strobilar proglottids (as for instance in species presenting postgravid proglottids). If the material contains gravid and ungravid or incomplete specimens, measures must not be mixed but given independently for each kind of specimens. A drawing (or photograph) of a whole complete specimen is sometimes useful, above all in species presenting unusual strobilar morphological or developmental characteristics (see for instance MAS-COMA *et al.*, 1986 a).

Scolex: An accurate description of the scolex shall include the description and measures of the scolex itself, rostellum (if any), rostellar hooks (if any) and suckers. Concerning the scolex, its length and maximum width must be given and attention must be paid to any peculiar scolex appearance.

Concerning the rostellum, if this organ is not present its absence must be stressed. If present its length and maximum width must always be given, even in cases of the so-called «rudimentary or vestigial» rostellum. Length and maximum width of rostellum as well as rostellum sheet must be taken in both scolex with an invagined and with a protruded rostellum, if possible from the material available. The shape of the rostellum and even the level which its base reaches may be specified in cases of a long rostellum. Drawings illustrating whole scolex in both situations (with an invagined and with a protruded rostellum) may be figured whenever possible.

Concerning hooks, the following must be included in the description: hook shape (accurate morphological description in different angles from lateral to completely frontal or apical), size (trying to include the maximum intraspecific variability by measuring hooks from different scolex if available; measures as already stated before; care must be taken in species bearing hooks of different sizes in the same individual), number (including extreme values and mean after counting in different scolex if available; care must be taken in species in which the hooks appear to be easily caducuous, above all in protruded rostellums; the loss of a hook can sometimes be detected by the free space it has left in the crown) and distribution (regular or irregular —at different levels— disposition in rostellum; hook disposition in the invaginated and in the protruded rostellum, if possible). Drawings representing several rostellar hooks from different angles (from lateral to completely frontal or apical) are imperative.

Concerning suckers, in normal cases it is enough to describe their location on the scolex and their size (measurements as stated above; for intraspecific variability purposes, always suckers from different scolex must be measured). An accurate description of the suckers is needed when special because of being armed with spines or hooks.

Strobila: The presence of a more or less evident neck zone must be described including its length and maximum width, specifying at what level (immediately after the scolex, before the appearance of the first visible proglottid, etc.) this maximum width is found. Concerning the strobila itself, the number of total segments must be counted in gravid specimens (the number of terminal proglottids separated for egg study must not be forgotten) and intraspecific variability must cover all the specimens available, with care not to mix complete gravid individuals with incomplete specimens not yet bearing mature eggs. Of course, if a peculiar strobilar shape is there, it must be described accurately (and also figured with a drawing of a complete specimen).

Concerning the general proglottid type, the shape of the segments must de described specifying symmetry/asymmetry, acraspedote/craspedote appearance and proglottid level in which the maximum width is found (care must be taken here in somewhat contracted specimens). Attention must be paid to accurately describe rare morphologies (presence of spines, lack of external segmentation despite the presence of an evident internal metamerism, etc.) or developments (strobila presenting well-distinguishable zones of markedly different proglottid shape, hiperapolysis, etc.). Measures must not be given for only a representative proglottid, but for each one of the different intrastrobilar proglottid types which may be distinguished in the strobila of the species in question (see below).

Worth mentioning is the need to distinguish between the different intrastrobilar proglottid types. As a rule the following can be listed: young, premature, mature, postmature, pregravid and gravid proglottids. Sometimes there are even postgravid proglottids. The way by which these different proglottid types are distinguished by the authors must be clearly specified in each paper, as one or other characteristics may be used depending from species. Young proglottids generally refer to proglottids already presenting external division or segmentation, but with no distinguishing internal differentiated structures or organs (as in *Hymenolepis claudevaucheri* and *H. cerberensis* —see Mas-Coma *et al.*, 1984, 1986 b). Sometimes, however, they may be defined as proglottids which, although they have no visible external lateral segmentation, can be differentiated by an outline distinguishing their internal structures but lacking individualized testicular primordia (as in *H. banyulsensis* —see Mas-Coma *et al.*, 1986 a). Premature proglottids are those presenting internal sexual structures and organs not yet having reached their maturity (as in *Hymenolepis claudevaucheri* and *H. cerberensis* —see Mas-Coma *et al.*, 1984, 1986 b), but in other species they may de defined by the already marked external lateral segmentation and the presence of internal sexual organs not yet having reached their apparent maturity, although with well individualized testes and vitellarium (as in *H. banyulsensis* —see Mas-Coma *et al.*, 1986 a). Care must be paid to premature segments in hymenolepidids in which a patent protandry is present (measures of testes at the levels of the first and the last premature segments can be given to illustrate protandry, as for instance in *H. cerberensis* — see Mas-Coma *et al.*, 1986 b). Mature proglottids are the segments presenting well-differentiated sexual organs, but with uterus not yet visible, the origin of a first uterus small outline marking the end of the premature proglottid zone. Sometimes the mature proglottids are difficult to differentiate from the last premature segments, taking into account the slow and gradual evolution of the inner structures and that these premature segments are already characterized by the presence of apparently well-differentiated sexual organs (as in *H. banyulsensis* —see Mas-Coma *et al.*, 1986 a). At any rate, a long

microscopical study always allows the researchers to decide where to make the separation. Postmature proglottids refer to those segments presenting a young uterus (the detection of a first uterus small outline marks the first postmature proglottid), whose external outline has not yet reached its definitive expansion and which contains no eggs, the appearance of the first immature eggs marking the end of the postmature proglottid zone (as in *Hymenolepis claudevaucheri* and *H. cerberensis* —see MAS-COMA *et al.*, 1984, 1986 b). There are however species in which immature eggs appear very quickly, and in these cases any visible gonad remains (with for instance testes as the last disappear) can be used to establish the end of the postmature proglottid zone (as in *H. banyulsensis* —see MAS-COMA *et al.*, 1986 a). Pregravid proglottids are those with the uterus already presenting its definitive expansion but yet bearing eggs in formation (as in *Hymenolepis claudevaucheri* and *H. cerberensis* —see MAS-COMA *et al.*, 1984, 1986 b). The total disappearance of given structures, such as gonads and vitellarium, can be helpful in establishing the end of the pregravid proglottid zone (as in *H. banyulsensis* —see MAS-COMA *et al.*, 1986 a). Gravid proglottids concern the final strobilar segments presenting a definitive uterus and mature eggs, the appearance of the first mature eggs marking the beginning of the gravid proglottid zone. In given species, as in *H. banyulsensis* (see MAS-COMA *et al.*, 1986 a), even postgravid proglottids may be distinguished. They are the last strobilar segments in which the uterus appears empty, sometimes showing isolated mature eggs in transit towards their exit across the last proglottids.

For each one of the above-mentioned intrastrobilar proglottid types, the number and size (length and maximum width) must be given. Extreme values and means of both number and size, obtained through the study of different specimens, are of great importance. The faster method to measure the different intrastrobilar proglottids is always to measure the first and the last of each proglottid type zones (they usually correspond to the smallest and the largest segments of each type; care must be taken if this is not the case in specimens more or less deformed by fixation or in species in which a given proglottid type zone induces a marked change in the strobilar general shape), so that the segment following the last largest segment of a given proglottid type zone will be the first and smallest segment of the subsequent proglottid type zone. In this way a logical succession of measures is obtained which finally allows an easy understanding of the specific intrastrobilar proglottid development characterizing the species in question. The number of proglottids of each intrastrobilar proglottid zone, although usually ranging between large intervals, offers the possibility of obtaining very valuable information on the development speed of the different structures and organs, when describing the genital system accurately and referring to the intrastrobilar proglottid type level. Distinguishing these different successive intrastrobilar proglottid zones establishes the basis for a detailed description of the evolution of all

structures along a strobila. Detailed drawings of at least one of each proglottid type present in the species under description should be included in multifigure plates whenever possible.

Finally, counting of the muscle fibers (mainly the longitudinal muscles) may be carried out in transversally hand-sectioned, separately mounted proglottids in apical view, if considered opportune. A detailed figure of a mature proglottid in such a view can be useful.

Excretory system: The description of the excretory sytem is highly important. The detailed origin of the lateral excretory canals at scolex level must be described and figured if observed. At strobilar level, care must be taken to detect, describe and draw the exact situation of the ventral and dorsal excretory canals in all types of intrastrobilar proglottids, above all concerning their location with respect to the different sexual structures and organs. Sometimes difficulties appear in detecting the presence of the lateral excretory canals in terminal gravid proglottids in which the uterus sac completely fills the internal segment space. But any failure to detect these canals must also be noted in the description. Measures of the diameter of each ventral and dorsal canal must be given. In species in which these canals appear to be uniform, it is enough to note the minimum and maximum diameters of each one along the whole strobila, but in cases in which large differences of their diameter are detected, it would be preferable to particularize the minimum and maximum diameters of both at each one of the different types of intrastrobilar proglottids. Transversal anastomoses of the ventral lateral canals may also be described, figured and measured if detected. Care must be taken to make a complete description of the excretory system in species in which the number of excretory canals differs from the usual two pairs, or abnormal transversal anastomoses appear. Drawings of transversely hand-sectioned whole sexually mature proglottids are sometimes of interest to emphasize the relative situation of the different structures and organs with respect to the lateral excretory canals (the same isolated proglottids mounted for muscle fiber countings may be used).

Genital system: The exact position (anterior, in the first third part, median or equatorial, at a more or less midlevel, in the posterior third, posterior, etc.) of the genital pore along the lateral margin of the proglottid must be determined in mature proglottids analyzed in a completely lateral view. This is easily established by verifying the presence of the opening of the genital pore exactly at the lateral margin of the proglottid. It must be taken into account that contraction can induce modifications of the opening level of the genital pore. In hymenolepidids, as a rule (with very rare exceptions) genital pores are always unilateral, but this character in a given species must be better verified by studying different specimens.

The genital atrium must be described in detail, above all in species presenting peculiarities (very deep, spined)

or additional structures such as accessory sac(s) (smooth, armed with spines or hooks, etc.). Measurements of such structures must be noted whenever possible. Particular drawings figuring such structures may be helpful.

Finally, and for an appropriate description of the male and female genital systems, it is important to determine the ventral or dorsal disposition of the strobilar proglottids mounted in lateral view on the microscopic slide, which can be achieved simply by analyzing the relative disposition of both ventral and dorsal excretory lateral canals.

Male genital organs: Testes number (in species presenting a variability in this number, the main testes number per proglottid must be given, besides other testes numbers present, followed by the number of proglottids per strobila which present these abnormal testes numbers), intraproglottid distribution (distributional pattern: triangular, in line, etc.), intraproglottid situation (mainly with respect to other sexual structures and lateral excretory canals: aporal/median/poral with respect to ovary, inside/outside excretory canals), testes shape (oval, lobated) and testes size must be described and noted, always making reference to the intraspecific and intrastrobilar variability ranges detected when studying different strobila and different proglottids along individual strobila, respectively. Studies of transversally whole mature proglottids are sometimes of interest to emphasize the relative situation of testes regarding the other structures and organs (the same isolated proglottids mounted for muscle fiber countings and excretory lateral canal studies may be used). These variation observations are of interest above all in order to establish the testes distribution pattern of the species in question. Concerning testis measurements, they must be taken in mature proglottids (if also measured in other proglottid types, such as in premature or postmature, this condition must be clearly noted) and care should be taken in species in which a given testis shows a markedly different size compared to the other testes. In such cases, measures of all three testes should not be mixed, but given separately.

The study of the premature proglottids makes it possible to distinguish whether there is a more or less pronounced phenomenon of protandry (testes appearing, developing and degenerating largely before the ovary reaches its maturity). If present, such a phenomenon must be described accurately by exactly establishing the proglottid type levels in which testes appear, develop and degenerate, including specific testes measures at the different given proglottid levels. An usually small intraspecific variation can also be detected in this character when studying different strobila.

The cirrus pouch must be described very accurately, above all concerning its extent regarding other internal structures (mainly the poral excretory lateral canals and, in cases of a large sized cirrus pouch, regarding the midline of the proglottid or even the aporal excretory lateral canals). In this sense, care must be taken to describe

the extent of the cirrus pouch when it appears fully developed in mature segments, as in premature segments this pouch has not yet reached its maximum development. Similarly, the cirrus pouch should only be measured in those mature proglottids in which it has achieved its definitive size. The thickness of the cirrus pouch wall may be measured in species in which it appears to be unusually thick. Sometimes it becomes useful to study the spatial distribution of the cirrus pouch in order to verify its location with respect to the other sexual structures, in transversally whole mature proglottids in apical view (in hymenolepidids the cirrus pouch, together with the female ducts, are always located dorsally to the poral excretory lateral canals).

The cirrus characteristics (smooth/armed, with small/long spines, distal/total/proximal distribution of spines, with/without a stylet, short/long stylet, invaginated coiled/non-coiled stylet, length and maximum width of the cirrus, length of the stylet) must be described and measured only in protruded cirri. Great care must be taken to ascertain the cirrus characteristics from invaginated cirri. Particular detailed drawings figuring the protruded cirrus and related structures may be helpful in complex cases.

Internal and external seminal vesicles may be described (attention must be paid to the possible presence of glandular cells surrounding the external seminal vesicle) and their length and maximum width should be measured whenever possible (if a rare case of absence of one, other or both seminal vesicles is detected, emphasis must be given to the confirmation of this absence and this absence must be stressed in the description).

The evolution (appearance at maturity and progressive disappearance) of all male genital structures and organs must be figured in detail in the drawings of at least premature (if protandry is present), mature, postmature, pregravid and gravid segments. An additional drawing of a transversally whole mature proglottid in apical view is sometimes useful to illustrate the inner spatial distribution of sexual structures and organs, above all in species in which a peculiar ventral/dorsal location of a given structure or organ is observed.

Female genital organs: Shape, size and exact intraproglottidean location (in relation to the whole proglottid as well as in relation to the other structures and organs) of the ovary and the vitellarium should be described in detail. A minimum study on intraspecific variability concerning all the above-mentioned aspects of ovary and vitellarium, obtained from different proglottids along a strobila and also from different specimens, must be carried out and results carefully noted in the description (concerning the vitellarium, if a large shape intraspecific variability is detected, it can be best illustrated with a separate drawing). Their ventral/dorsal location can sometimes be better figured with a drawing of a transversally sectioned mature proglottid in apical view.

The location of the vagina opening (posterior, ventral,

rarely anterior) with respect to the orifice of the male duct must be given and figured. When accessory vaginal structures are present (funnel-like copulatory part of the vagina; distal, sclerotized clamp; powerful vaginal sphincter) they should be described and figured (and even measured if possible) in detail. The presence or absence of a receptaculum seminis must be stressed. The development of the receptaculum seminis usually showing large differences in size along a strobila, its shape, size and expansion regarding other structures may be detailed in each type of intrastrobilar proglottids.

The uterus is a structure whose whole development along a strobila, from its origin to its final stage, must be carefully studied, described and appropriately illustrated in figures to establish its origin pattern, development type and final morphological pattern. The first postmature proglottid, in which a recently appearing young uterus can be distinguished, should be found. In the first postmature proglottids a detailed study should be carried out to ascertain the uterus origin pattern of the species (irregularly lobed median sac, elongate longitudinal sac, transverse lobed double sac, tube-sac, inverse U shaped, bilobed, etc.). A postmature segment in which this uterine origin is clearly appreciable must be drawn.

Along the following postmature and pregravid proglottids the intermediate development of the uterus must be determined (reticular or non-reticular evolution; slow or rapid development up to final gravid stage, that is, whole uterine maturation taking place respectively along a large number of segments or a very few proglottids; uterus intermediate stage either surpassing the excretory canals bilaterally or not; appearance and disappearance of trabecules inside the uterus; non-lobated, oval uterus development; more or less pronounced lobated appearance of the development of the uterus; uterus development as a transversal lobated sac or tube; initial bilobed uterine sac developing as an inverse U or horseshoe; uterus giving rise to an irregular ring; uterus development up to final gravid stage only in free segments precociously detached from strobila; etc.). Usually at least two figures of a postmature and a pregravid proglottid illustrating the intermediate uterus development are needed.

Terminal gravid proglottids showing the definitive shape, extent and appearance of the final uterus stage must be described in detail (reticulate appearance; saccate shape; occupying all or almost all of the inner space of the proglottid; uterus distending irregularly to the external walls of gravid segment whose outline can therefore even be deformed due to the growth of eggs; small lobated uterus occupying only half of the width of the proglottid; thin or thick walled uterus; uterus presenting few or many eggs; final uterus either surpassing the excretory canals bilaterally or not; gravid uterus forming two lobated or non-lobated sacs, which may be joined by a narrow isthmus; very thick-walled, oval capsule-like sac; uterus wall with a pronounced thickening giving rise to a regular elipsoidal sac which detaches from the pro-

glottid thus becoming free; sacciform uterus becoming a thick-walled capsule inducing gravid segments to become oval and detach individually from the strobila to continue separate development; uterine interproglottidean thickened walls disappearing, so that eggs of several segmens reunite in the common multisegmental muscular cover; etc.). At least a drawing of one of these gravid proglottids shall be included.

If postgravid proglottids are present, they must also be described (uterus of the last strobilar proglottids appearing whether empty or including only a very few eggs) and a figure of one postgravid segment may be included in the plate.

In the descriptions of the whole uterus evolution along postmature, pregravid and gravid (and postgravid if any) segments, special attention should be paid to the other male and female sexual structures which are following respective degeneration and disappearance processes. Such processes concerning testes, cirrus sac, seminal vesicles, vitellarium, receptaculum seminis, etc., should be carefully followed and described parallel to the uterus development to define the pattern (= order) of structure-organ degeneration and disappearance. Special care must be taken to illustrate these degenerating structures and organs in the figures of the above mentioned proglottid types.

Eggs: Only mature eggs isolated from terminal gravid proglottids and prepared according to the above-mentioned mounting specifications can be used. Description and measures should only be made in eggs observed in totally lateral view. All different egg structures must be defined accurately. Measures must be taken at least of the external egg shell, embryophore, oncosphere (length and maximum width) and oncospheral hooks (length is enough). The width of egg shell and embryophore walls may also be added if thick. Different types of oncospheral hooks may be distinguished if present and then hook length must be given independently for each type. For intraspecific variability purposes, eggs coming from different strobila may be measured whenever possible. Drawings of at least a complete egg in lateral view and of one example of each hook type present must be included.

DISCUSSION

In conclusion, the proper characteristics of a correct description of hymenolepidid cestodes are the following:
A) *availability of appropriate material*: specimens must not be contracted by fixation and complete individuals not broken; specimens must include final gravid proglottids; if specimens available are broken in parts, it must be remembered that host individuals can be parasitized by different hymenolepidid species raising the possibility of errors in mixing strobilar parts that actually correspond to different species, as already stressed by BAER (1973);

B) *complete description*: the description must include the scolex, the different proglottid types of the whole strobila, and finally the eggs, together with their respective structures; the usual descriptions comprising only scolex and sexually mature proglottids are insufficient; rostellar hooks, proglottid musculature and egg structures must be appropriately described from specially prepared materials and not from *in toto* mounted specimens;

C) *detailed description*: the inner morphoanatomy of all intrastrobilar proglottid types must be accurately described (shape and size of all organs and structures in each one of the young —if there is something remarkable—, premature, mature, postmature, pregravid, gravid and postgravid —if any— proglottids), paying special attention to the location of the different structures in relation to the other structures or organs; worth noting also is the importance of mentioning the absence of given structures (often the problem is posed simply because in an old description a structure was not mentioned, so that it becomes impossible to know if this structure is really absent or simply was not seen or noted by the authors);

D) *intraspecific variability*: a minimum intraspecific variability study must be carried out concerning important but well-known variable structures and organs (number, shape, size and situation of rostellar hooks, number and location of testes, shape of ovary and vitellarium, size of egg structures, etc.); hymenolepidids are characterized by presenting an intraspecific variability which concerns given structures but which remains within certain more or less narrow ranges characteristic of each species; if only a small number of specimens are available, at least an intrastrobilar proglottid variability description must be given;

E) *need for drawings*: drawings are indispensable and should represent at least scolex (in armed species, if possible a scolex with evaginated rostellum and another scolex showing an invaginated rostellum), rostellar hooks (if any; if present in all the different angles), whenever possible one of each premature (if necessary because of, for instance, protandry), mature, postmature, pregravid, gravid and postgravid (if any) proglottids (usually no drawings of young proglottids are needed), and the egg and oncospheral hooks; descriptions in which the drawings are restricted, as usual, to only the scolex, a hook in lateral view and a sexually mature proglottid, must be avoided.

According to the above short review on the morphoanatomy of the adult stage in hymenolepidids, it is evident that such complete descriptions provide the simplest way to allow appropriate comparative studies and differentiation of species which were impossible up to the present. As already stressed by Baer (1973), unfortunately the preparation of the necessary basis with correct descriptions of species (which means not only beginning to describe appropriately the new species appearing in future research, but also the necessary review of old materials included in collections) will require a long time, but only then would an acceptable realistic system of the hymenolepidids be envisaged. The very long lists of hymenolepidid species which could not be generically classified by Schmidt (1986) is discouraging. Helminthologists must try to begin with this enterprise. Worth mentioning in this sense is the role of collections and museums in making specimens available for study and review, above all concerning old materials (see Pritchard & Kruse, 1984). The work of specialists such as, for instance, Prof. Dr. Bogdan Czaplinski (Warsaw, Poland), who has for several years been redescribing insufficiently known species by reviewing old materials from different collections, is worth encouraging.

The present standardization proposal has the purpose and the capacity to facilitate, stimulate and guide future research on hymenolepidids. As can be seen, the present proposal is not extraordinary, which is precisely its most important attribute. The main aim is to appropriately guide the first steps or sporadic incursions of non-specialist researchers in this problematic cyclophyllidean group. Hopefully this standardization proposal will receive more acceptance and application than the one by Baer (1973), which had the problem of being published only in a conference proceedings, thus remaining only available to a few specialists.

The standardization proposal here in question, besides its obvious advantages, unfortunately presents two disadvantages. These disadvantages are not important for the application of the proposal, but should not be underestimated. On the contrary, they must be taken into account in order to undertake the efforts necessary to resolve the present problem of hymenolepidid desorganization.

A) *Time consumption*: The type of study here proposed is undoubtedly time-consuming, clearly longer than the time needed for a hymenolepidid species description according to the most usual recently-published papers. But one cannot forget that cestodes are polyzoic animals and consequently their correct complete study will always comprise the study of the different intrastrobilar proglottids (=individuals of the polyzoic worm). In reality, thanks must be given to adult cestodes for being polyzoic, as no other helminth life cycle stage offers such extensive information. We must be able to take advantage of this; we cannot think of it as a digenean adult stage. When enough complete descriptions are available, the numerous morphologic and anatomic aspects known in cestode adults will evidently facilitate the work of systematic classifications, taxonomic studies, and evolutionary and phylogenetic approaches (together with the additional knowledge on ontogenies, life cycles, host specificities and biogeography). Non-specialist authors must understand that the scientific satisfaction in the description of a new species does not only lie in proposing a new species, but also in the acceptance of a reasonable, relatively long manuscript by a good journal.

B) *Space consumption*: The type of complete morphoanatomic descriptions here proposed is inevitably page- consuming. Specialized journals shall understand the need for complete, long descriptions when dealing with species pertaining to cestode groups presenting such a large problematic as hymenolepidids. Already published in a recent standard journal, such a complete description, independent of other parts of the paper (introduction, discussion, references, etc.), takes about 1,5-3 whole written pages plus 2 whole pages for multifigure plates and corresponding legends (see for instance MAS-COMA *et al.*, 1984, 1986 a, b), which is, at any rate, perfectly acceptable and far from excessive. Thus, efforts must not only be made to accept and encourage the submission of papers including such descriptions, but also to reject those papers including descriptions which, because of being too short, are insufficient. Referees and editors must always take into consideration the huge problems which afterwards derive from such insufficient descriptions, as has been clearly demonstrated in this paper. Papers on morphoanatomy are evidently today not among the most vanguardist parasitological studies, but scientific editors must keep in mind their scientific responsibility when defending such traditional papers as opposed to others dealing with recent more popular research fields owing to inevitable commercial guidelines.

CONCLUSIONS

The present availability of data undoubtedly makes it impossible to attempt an appropriate classification of the hymenolepidids reflecting the natural evolution and phylogeny of this complicated group comprising a large number of species. The only correct way to remedy such a situation, as already emphasized by VAUCHER (1971) and BAER (1973), is the appropriate study of old, recent and new materials and the corresponding appropriate and complete redescription of each species. Of course, this will require a very long time, but there is no other way to attempt a correct rearrangement of the systematics and taxonomy of the Hymenolepididae.

Besides the traditional methods here in discussion, there are evidently other more sophisticated technologies today available, such as biochemical and genetic techniques proper to molecular biology (BRYANT & FLOCKHART, 1987; THOMPSON, 1988), mainly the isoenzyme analysis by electrophoresis and isoelectric focusing allowing species and even strain differentiation, already applied to a few hymenolepidid species (DIXON & ARAI, 1985, 1986; HERRERO *et al.*, 1989, 1990, 1991; PASCUAL *et al.*, 1989; ANDREWS *et al.*, 1989; NOVAK, TAYLOR & PIP, 1989) and the more modern techniques of nucleic acid probes for species identification (BLAIR & MC MANUS, 1989) or relative small supraspecific taxa distinction (SARICH, SCHMID & MARKS, 1989). But even recognizing the extensive information that these techniques can and will undoubtedly provide in the near future, it is clear that these techniques continue today to be far from available to every parasitologist working in cestode systematics and faunistics, above all because of technological and pronounced cost questions.

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