Chapter 12

Phylogeny among orders of the Eucestoda (Cercomeromorphae): Integrating morphology, molecules and total evidence

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Advances in our understanding of genealogy among the orders of the Eucestoda have been based on independent approaches linked to comparative morphology and analysis of molecular sequence data, particularly from 18S rDNA. Parsimony analyses of molecular or morphological databases have yielded largely concordant trees supporting monophyly for the Eucestoda: 1) monozoic Caryophyllidea are basal; 2) difossate and segmented forms such as Pseudophyllidea are the sister for the remaining orders; and 3) tetrafossates including the paraphyletic Tetraphyllidea, Proteocephalidea, Nippotaeniidea, Tetrabothriidea, Mesocestoidata, and Cyclophyllidea are highly derived. Hypotheses by Hoberg *et al.* (1997c) and Mariaux (1998) differed in placement of the Diphyllidea and the Trypanorhyncha. A 'total evidence' approach now combines substantial components of currently available morphological and molecular data and additional taxa to further examine the putative relationships among the Eucestoda using two complementary strategies: 1) a top-down analysis employing a 'consensus' or reduced matrix for molecular and morphological data for the ingroup across 11 ordinal-level taxa, three families of Tetraphyllidea and two families of Pseudophyllidea; and 2) a bottom-up analysis employing character data for individual, representative genera and species including 48 ingroup taxa across 16 ordinal and family-level taxa in a 'comprehensive' matrix. Parsimony analysis of the consensus matrix resulted in two most-parsimonious trees (MPTs) (CI = 0.671, RC = 0.378) largely similar to general structure outlined by Hoberg *et al.* (1997c) and Mariaux (1998). Analysis of the comprehensive matrix resulted in 48 equal-length trees (CI = 0.484, RC = 0.378) congruent to the MPTs derived from analysis of the consensus matrix in diagnosing the orders and putative relationships of the eucestodes. Results overall contrasted minimally with Hoberg *et al.* (1997c) or Mariaux (1998). Comparative data from morphology, ontogeny and ultrastructure are validated; a complementary nature is emphasized for: 1) morphological and molecular characters; and 2) top-down versus bottom-up approaches. Phylogenetic resolution among the Eucestoda will lead to development of model systems for evolutionary biology, cospeciation analysis and historical biogeography.

A history and background for tapeworm phylogenetics

Historically, the phylogeny for the tapeworms has been problematic and unresolved with numerous competing hypotheses having been presented over the past century (e.g., Loennberg 1897; Fuhrmann 1931; Skrjabin 1940; Baer 1950; Spasskii 1951, 1958; Euzet 1959, 1974; Freeman 1973; Dubinina 1980; Euzet *et al.* 1981; Brooks *et al.* 1991). Although the morphological limits for most orders are apparent (e.g., Wardle and McLeod 1952; Yamaguti 1959; Schmidt 1986; Spasskii 1992; Khalil *et al.* 1994) there has been disagreement over the validity and rank of certain taxa. The contentious nature of these hypotheses has been driven by a variety of issues: 1) concepts for relationships were often based on assessments of single characters or structural/ontogenetic attributes; 2) assumptions about putative coevolutionary linkages among tapeworms and their hosts strongly influenced concepts for parasite phylogeny (e.g., Wardle and McLeod 1952; Brooks *et al.* 1991; Klassen 1992); 3) philosophical differences over the evolutionary process led to divergent interpretations of relationship; 4) adequacy and applicability varied for a diversity of classes of characters as indicators of relationship (e.g., morphology, ontogeny, etc.); 5) interpretations for homology were contradictory; and 6) the methods used to develop and assess competing phylogenetic hypotheses were often not directly comparable. Although recent diagnostic keys have provided new critical data and interpretation extending to generic-level taxa, there has been no general attempt to reflect evolutionary history (Schmidt 1986; Khalil *et al.* 1994). Such concerns led to recognition that a standardized approach, emphasizing cladistic methodology (Hennig 1950, 1966; Wiley 1981; Wiley *et al.* 1991) was requisite for resolution and formulation of a synoptic understanding of the history and genealogical relationships for the Eucestoda (Hoberg *et al.* 1997b).

Phylogenetic studies of cestodes, first initiated in the late 1970s (e.g., Brooks 1978), have been limited in taxonomic scope to families, genera and species (summarized in Brooks and McLennan 1993a) and higher-level systematics was not addressed in detail (Mariaux 1996). Thus, phylogenetic reconstruction until recently had evaluated intraordinal relationships for some Proteocephalidea (Brooks 1978, 1993), Tetraphyllidea (Brooks *et al.* 1981; Brooks 1992), Tetrabothriidea (Hoberg 1989, 1995; Hoberg and Adams 1992), and Cyclophyllidea (Hoberg 1986, 1992; Moore and Brooks 1987). Brooks *et al.* (1991) and Brooks and McLennan (1993a) were the first to apply cladistic methods to develop a synoptic hypothesis for the phylogeny of the major lineages and orders of the Eucestoda.

Over the years since 1996, the focus on phylogenetic studies among the Eucestoda has increased dramatically (Hoberg *et al.* 1997b). New working hypotheses for relationships of the orders (Figure 12.1) were developed based on comparative morphology (Hoberg *et al.* 1997c, 1999b) and molecular sequence data (Mariaux 1998; Olson and Caira 1999). Justine (1998b) evaluated an extensive literature and examined the utility of spermatozoon ultrastructure for phylogenetic reconstruction. Concurrently, Hoberg *et al.* (1997c, 1999b) outlined, summarized and compared prior explicit concepts for phylogeny. Mariaux and Olson (2001, this volume) summarized progress in molecular systematics studies of tapeworms.

Phylogenetic reconstruction has now been conducted at the intraordinal level to examine relationships within eight of

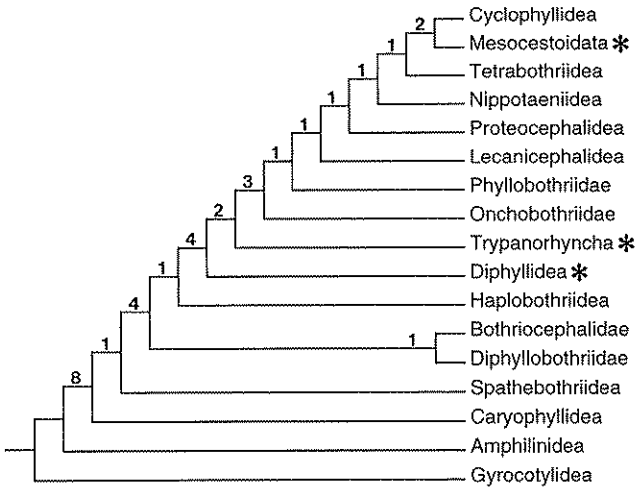

Figure 12.1 Phylogeny for the Eucestoda based on comparative morphology. Shown is one of two MPTs (length = 159; CI = 0.803; RC = 0.645) that is largely congruent with prior hypotheses (Hoberg et *al.* 1997c, 1999b); an alternative hypothesis places the Diphyllobothriidae basal to the Bothriocephalidae and remaining eucestodes. Contrasting with Hoberg et *al.* (1997c), this hypothesis now includes the Mesocestoidata, Bothriocephalidae and Diphyllobothriidae as independent taxa; Litobothriidae is not included here, as data are unknown for 22 of 51 characters (spermatozoa, spermiogenesis, ontogeny and eggs). Departures from the topology reported by Mariaux (1998) based on 18S rDNA are denoted by asterisks. Reconciliation of the morphological hypothesis with that from molecular analysis requires 18 additional steps in the former tree (length = 178; CI = 0.72; RC = 0.50). Bremer decay values are shown above each node.

12–13+ currently recognized orders: Tetrabothriidea (Hoberg 1989; Hoberg and Adams 1992); Pseudophyllidea (Bray *et al.* 1999); Trypanorhyncha (Beveridge *et al.* 1999); Tetraphyllidea and Lecanicephalidea (Caira *et al.* 1999; Olson and Caira 1999) where recognition of the ordinal level diversity within this group is now being highlighted; Proteocephalidea (Rego *et al.* 1998; Zehnder and Mariaux 1999); Diphyllidea (Ivanov and Hoberg 1999); and Cyclophyllidea (Hoberg *et al.* 1999a; von Nickisch-Rosenegk *et al.* 1999). Studies within the Spathebothriidea, Caryophyllidea and Nippotaeniidea, continue to be lacking. These represent a suite of testable hypotheses for in-depth analysis of the phylogeny for the Eucestoda.

Independent analysis of molecular and morphological data using parsimony has yielded largely congruent trees supporting monophyly for the Eucestoda: 1) monozoic Caryophyllidea are basal; 2) difossate and segmented forms such as Pseudophyllidea are the sister for the remaining orders; and 3) tetrafossates including the Tetraphyllidea, Proteocephalidea, Nippotaeniidea, Tetrabothriidea, Mesocestoidata, and Cyclophyllidea are highly derived (Figure 12.1). Hypotheses by Hoberg *et al.* (1997c) and Mariaux (1998) were largely congruent and differed primarily in placement of the Diphyllidea and the Trypanorhyncha and whether or not the Mesocestoidata should be subsumed within the Cyclophyllidea. Alternatively, Olson and Caira (1999) found the Spathebothriidea to be basal, a possible separation between lineages containing difossate versus tetrafossate taxa, and a variable position for the Trypanorhyncha and Diphyllidea. It is now clear that the Tetraphyllidea is paraphyletic (Euzet *et al.* 1981; Hoberg *et al.* 1997c; Caira *et al.* 1999; Olson and Caira 1999). There is also some indication that Mesocestoidata and Litobothriidae should be resurrected at the ordinal level (see Mariaux 1998; Hoberg *et al.* 1999a; Miquel *et al.* 1999; Olson and Caira 1999). Apparent resolution over the relationships of the Tetrabothriidea as the putative sister of the Cyclophyllidea or of the Mesocestoidata + Cyclophyllidea (Hoberg *et al.* 1997c, 1999a; Mariaux 1998; Olson and Caira 1999) contrasts with a diversity of opinions over the past 100 years (Baer 1954; Spasskii 1958, 1992; Temirova and Skrjabin 1978; Galkin 1987, 1996; Hoberg 1987, 1994).

The current studies outlined in this chapter are designed to further elucidate the higher-level hypotheses for the Eucestoda. The most recent consensus (Khalil *et al.* 1994) recognized 12 orders of the Eucestoda, and 9–19 orders have been distinguished by taxonomic consensus in the past (Mariaux 1996). It is suggested that ordinal-level diversity may reside between these extremes. A 'total evidence' approach (Kluge 1989; de Queiroz *et al.* 1995; Sanderson *et al.* 1998) combining the currently available morphological and molecular databases (18S rDNA only) was used to examine the putative relationships among the Eucestoda using two complementary strategies: 1) a top-down analysis employing a 'consensus' or reduced matrix for molecular and morphological data for 16 ordinal and family-level taxa of the ingroup; and 2) a bottom-up analysis employing character data for individual, representative genera and species including 48 in-group taxa in a 'comprehensive' matrix. The limiting factor for inclusion of taxa was based on the availability of molecular sequence data which are lacking for inclusive families within the paraphyletic Tetraphyllidea (see Euzet 1994). The current analyses extend those of Hoberg *et al.* (1997c, 1999b) and Mariaux (1998) with the addition of members of previously unrepresented families and orders and address: 1) examination of the monophyly for orders of the Eucestoda; 2) development of a more robust hypothesis for relationships among the major taxa based on these data; and 3) definition of a clear working hypothesis for phylogeny that will be useful in delineating areas of future research linked to systematics, classification, and historical ecological research in coevolution, biogeography and ecology of the tapeworms.

Foundations for the analyses: taxa and characters

Relationships among 16 putative orders and several families of the Eucestoda were evaluated based on data derived from comparative morphology and molecular sequences of 18S rDNA. Taxa and characters included those in Hoberg *et al.* (1997c) and Mariaux (1998) with sequences for two additional taxa from Olson and Caira (1999); details of outgroups and polarity argumentation are presented in these papers. Mesocestoidata is treated here as an independent taxon based on recent studies by Mariaux (1998), Hoberg *et al.* (1999a) and Miquel *et al.* (1999). Tetraphyllidea is deconstructed to represent the Onchobothriidae, Phyllobothriidae and Litobothriidae. Pseudophyllidea is represented by two putative lineages encompassing the Diphyllobothriidae and Bothriocephalidae, with the latter including Triaenophoridae, Echinophallidae, Philobythiidae and Cephalochlamididae (consistent with Bray *et al.* 1999). Characters for spermatozoons and spermiogenesis are included for the Mesocestoidata (Miquel *et al.* 1999) and Lecanicephalidea (personal communication J.-L. Justine and L. Euzet). Additionally, molecular sequences from species of Haplobothriidea (*Haplobothrium globuliforme*), Litobothriidae (*Litobothrium janovyi*), Lecanicephalidea (*Eniochobothrium gracile*), and Onchobothriidae (*Calliobothrium* sp.), kindly provided by P. D. Olson, were

included in the current analysis, otherwise data and sequence alignments are consistent with Mariaux (1998).

'Total evidence' or combined analysis

Molecular and morphological data were combined in the current analysis in accordance with rationale established for 'total evidence' and phylogenetic reconstruction among other taxa (e.g., Kluge 1989; de Queiroz *et al.* 1995; Huelsenbeck *et al.* 1996; Siddall 1997; Blair *et al.* 1998; Sanderson *et al.* 1998; Littlewood *et al.* 1999a). Because the original data did not contain the same taxa, and the numbers of taxa were relatively limited, we initially used a 'supermatrix' approach in which the matrices were combined (Kluge and Wolf 1993; Sanderson *et al.* 1998). Additionally, separate data were compared for heterogeneity according to the Partition Homogeneity Test (PHT) as implemented in PAUP* (Swofford 1998).

Consensus matrix

The 'consensus' or 'reduced' matrix was designed to address relationships among putative orders in a top-down analysis where supraspecific taxa are used as terminals (see for example discussion in Bininda-Emonds *et al.* 1998). There were 16 ingroup taxa and two outgroups (consistent with Hoberg *et al.* 1997c, plus the Mesocestoidata, Litobothriidae, Bothriocephalidae and Diphyllobothriidae). The Tetraphyllidea, recognized to be paraphyletic (e.g., Hoberg *et al.* 1997c; Caira *et al.* 1999) was deconstructed to the family level to represent constituent taxa. Explicitly, the current analysis does not address the relationships for the diversity of minor 'tetraphyllidean' families (e.g., Cathetocephalidae, Chimaerocestidae, Disculicipitidae, Prosobothriidae and Dioecotaeniidae), nor the monophyly of these inclusive groups. Included were 51 binary and multistate characters from comparative morphology (Appendix 12.1) (consistent with Hoberg *et al.* 1997c, 1999b), and 1102 aligned nucleotide sites representing bases from partial sequences of 18S rDNA (consistent with Mariaux 1998; Olson and Caira 1999); 144 characters were informative for parsimony analysis, respectively, 100 molecular and 44 morphological.

Multistate taxa were coded as polymorphic for both morphological and molecular data, where families, genera or species possessed alternative character states. The potential influence of coding for polymorphism in multistate taxa, was considered (see Maddison and Maddison 1992; Swofford 1993). Estimation of ancestral states based on a prior phylogeny such as that outlined by Yeates (1995) or Bininda Emonds *et al.* (1998) was not applied to supraspecific taxa in this analysis. Although this method for coding would eliminate polymorphism by explicitly recognizing the ancestral state for each supraspecific taxon, decisions could not be based on application of a consistent convention.

Comprehensive matrix

Alternatively, a 'comprehensive' matrix included data for representative species or exemplars for 48 in-group taxa across eucestode ordinal diversity, and two outgroups in a bottom-up analysis. Generic and species-level taxa are consistent with Mariaux (1998) and Olson and Caira (1999) and a complete list of taxa is included in the former study. Ordinal-level taxa were deconstructed to the species level with respect to morphological characters; 113 binary and multistate characters were derived from comparative morphology (data summarized in Hoberg *et al.* 1997c, 1999a; Rego *et al.* 1998; Bray *et al.* 1999); autapomorphies were generally excluded (Appendices 12.1, 12.2). Due to limited representation for the orders Diphyllidea, Trypanorhyncha, Lecanicephalidea, and Tetraphyllidea, morphological data for species and genera from the following studies were not included in this matrix: Beveridge *et al.* (1999); Ivanov and Hoberg (1999); Caira *et al.* (1999). A total of 1102 nucleotide sites represented bases from partial sequences of 18S rDNA (consistent with Mariaux 1998); 1215 total characters, and 271 informative for parsimony analysis. Sequence alignments have been deposited in EMBL/GenBank and a complete list of genera and species and their GenBank accession numbers are documented (see Mariaux 1998; complete alignments are also available from J.M.). GenBank data for additional taxa in the current analysis are as follows: *Calliobothrium* sp. (AF124469); *Litobothrium janovyi* (AF124468); *Haplobothrium globuliforme* (AF124458); *Eniochobothrium gracile* (AF124465).

Parsimony analysis

The two contrasting matrices allowed examination of the influence of character coding and different strategies of analysis (e.g., top-down employing supraspecific taxa versus bottom-up employing a series of genera and species as representatives of higher taxa) on tree structure and stability along with recovery and diagnosis of higher taxa. We examined the issue of maintenance of position for terminal supraspecific taxa in a cladogram with respect to a solution involving 'all' species (Bininda-Emonds *et al.* 1998; Wiens 1998).

Analysis of the matrices, written with MacClade 3.05 (Maddison and Maddison 1992), was conducted using PAUP 3.1.1, and PAUP* 4.0 (Swofford 1993, 1998). Analyses were done initially in a heuristic search mode (HS), with step-wise addition = simple and branch swapping either by nearest neighbour interchanges (NNI) or by tree bisection-reconnection (TBR); results were confirmed with branch and bound (B&B) for the consensus matrix. In HS and B&B, multistate characters were unordered; character weights were not applied; multistate taxa were designated as polymorphic; gaps in sequence alignments were treated as missing data, however, handling these as a fifth base had no influence on results; optimization was by ACCTRAN. Results are shown as a phylogenetic tree(s) with associated statistics, including the consistency index (CI), and rescaled consistency index (RC), or as strict consensus trees as defined by Swofford (1993). As implemented in PAUP* (Swofford 1998), resulting hypotheses were further evaluated via bootstrap and jack-knife resampling (Farris *et al.* 1996). Decay or Bremer-support indices (Bremer 1994) were calculated using AutoDecay 3.0.3 (distributed by the authors, T. Eriksson and N. Wikström 1995).

Host–parasite coevolution

Putative coevolutionary associations of definitive hosts and eucestode taxa were examined by mapping extant vertebrate taxa (e.g., Chondrichthyes, Holocephali, Actinopterygii, Teleostei, Amphibia, Chelonia, Mammalia, Lepidosauria, and Aves) onto the parasite tree. A host-matrix (not shown) was written with MacClade 3.05 and hosts as characters were

optimized onto the phylogeny of the Eucestoda (Maddison and Maddison 1992).

Total evidence and a phylogeny for the Eucestoda

Data set heterogeneity

The PHT revealed that the partitions (molecular versus morphological) were not homogeneous ($P < 0.01$). We were aware, however, of areas of conflict in these data, particularly in the placement of the Diphyllidea. With the Diphyllidea excluded, homogeneity was indicated with values dependent on the matrix and conditions of analysis ($0.08 > P > 0.02$).

Phylogeny of the Eucestoda

Parsimony analysis of the consensus matrix (Figure 12.2) resulted in two most-parsimonious trees (MPT) (excluding uninformative characters: CI = 0.671, RC = 0.378); monophyly for the Eucestoda was strongly supported. The MPTs were fully resolved except for a polytomy linking the Haplobothriidea with the Diphyllobothriidae and Bothriocephalidae. Trees were largely similar in general structure to those outlined by Hoberg *et al.* (1997c) or Mariaux (1998) but contrasted as follows: 1) Haplobothriidea + Pseudophyllidea as sister groups; 2) Trypanorhyncha placed basal to the tetrafossates (consistent with Hoberg *et al.* 1997c); 3) Litobothriidae and Lecanicephalidea as groups basal to the 'Tetraphyllidea' + remaining tetrafossates; and 4) Diphyllidea as the sister-taxon of the Proteocephalidea (consistent with Mariaux 1998). Bootstrap and jack-knife values were generally within a range of 70–100% except for three nodes (Figure 12.2).

Parsimony analysis of the comprehensive matrix resulted in 48 equal-length trees (CI = 0.484, RC = 0.378). The strict consensus was fully resolved (except for a polytomy among crown groups in the Cyclophyllidea) and congruent to the MPTs derived from analysis of the reduced matrix (Figure 12.3); the tree is consistent with phylogenetic diagnoses of a minimum of 16 orders. Bootstrap and jack-knife resampling revealed equivocal support in two sectors of the tree: 1) in relationships of the relatively basal Haplobothriidea + Pseudophyllidea (including Bothriocephalidae and Diphyllobothriidae); and 2) within the Cyclophyllidea.

Based on separate analyses (e.g., Hoberg *et al.* 1997c; Mariaux 1998) and the results of these combined, total evidence, analyses (Figures 12.1–12.3) the following observations are supported: 1) monophyly for Eucestoda; 2) a basal position for the monozoic Caryophyllidea; 3) Pseudophyllidea and Haplobothriidea as basal, polyzoic taxa with separation of the Diphyllobothriidae from the Bothriocephalidae and remaining pseudophyllideans; 4) Trypanorhyncha as the sister for the Litobothriidae and the tetrafossates; 5) Tetraphyllidean paraphyly; and 6) unequivocal support for the relationships and placement of the Nippotaeniidea + Tetrabothriidea + Mesocestoidata + Cyclophyllidea. In contrast to Hoberg *et al.* (1997c), the Pseudophyllidea + Haplobothriidea are sister-groups, the Lecanicephalidea are the sister-group for the remaining tetrafossates, and the Diphyllidea are the putative sister of the Proteocephalidea. In contrast to Mariaux (1998), the Trypanorhyncha are postulated as the sister of the Litobothriidae + tetrafossate tapeworms and Mesocestoidata are the sister of the Cyclophyllidea. Haplobothriidea, Litobothriidae, Lecanicephalidea, and Onchobothriidae had not been represented in the original analysis of sequences from 18S rDNA.

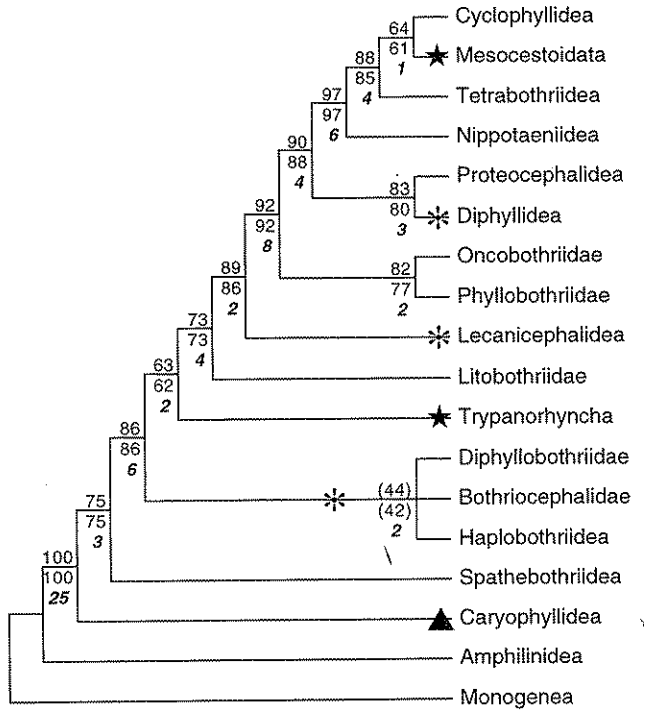

Figure 12.2 Phylogeny for the Eucestoda based on the 'consensus' matrix. Shown is the strict consensus of two MPTs resulting from analysis of total evidence combining morphological and molecular databases (length = 578; CI = 0.671; RC = 0.378). Incongruence with the morphologically based hypothesis (Figure 12.1; and Hoberg *et al.* 1997c, 1999b) is indicated by asterisks and is evident in the following areas: 1) placement of the Pseudophyllidea basal to the Haplobothriidea; 2) Diphyllidea as the sister of Trypanorhyncha + remaining eucestodes; and 3) Lecanicephalidea as the sister of the Proteocephalidea + remaining eucestodes. Departures from the molecular-based hypothesis (Mariaux 1998) are indicated by stars and include: 1) Trypanorhyncha as the sister of the Pseudophyllidea + remaining eucestodes; and 2) Mesocestoidata as the sister of the Tetrabothriidea + Cyclophyllidea. A major contrast with respect to the hypothesis by Olson and Caira (1999) is the alternative placement of the Spathebothriidea and Caryophyllidea as indicated by a triangle. Indices shown on the strict consensus tree: 1) bootstrap, above branches (1000 replicates with 10 repeats each, values < 50% shown in brackets); 2) jack-knife, below branches (1000 replicates with 10 repeats, HS; Jac emulation < 50% in brackets); 3) Bremer decay indices below branches, in bold italics.

Host–parasite relationships

Hosts were mapped onto a tree that summarizes the putative relationships for eucestodes based on analysis of the comprehensive matrix (Figure 12.4). A complex history involving cospeciation, colonization and extinction is indicated by this hypothesis. Actinopterygians are postulated as basal or ancestral hosts for eucestodes. Patterns of occurrence for cestodes are indicative of episodes involving serial colonization followed by rapid and potentially explosive radiations in fishes (e.g., neoselachians and teleosts), tetrapods, and amniotes (lineages leading to extant amphibians, mammals, chelonians, lepidosaurians, and birds).

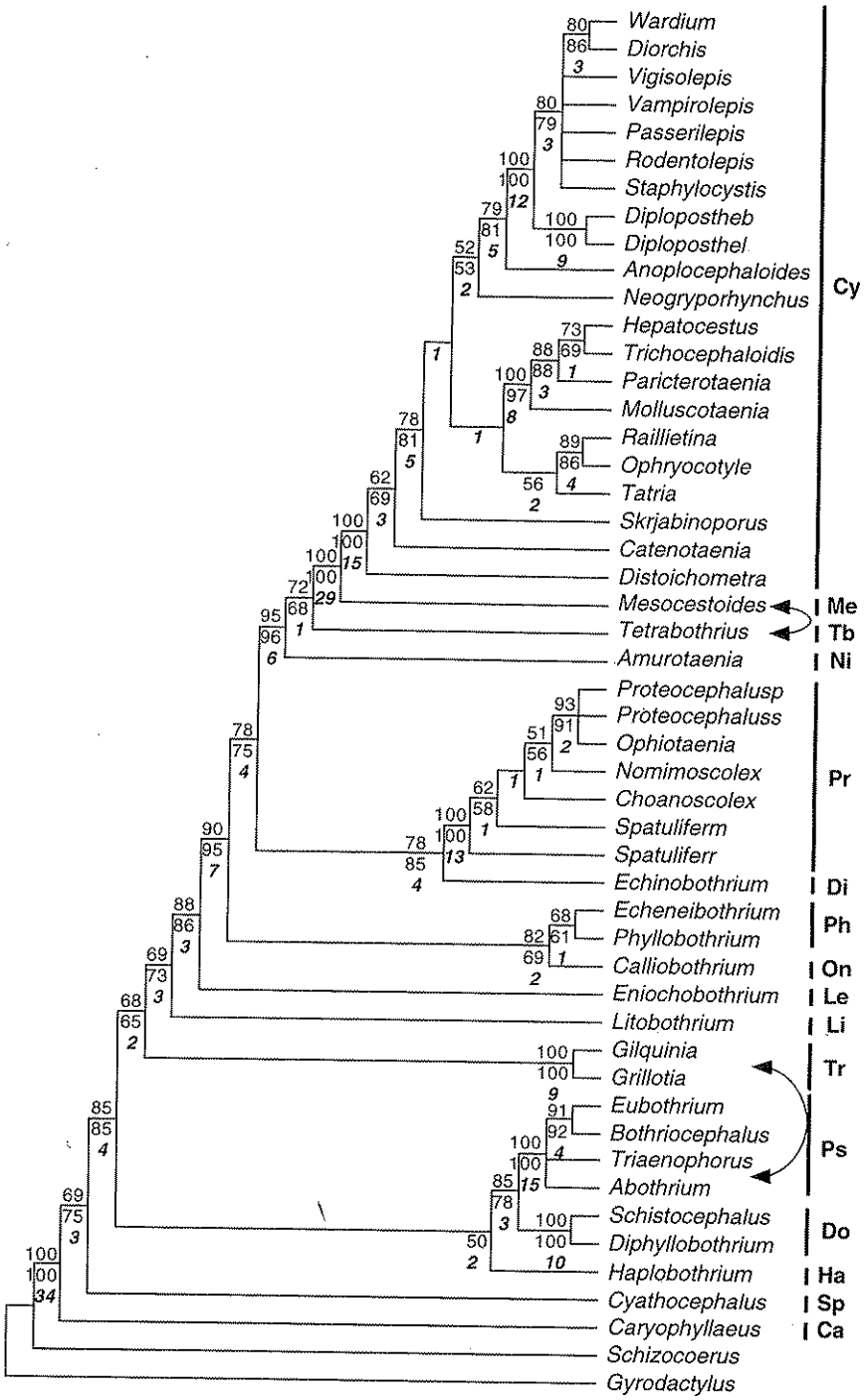

Figure 12.3 Phylogeny for the Eucestoda, based on total evidence and a 'comprehensive' matrix. The strict consensus is based on 48 MPTs (length = 1124; CI = 0.484; RC = 0.376). Note general congruence with relationships among ordinal level taxa in the 'consensus'/total evidence analysis (Figure 12.2). Bi-directional arrows show alternative placement of Pseudophyllidea/Trypanorhyncha and Tetrabothriidea/Mesocestoidata based on the comprehensive dataset for 18S rDNA (Mariaux 1998); departures in placement of Diphyllidea and Lecanicephalidea relative to the morphological hypothesis (Figure 12.1; Hoberg *et al.* 1997c) have been indicated in Figure 12.2. At a minimum, 16 orders may be diagnosed, with a clear separation of the Diphyllobothriidae from the Bothriocephalidae and Triaenophoridae in the Pseudophyllidea, and paraphyly for the Tetraphyllidea. Indices include: 1) bootstrap, above branches (100 replicates with 10 repeats each, HS; values < 50% shown in brackets); 2) jack-knife, below branches (100 replicates with 10 repeats each, HS; jac emulation < 50% in brackets); 3) Bremer decay indices in bold italics. Family and ordinal-level taxa, in phylogenetic order, are indicated as follows:
Ca = Caryophyllidea;
Sp = Spathebothriidea;
Ha = Haplobothriidea;
Do = Diphyllobothriidae;
Ps = Pseudophyllidea (including: Bothriocephalidae, Triaenophoridae);
Tr = Trypanorhyncha;
Li = Litobothriidae;
Le = Lecanicephalidea;
On = Onchobothriidae;
Ph = Phyllobothriidae;
Di = Diphyllidea;
Pr = Proteocephalidea;
Ni = Nippotaeniidea;
Tb = Tetrabothriidea;
Me = Mesocestoidata;
Cy = Cyclophyllidea.

Interpreting the phylogeny of the Eucestoda

Monophyly, characters and ordinal level relationships

Monophyly for the Eucestoda is independently corroborated based on molecular, comparative morphological, ontogenetic and ultrastructural characters (Ehlers 1984, 1985a,b, 1986; Brooks *et al.* 1985b, 1991; Brooks 1989a,b; Justine 1991a, 1998b; Brooks and McLennan 1993a; Hoberg *et al.* 1997c, 1999b; Mariaux 1998; Littlewood *et al.* 1999a). Phylogenetic trees resulting from separate (Hoberg *et al.* 1997c; Mariaux 1998) or combined analysis and from either a consensus or comprehensive matrix were well resolved and diagnosed largely congruent relationships for major taxa (Figures 12.1–12.3).

Given the results emanating from molecular data only (e.g., Olson and Caira 1999), we cannot exclude a fundamentally different scenario for the evolution of the eucestodes. Several lines of information (based on different weighting schemes in Mariaux 1998) from the current analysis and that of Olson and Caira (1999) would support diagnosis of largely difossate and tetrafossate clades (see also Mariaux and Olson 2001, this volume). A further contrast with the current analysis is the basal placement of the Spathebothriidea resulting from

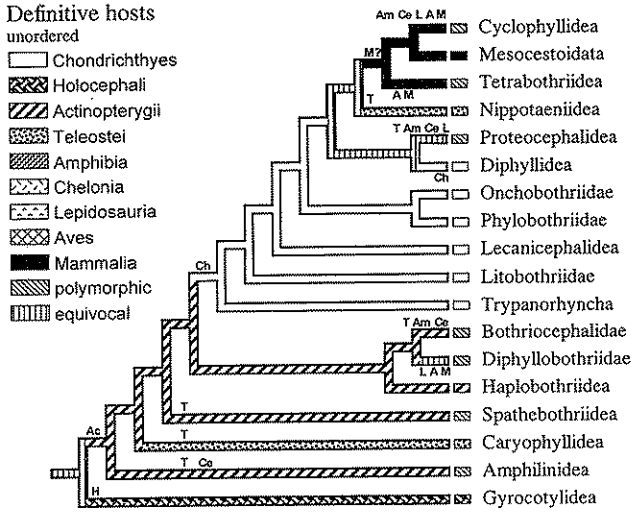

Figure 12.4 Phylogenetic hypothesis for the Eucestoda based on total evidence, showing the distribution of major vertebrate definitive hosts. Host taxa are mapped and optimized on the tree representing the 'consensus' analysis, with further resolution of relationships summarized from Figures 12.1–12.3, with MacClade 3.05 (Maddison and Maddison 1992). Host distributions are indicative of an early association with basal actinopterygian fishes, multiple colonization events of basal teleosts, and a secondary colonization of and radiation in chondrichthyans; colonization also accounts for the distribution of the tetrabothriideans in marine mammals and seabirds (Hoberg *et al.* 1997c, 1999a,b). Although the root of the subclade for Tetrabothriidea, Mesocestoidata + Cyclophyllidea optimizes to mammalian hosts, the associations of these groups with tetrapods appear to be older than implied and may reflect radiations in now extinct host groups (Hoberg *et al.* 1999a,b). The broader aspects of the putative history for these associations is not refuted by alternative placement of the Lecanicephalidea or Diphyllidea and inclusion of the Litobothriidae (Hoberg *et al.* 1999b). Host taxa are indicated as follows: A = Aves; Ac = Actinopterygii; Am = Amphibia; Ce = Chelonia; Ch = Chondrichthyes; H = Holocephali; L = Lepidosauria; M = Mammalia; T = Teleostei.

analysis of *Elongation factor* -1α and 18S rDNA (Olson and Caira 1999). Some aspects of these hypotheses appear weakly corroborated, however, and may be contradicted by both comparative morphology and total evidence. Additionally, the placement of the Diphyllidea with the Proteocephalidea in the current analysis and that of Mariaux (1998) seem ambiguous, given that this topology has not been observed in any other phylogenetic studies of molecular or morphological data.

Prior hypotheses for relationships among orders of the eucestodes represent two basic patterns (reviewed in Hoberg *et al.* 1997c; Mariaux 1998). Loennberg (1897) and Baer (1950) proposed a dichotomous and hierarchical phylogeny. In contrast, major lineages, diagnosing separate difossate and tetrafossate groups derived from a common ancestor, were defined by Fuhrmann (1931), Euzet (1959, 1974), Dubinina (1980), Euzet *et al.* (1981), and Olson and Caira (1999). Among difossate or tetrafossate taxa Freeman (1973) recognized five distinct lineages. Brooks *et al.* (1991), and Brooks and McLennan (1993a) defined a difossate lineage and a tetrafossate lineage with three coordinate sister-groups. Based on either separate or combined analyses, however, there is no apparent support for the diagnosis of distinct clades or lineages for difossate versus tetrafossate tapeworms. Detailed comparisons among this range of hypotheses based either on comparative morphology or sequence data have been considered previously (Hoberg *et al.* 1997c, 1999b; Mariaux 1998; Mariaux and Olson 2001, this volume).

The following areas of concordance are notable with respect to the current and prior hypotheses: 1) The caryophyllids are basal with monozooy postulated as ancestral (Llewellyn 1965; Mackiewicz 1972; Dubinina 1980; Ehlers 1986; Hoberg *et al.* 1997c; Mariaux 1998); 2) difossate forms are primitive and basal to the tetrafossate groups of the higher tapeworms, and the difossate forms (e.g., pseudophyllideans) are the sister-group of the strongly polyzoic tapeworms (Brooks *et al.* 1991; Hoberg *et al.* 1997c); 3) Pseudophyllidea contains two distinct lineages represented by Diphyllobothriidae and Bothriocephalidae (Bray *et al.* 1999); 4) the Pseudophyllidea and Haplobothriidea are closely related (Olson and Caira 1999); 5) Trypanorhyncha are the putative sister for the Litobothriidae + higher tetrafossates; 6) higher tapeworms or tetrafossates, e.g., lecanicephalideans, onchobothriids, phyllobothriids, proteocephalideans (+ diphyllideans), nippotaeniideans, tetrabothriideans and mesocestoidatans + cyclophyllideans, are closely related or potentially coordinate groups (Loennberg 1897; Fuhrmann 1931; Baer 1950; Spasskii 1958, 1992; Euzet 1959; Freeman 1973; Dubinina 1980; Brooks *et al.* 1991; Brooks and McLennan 1993a; Hoberg *et al.* 1997c; Mariaux 1998; Olson and Caira 1999); 7) the tetraphyllideans do not constitute a natural group but are paraphyletic (Loennberg 1897; Euzet *et al.* 1981; Hoberg *et al.* 1997c, 1999b; Caira *et al.* 1999); 8) nippotaeniideans are derived within the higher tapeworms (Dubinina 1980; Hoberg *et al.* 1997c; Mariaux 1998; Olson and Caira 1999); and 9) the tetrabothriideans are the putative sister-group of the cyclophyllideans (Dubinina 1980; Hoberg *et al.* 1997c, 1999a; Olson and Caira 1999) or the mesocestoidatans + cyclophyllideans (Mariaux 1998). The status of the Mesocestoidata as an independent order, or as the basal member of the Cyclophyllidea may require further examination (see Mariaux 1998; Miquel *et al.* 1999; Hoberg *et al.* 1999a), although unequivocal separation from tetrabothriideans and cyclophyllideans is apparent (Figures 12.1–12.3).

The current study has minimal bearing on resolving the placement of the minor constituent taxa of the paraphyletic Tetraphyllidea (see Hoberg *et al.* 1997c; Caira *et al.* 1999). Although morphological characters have been studied for a diversity of species and genera among these taxa (e.g., Caira *et al.* 1999), a completely comparable molecular database is currently under development (Olson *et al.* 1999). Relationships of these taxa could have a bearing on understanding broader issues within the Eucestodes, if (1) they do not represent a domain in the tree or a series of coordinate taxa; or (2) other groups such as the Proteocephalidea and Lecanicephalidea are found to be paraphyletic- or subsumed within one or another of the 'tetraphyllidean' groups (see Caira *et al.* 1999; Olson and Caira 1999). Evidence presented from analyses of total evidence is compatible with the former contention in postulating a close relationship for 'tetraphyllideans', the Litobothriidae and Lecanicephalidea. Proteocephalideans have been regarded as monophyletic in most recent analyses (Rego *et al.* 1998; Zehnder and Mariaux 1999) although this requires more complete examination. Paraphyly for the Proteocephalidea, however, would in part be consistent with the systematics proposed by Spasskii (1958) in which it is placed as a suborder in the Tetraphyllidea with Phyllobothriata, Tetrabothriata, and Nippotaeniata.

Comparative data from morphology, ontogeny and ultrastructure are validated; a complementary nature is emphasized for: 1) morphological and molecular characters; and 2)

top-down versus bottom-up approaches (see Yeates 1995; Bininda-Emonds *et al.* 1998; Wiens 1998). Recognition of a robust phylogenetic signal and support for these hypotheses is indicated, based on both consensus and comprehensive data, within the context of a total evidence approach (Kluge 1989; de Queiroz *et al.* 1995; Sanderson *et al.* 1998). This is consistent with the contention of Bininda-Emonds *et al.* (1998) that analysis of supraspecific taxa as terminals can be phylogenetically informative. Additionally, this suggests that in studies of the Platyhelminthes, there is no compelling reason to exclude certain classes of morphological characters – and in essence select only those that give solutions (or resolution) congruent to that based on molecular sequence data (e.g., see arguments in de Queiroz *et al.* 1995).

Trends in character evolution

Major conclusions about morphological characters and their evolution (origin of a segmented strobila; ovarian, vitelline and uterine development; eggs; spermatozoa and spermiogenesis) have not dramatically changed from those presented in Hoberg *et al.* (1997c) and Mariaux (1998). Certain points, particularly those related to the origin of polyzooy and the structure of ancestral cestodes can be reiterated.

Based on the monozoic form of the Amphilinidea, the putative sister-group of the tapeworms and the basal position of the Caryophyllidea, an unsegmented strobila is postulated as plesiomorphic based on the analyses herein. A monozoic strobila as ancestral for the eucestodes is consistent with hypotheses presented by Llewellyn (1965), Rees (1969), Mackiewicz (1972), and Ehlers (1984, 1985a,b, 1986). A close relationship for the caryophyllids and spathebothriids may also be suggested by karyological characters (Petkeviciute 1996). Thus, the suggestion that these groups are subsumed within the Pseudophyllidea and that monozooy or the tendency toward monozooy is secondary in these orders (e.g., Baer 1950; Freeman 1973; Brooks *et al.* 1991; Brooks and McLennan 1993a) is not supported (see discussion in Brooks *et al.* 1991). This may refute the contention by Wardle and McLeod (1952) for convergence of the polyzoic strobila in difossate and tetrafossate lineages. Polyzooy appears to have been derived once among the eucestodes, initially in the common ancestor of the Pseudophyllidea + strobilate tapeworms.

We should note, however, that Olson and Caira (1999) have proposed a basal position for the Spathebothriidea, a contention in part supported by their molecular analyses of two independent gene loci and by a shared deletion in the *Ef*-1α gene among their spathebothriidean-exemplar and platyhelminth outgroups. Within the context of phylogeny for the outgroups, cestodarians and eucestodes, however, absence of the intron in *Ef*-1α represents the plesiomorphic condition and thus is equivocal in diagnosing support for a basal position for the Spathebothriidea. In essence, the presence of the intron is synapomorphic for a restricted group of eucestodes, but as a consequence absence may not be phylogenetically informative with respect to the Spathebothriidea.

If the spathebothriideans are the basal lineage of the tapeworms a single origin of polyzooy among the eucestodes remains supported. The monozoic condition in the caryophyllideans, as a component of the pseudophyllidean/ haplobothriidean lineage, would be consistent with a single reversal to monozooy in the former group (Olson and Caira 1999). Results outlined herein, however, and those from independent analyses (Hoberg *et al.* 1997c; Mariaux 1998) support a basal position for the caryophyllideans that is bolstered by strong Bremer and bootstrap indices, and fail to diagnose a relationship between the pseudophyllidean and caryophyllidean lineages.

Holdfast structures among the eucestodes are diverse. The single apical sucker constitutes a deep plesiomorphy with respect to the structure observed in the amphilinids (Brooks *et al.* 1991; Littlewood *et al.* 1999a). Ancestral tapeworms have been regarded as either tetrafossate, such as the Tetraphyllidea or Proteocephalidea (e.g., Wardle and McLeod 1952), or difossate such as the Pseudophyllidea (e.g., Joyeux and Baer 1961). It is apparent, however that definable suckers are lacking in the basal groups of eucestodes.

Current analyses are compatible with an ancestral condition being represented by a unifossate (and monozoic) tapeworm, as defined by Freeman (1973). Among polyzoic cestodes, difossate forms, with bilateral symmetry and bothria (Pseudophyllidea, Haplobothriidea) are derived relative to the Caryophyllidea and Spathebothriidea. Subsequent development resulted in tetrafossate forms with bothridia (Trypanorhyncha), suckers (Lecanicephalidea and later Proteocephalidea–Cyclophyllidea) or bothridia + suckers (Onchobothriidae, Phyllobothriidae). Relative placement of the Trypanorhyncha would suggest that bothridia are plesiomorphic among the tetrafossate tapeworms, and that suckers are derived from bothridial margins, in contrast to Brooks *et al.* (1991). Difossate forms with bothridia such as the Diphyllidea, the putative sister of the Proteocephalidea remain enigmatic (Ivanov and Hoberg 1999). Tetraphyllidean and tetrabothriidean bothridia, or bothridia-like suckers with auricular appendages, are not homologous, and more definitive studies of the structure of tetrabothriidean 'bothridia' are required (Rees 1956; Andersen and Lysfjord 1982; Caira *et al.* 1999). Current placement of the Nippotaeniidea is consistent with paedomorphic development for the apical sucker, a character that may show ontogenetic convergence in the Litobothriidae.

Continued resolution of relationships at the ordinal and intraordinal levels for eucestodes is dependent on exploitation of new and poorly studied classes of characters (Mariaux 1996; Hoberg *et al.* 1997b,c; Caira *et al.* 1999; Olson and Caira 1999). A wealth of data remains to be revealed and evaluated within the context of homology for the ultrastructure of organ systems, structure and ontogeny of complex organs such as the uterus and rostellum (e.g., among the Cyclophyllideans), life history and larval stages, spermatozoons and spermiogenesis, and karyology. Integration with a rapidly expanding database for molecular sequences from multiple gene systems may dramatically contribute to confidence in resolving and reconstructing the evolutionary history for the eucestodes.

Parasite–host coevolution and systematics

Hypotheses for the phylogeny of the eucestodes have been strongly tied to concepts of host–parasite specificity as an indicator of extended and extensive coevolutionary histories of these assemblages (e.g., Fuhrmann 1931; Wardle and McLeod 1952; Dubinina 1980; discussed in Brooks *et al.* 1991) where extant representatives of primitive fishes, e.g., chondrichthyans, were considered to be hosts for the most ancestral taxa of tapeworms (Loennberg 1897). Results of the analyses currently presented, which place the Caryophyllidea, Spathebothriidea, Pseudophyllidea, and Haplobothriidea as basal to the 'higher tapeworms' fail to support this contention.

Examination of host distribution within the context of the current phylogeny for the eucestodes suggests a basal association

with actinopterygian fishes and independent colonization(s) and secondary radiation among chondrichthyans, teleosts, and tetrapods (Figure 12.4) (Hoberg *et al.* 1999a,b). This emphasizes the putative great age for origin of the eucestodes, and a temporally deep association with their hosts extending perhaps to the Devonian, ≥ 350–420 Ma. Hypotheses for deep age of the eucestodes and the relative contributions of cospeciation, host-switching and extinction as determinants of the structure of the contemporary fauna were initially outlined in studies of the higher phylogeny for eucestodes and the intraordinal relationships of cyclophyllideans (Hoberg *et al.* 1997c, 1999a,b). Independent estimates for the age of divergence for disparate segments of the parasite tree(s) were based on an integration of parasite and host phylogenies, host-distribution, biogeography for host–parasite assemblages, and historical geological data (Hoberg 1997). Archaic radiations previously postulated for the Monogenea, Digenea, Gyrocotylidea and Amphilinidea are consistent with these temporal estimates (e.g., Brooks 1989b; Brooks and McLennan 1993a; Boeger and Kritsky 1997). Conceptually, this theoretical framework has recently received corroboration through investigations on the broader history of the Platyhelminthes (Littlewood *et al.* 1999b).

Total evidence and concordant relationships

There is a general concordance in the relationships observed in trees derived from separate analysis of morphological and molecular data (Hoberg *et al.* 1997c; Mariaux 1998; Olson and Caira 1999; Mariaux and Olson 2001, this volume), and in those from a total evidence approach (Figures 12.1–12.3). Recognition of discrete lineages or clades for difossate and tetrafossate taxa is not generally supported, although such has been demonstrated in analyses of some molecular data (Olson and Caira 1999).

Principle conclusions derived from separate and combined analyses are the following: 1) Caryophyllids are basal within the Eucestoda and monozooy is ancestral; 2) Pseudophyllidea includes two distinct lineages represented by the Diphyllobothriidae and the Bothriocephalidae, Triaenophoridae and other families; 3) Pseudophyllidea + Haplobothriidea are the sister-group of the strongly polyzoic tapeworms and difossate forms are relatively primitive; 4) Trypanorhyncha is a relatively basal taxon; 5) Litobothriidae is the sister-group for the tetrafossates; 6) tetrafossates or higher tapeworms (Lecanicephalidea, 'Tetraphyllidea', Proteocephalidea + Diphyllidea, Nippotaeniidea, Tetrabothriidea, Mesocestoidata and Cyclophyllidea) are strongly diagnosed; 7) Tetraphyllidea is paraphyletic; 8) Nippotaeniidea is highly derived; and 9) Tetrabothriidea is a distinct order and the sister-group of the Mesocestoidata + Cyclophyllidea. Also emphasized is the putative deep age for origin and initial radiation of the eucestodes in the Paleozoic. The generality of these conclusions appears robust, based on the data available.

Phylogenetic studies of the Eucestoda are integral to biodiversity assessment and refinement of historical research programmes linking ecology and biogeography (e.g., Brooks and McLennan 1991, 1993a; Hoberg 1997; Hoberg *et al.* 1997a,b,c). Survey and inventory in biologically critical habitats is required in formulating a synoptic view of the history, structure and evolution of global biodiversity (Brooks and Hoberg 2000). Elucidation of coevolutionary and biogeographic histories for host–parasite assemblages involving cestodes, lends relevant information to programmes in conservation biology. Predictions about the age and duration of specific faunal associations (e.g., Hoberg *et al.* 1999a,b), recognition of regions of endemism and evolutionary 'hot spots' and the historical structure of ecosystems and communities emanate directly from phylogenetic studies of tapeworms (Hoberg 1997). Our phylogenetic knowledge of cestodes is an integrative framework to be applied to questions of the origin, maintenance and distribution of organismal diversity.

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Appendix 12.1. Morphological characters for analysis using supraspecific taxa as terminals, and the foundation for the 'consensus' matrix. Character descriptions, justification, polarity, and numbering are consistent with higher-level analyses among the Eucestoda (Hoberg *et al.* 1997c, 1999a).

Orders of the Eucestoda. 51 characters (characters 160–210 for consensus matrix; 1103–1153 for comprehensive matrix). Corresponding to Hoberg *et al.* (1997c, 1999a). Numbers correspond to those for characters in original papers. Polarity is discussed and defined in Hoberg *et al.* (1997c, 1999b). Morphological characters were polarized by taxonomic outgroup criteria (Watrous and Wheeler 1981; Maddison *et al.* 1984; Wiley *et al.* 1991), with reference to the Monogenea, Gyrocotylidea and the Amphilinidea, groups recognized as basal to the Eucestoda (Ehlers 1984, 1985a,b, 1986; Brooks *et al.* 1985b; Brooks 1989a,b; Brooks *et al.* 1991; Justine 1991a; Brooks and McLennan 1993a).

1. UTERUS (structure at initial stage of development). 4 states. 0 = tubular, coiled, sinuous; 1 = tubular, straight; 2 = granular or cellular Anlagen, which expands to form tubular and saccate structure; 3 = saccate, bilateral.
2. UTERUS (structure when gravid). 4 states. 0 = tubular, including straight and coiled forms; 1 = tubular, with anterior saccate expansion; 2 = saccate, without bilateral expansion; 3 = saccate, bilateral, usually with distinct diverticula, and including modifications from saccate condition. Seen in the Cyclophyllidea (including, reticulate, paruterine organs, capsules).
3. UTERINE PORE (structure). 4 states. 0 = permanent, ventral; 1 = dehiscence, ventral; 2 = dehiscence, dorsal; 3 = absent.
4. UTERUS (position). 2 states. 0 = ventral; 1 = dorsal.
5. GENITAL PORE (position). 3 states. 0 = marginal and separate; 1 = median; 2 = marginal and single.
6. GENITAL PORES (position and fusion). 3 states. 0 = male and female pores separate; 1 = separate or fused but opening in common atrium; 2 = fused.
7. ANTERIOR HOLDFAST (orientation and structure in adult). 3 states. 0 = apical sucker, single; 1 = bilateral, difossate; 2 = bilateral, tetrafossate.
8. ANTERIOR HOLDFAST (adult, structure of adhesive organs). 4 states. ? = not applicable as character; 0 = bothria; 1 = bothridia only; 2 = bothridia + suckers; 3 = suckers only; 4 = bothridia-like acetabulae with auricular appendages.

9. APICAL HOLDFAST (myzorhynchus). 2 states. 0 = absent; 1 = present.
10. ROSTELLUM. 2 states. 0 = absent; 1 = present and either non-retractable or retractable.
11. BOTHRIDIAL MARGINS (adult scolex). 3 states. 0 = absent; 1 = flimsy; 2 = rigid.
12. SCOLEX TENTACLES. 2 states. 0 = absent; 1 = present.
13. SCOLEX HOOKS (adult). 3 states. 0 = absent; 1 = present, on bothridia; 2 = present, on region anterior to the bothridia or bothria.
14. APICAL HOOKS (adult). 2 states. 0 = absent; 1 = spines, or hooks present.
15. HOOKS (structure of true hooks with base, handle and blade). 4 states. 0 = absent; 1 = 'Diphyllidean' spines and prongs; 2 = 'Tetraphyllidean/Trypanorhynchan', prong-like; 3 = taenioid.
16. SCOLEX (ontogeny of adult form). 2 states. 0 = adult form in intermediate host with limited differentiation in definitive host; 1 = adult form in definitive host only.
17. SCOLEX (structure at base). 2 states. 0 = lacking pedunculate form; 1 = pedunculate.
18. LONGITUDINAL MUSCULATURE (adult). 2 states. 0 = weakly developed; 1 = well developed, with clear demarcation of the cortical and medullary regions.
19. EGG DEVELOPMENT. 2 states. 0 = polylecithal; 1 = oligolecithal.
20. EGG (operculum). 2 states. 0 = present; 1 = absent.
21. EGG (quinone tanning). 2 states. 0 = present; 1 = absent.
22. EMBRYONIC MEMBRANES. 2 states. 0 = single membrane formed by embryo; 1 = 2 membranes with embryophore.
23. PROTONEPHRIDIUM (in hexacanth). 2 states. 0 = present; 1 = absent.
24. EMBRYOPHORE. 3 states. 0 = ciliated, developed as a coracidium; 1 = nucleated, non-rigid; 2 = rigid.
25. EMBRYOGENESIS. 2 states. 0 = not delayed; 1 = delayed.
26. HEXACANTH. 2 states. 0 = hexacanth oncosphere absent; 1 = present.
27. OVARY (structure in transverse section). 2 states. 0 = flat, lobate, globular; 1 = 'X'-shaped.
28. VITELLARIUM (position). 3 states. 0 = cortical; 1 = medullary; 2 = paramuscular.
29. VITELLARIUM (distribution, and form). 3 states. 0 = lateral, follicular; 1 = median, preovarian, globular; 2 = median, postovarian, globular.
30. VITELLARIUM (structure and disposition of ducts). 3 states. 0 = follicular, with multiple ducts; 1 = bilobed, globular, connected by two ducts, narrow isthmus and reservoir; 2 = compact, globular, with single duct.
31. STROBILA (external segmentation). 2 states. 0 = absent (monozoic); 1 = present (polyzoic).
32. STROBILA (internal segmentation). 2 states. 0 = absent; 1 = present.
33. STROBILA (segment structure). 3 states. 0 = monozoic; 1 = acraspedote; 2 = craspedote.
34. TESTES (position). 2 states. 0 = cortical; 1 = medullary.
35. CERCOID (ontogeny and structure). 2 states. 0 = larval scolex not invaginated (e.g. procercoids with bothria); 1 = larval scolex invaginated (cysticercoid, cysticercus, some cercoscolex).
36. CERCOID (ontogeny). 2 states. 0 = cercomer not forming cyst (acystic); 1 = cercomer forms cyst (cystic).
37. METACESTODE (apical). 2 states. 0 = apical sucker present; 1 = apical sucker absent.
38. METACERCOID (form). 6 states. 0 = absent; 1 = plerocercoid (bothriate); 2 = plerocercus (acetabulate type); 3 = caudate adults; 4 = neoplerocercus; 5 = acetabulo- or glandulo-procercoid.
39. SPERM (mitochondrion). 2 states. 0 = present; 1 = absent.
40. SPERM (crested-body). 2 states 0 = absent; 1 = present.
41. SPERM (peripheral microtubules). 2 states. 0 = parallel; 1 = twisted.
42. SPERMIOGENESIS. 4 states. 0 = flagellar rotation present, with 2 axonemes; 1 = Caryophyllidean type, single axoneme, with flagellar rotation and proximodistal fusion; 2 = single axoneme, flagellar rotation absent, with proximodistal fusion; 3 = single axoneme, without flagellar rotation or proximodistal fusion.
43. SPERM (periaxonemal sheath). 2 states. 0 = absent; 1 = present.
44. SPERM (formation and number of axonemes). 3 states. 0 = 2 axonemes; 1 = 1 axoneme, one free flagellum and flagellar bud + rootlet; 2 = 1 axoneme lacking rootlet structure.
45. ONTOGENY OF SCOLEX. 2 states. 0 = lacking heterochrony; 1 = with sequential heterochrony.
46. APICAL ORGAN (in adult). 3 states. 0 = absent; 1 = present as pit-like glandular structure at apex of scolex; 2 = present as a muscular cushion.
47. SPERM (striated root associated with each centriole). 2 states. 0 = present; 1 = absent.
48. SPERM (intercentriolar body). 2 states. 0 = present; 1 = absent.
49. SPERM (peripheral microtubules). 2 states. 0 = single arrangement of microtubules; 1 = dual arrangement of microtubules.
50. MICROTRICHES (scolex). 2 states. 0 = palmate structure absent; 1 = palmate structure present.
51. LARVAL CYST (structure). 2 states. 0 = lacking well-defined cyst; 1 = with well-defined cyst.

'Consensus' or reduced matrix for morphological characters (characters 1–51*).

New data represented here and for Appendix 12.2: 1) Pseudophyllidea are represented by constituent taxa as follows: Diphyllobothriidae and Bothriocephalidae (including morphological data for Triaenophoridae, Echinophallidae, Philobythiidae and Cephalochlamydidae); 2) Tetraphyllidea are represented by constituent taxa as follows: Onchobothriidae, Phyllobothriidae, and Litobothriidae ('minor families', Disculicipitidae, Prosobothriidae, Dioecotaeniidae, Chimaerocestidae, and Cathetocephalidae are not represented); 3) characters. 39–44 and 47–48 (sperm and spermiogenesis) for *Mesocestoides* based on Miquel *et al.* (1998) and Lecanicephalidea based on J.-L. Justine and L. Euzet (personal communication 1999); 4) all other characters for Mesocestoidata, which was originally subsumed within Cyclophyllidea (Hoberg *et al.* 1997c, 1999a); 5) character 47, striated root, was originally coded incorrectly for the Tetrabothriidea in Hoberg *et al.* (1997c). Codes: [n] = polymorphism; '?' = missing/unknown/inapplicable.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Monogenea	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphilinidea	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Caryophyllidea	0	0	0	0	1	[01]	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	[01]	0
Spathebothriidea	0	0	0	0	1	0	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Diphyllobothriidae	0	0	0	0	1	[01]	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Bothriocephalidae	0	1	0	0	[12]	1	1	0	0	0	0	0	[02]	[01]	0	0	0	0	0	[01]	0	0	0	[01]	1
Haplobothriidea	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Diphyllidea	1	1	3	0	1	1	1	1	0	0	1	0	2	1	1	0	1	0	0	1	?	?	?	1	0
Trypanorhyncha	1	2	[13]	0	2	2	2	1	0	0	2	1	0	0	2	0	1	0	0	[01]	0	0	1	0	1
Onchobothriidae	1	2	1	0	2	2	2	2	0	0	2	0	1	0	2	1	1	0	1	1	1	1	1	1	0
Phyllobothriidae	1	2	1	0	2	2	2	[12]	1	0	[12]	0	0	0	0	0	0	0	1	1	1	1	1	1	0
Litobothriidae	1	2	?	0	2	1	0	?	0	0	0	0	0	0	0	?	0	0	1	1	?	?	?	?	?
Lecanicephalidea	1	2	1	0	2	2	2	3	1	0	0	0	0	[01]	0	0	0	0	1	1	1	1	1	1	0
Proteocephalidea	2	3	1	0	2	2	2	3	0	[01]	0	0	0	[01]	[03]	0	0	[01]	1	1	1	1	1	[12]	[01]
Nippotaeniidea	1	2	3	0	2	2	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
Tetrabothriidea	2	2	2	1	2	2	2	4	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	0
Cyclophyllidea	3	3	3	[01]	2	2	2	3	0	[01]	0	0	0	[01]	[03]	[01]	0	1	1	1	1	1	1	2	0
Mesocestoidata	[13]	3	3	0	1	2	2	3	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	0

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
Monogenea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphilinidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caryophyllidea	1	0	[01]	0	0	0	0	0	0	0	0	1	3	1	1	0	1	0	1	0	0	0	0	0	0	0
Spathebothriidea	1	0	0	0	0	0	1	0	0	0	0	1	3	1	?	0	?	0	?	0	0	?	?	?	0	0
Diphyllobothriidae	1	0	0	0	0	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Bothriocephalidae	1	0	[01]	[02]	[02]	1	1	[12]	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Haplobothriidea	1	0	1	0	0	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Diphyllidea	1	0	0	0	0	1	1	1	1	0	?	?	?	1	1	0	[01]	0	[01]	0	0	0	0	0	1	1
Trypanorhyncha	1	[01]	0	0	0	1	1	[12]	1	0	0	1	4	1	1	0	0	?	0	0	0	0	0	0	1	1
Onchobothriidae	1	[01]	1	0	0	1	1	1	1	0	0	0	5	1	1	0	0	0	0	1	1	0	0	1	0	0
Phyllobothriidae	1	[01]	1	0	0	1	1	[12]	1	0	0	1	5	1	1	0	1	0	1	0	1	0	0	1	0	0
Litobothriidae	1	[01]	1	0	0	1	1	2	1	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?
Lecanicephalidea	1	0	1	0	0	1	1	1	1	0	0	1	5	1	1	0	1	0	1	0	0	0	0	1	0	0
Proteocephalidea	1	0	[012]	0	0	1	1	[12]	[01]	[01]	0	[01]	2	1	1	[01]	[01]	0	[01]	0	[01]	0	[01]	0	0	0
Nippotaeniidea	1	0	1	1	1	1	1	1	1	0	0	0	2	1	?	0	?	0	1	0	0	?	?	?	0	0
Tetrabothriidea	1	0	1	1	[02]	1	1	2	1	0	0	0	5	1	1	1	1	1	1	1	1	0	1	0	0	0
Cyclophyllidea	1	0	1	2	2	1	1	2	1	1	[01]	[01]	2	1	1	1	[23]	1	2	[01]	0	1	1	0	0	0
Mesocestoidata	1	0	1	2	2	1	1	2	1	1	0	1	2	1	1	0	1	?	1	0	1	0	0	0	0	0

Appendix 12.2. Morphological characters for analysis using generic and species level taxa as terminals, and the foundation for the 'comprehensive' matrix. Character descriptions, justification and polarity, and numbering are consistent with: 1) higher-level analyses among the Eucestoda (Hoberg *et al.* 1997c, 1999b); 2) Cyclophyllidea (Hoberg *et al.* 1999a); 3) Proteocephalidea (Rego *et al.* 1998); and 4) Pseudophyllidea (Bray *et al.* 1999).

Order Cyclophyllidea. 35 characters (characters 1154–1188 for comprehensive matrix). Corresponding to Hoberg *et al.* (1999a).

1. STROBILA (shape). 2 states. 0 = flattened, ribbon-like; 1 = cylindrical.
2. STROBILA (sexual development of proglottid). 2 states. 0 = hermaphroditic; 1 = dioecious.
3. STROBILA (segmentation). 2 states. 0 = strongly defined; 1 = absent or poorly defined.
4. STROBILA (segment structure). 2 states. 0 = acraspedote; 1 = strongly craspedote.
5. GENITAL PORE (position). 2 states. 0 = marginal; 1 = ventral, median.
6. ACCESSORY REPRODUCTIVE DUCTS. 2 states. 0 = absent; 1 = present.
7. TESTES (number). 2 states. 0 = numerous; 1 = generally not > 2 or 3.
8. SEMINAL VESICLE (internal). 2 states. 0 = absent; 1 = present.
9. SEMINAL VESICLE (external). 2 states. 0 = absent; 1 = present.
10. VAGINA. 2 states. 0 = present; 1 = absent.
11. GENITALIA. 2 states. 0 = single; 1 = double.
12. PROGLOTTID (ontogeny). 2 states. 0 = protandrous; 1 = proterogynous.
13. OVARY (position and form). 2 states. 0 = positioned in far posterior of proglottid, strongly bilobed and compact; 1 = not positioned in far posterior, and usually multilobate.
14. UTERUS (position relative to female organs). 0 = ventral; 1 = dorsal.
15. UTERUS (structure). 6 states. 0 = longitudinal sac with diverticula; 1 = tubular; 2 = initially transverse tubular, later saccate expanding to fill segment; 3 = saccate; 4 = reticulate; 5 = labyrinthine.
16. UTERUS (persistence). 2 states. 0 = persistent; 1 = ephemeral or transient.
17. PARUTERINE ORGAN. 2 states. 0 = absent; 1 = present.
18. EGGS (structure, striated embryophore). 2 states. 0 = embryophore not striated; 1 = embryophore striated.
19. EGGS (pyriform apparatus). 2 states. 0 = absent; 1 = present.
20. EMBRYOPHORE (polar processes). 2 states. 0 = absent; 1 = present.
21. EGGS (thin-walled capsules). 2 states. 0 = absent; 1 = present.
22. EGGS (fibrous capsules). 2 states. 0 = absent; 1 = present.
23. ROSTELLUM (structure). 5 states. 0 = absent; 1 = sucker-like; 2 = taeniid; 3 = sac-like; 4 = davaineid.
24. ROSTELLAR SHEATH. 2 states. 0 = absent; 1 = present.
25. ROSTELLAR HOOKS (presence). 2 states. 0 = absent; 1 = present.
26. ROSTELLAR HOOKS (number of rows). 4 states. 0 = absent; 1 = 1 row; 2 = 2 rows; 3 > 2 rows.
27. ROSTELLAR HOOKS (hammer form). 2 states. 0 = hammer-shaped hooks absent; 1 = hammer-shaped hooks present.
28. ROSTELLAR HOOKS (epiphyseal form). 2 states. 0 = hooks lacking well-demarcated epiphysis between handle and blade; 1 = hooks with epiphysis.
29. SUCKERS (armature). 2 states. 0 = consistently absent; 1 = present.
30. SCOLEX (structure during ontogeny). 3 states. 0 = retracted; 1 = invaginated; 2 = neither retracted nor invaginated.
31. LIFE CYCLE (number of hosts). 2 states. 0 = 3 hosts; 1 = 2 hosts.
32. PRIMARY LACUNA (larval ontogeny). 2 states. 0 = absent; 1 = present.
33. CERCOMER (larval ontogeny). 2 states. 0 = present (caudate); 1 = absent (acaudate).
34. METACESTODE (apical structure). 2 states. 0 = apical sucker present during development; 1 = apical sucker always absent.
35. METACESTODE ('cuticular hairs'). 2 states. 0 = metacestode with prominent 'cuticular hairs' (hair-like microtriches?); 1 = fibrous layer surrounding cysticercoid.

Order Proteocephalidea. 16 characters (characters 1189–1204 for comprehensive matrix). Corresponding to Rego *et al.* (1998).

3. OVARY (position). 3 states. 0 = medullary; 1 = initially medullary, developing cortically; 2 = cortical.
5. TESTICULAR FIELDS (position). 3 states. 0 = single field; 1 = two fields confluent in anterior; 2 = two distinctly separate fields.
6. UTERUS (position). 3 states. 0 = medullary; 1 = cortical; 2 = initially cortical developing medullary.
8. EGG (structure). 3 states. 0 = spherical to oval, external hyaline membrane present; 1 = internal polar circle-like structures present; 2 = polar filaments present.
10. VAGINAL SPHINCTER. 2 states. 0 = present; 1 = absent.
11. VAGINA (position relative to cirrus sac). 3 states. 0 = anterior; 1 = posterior; 2 = alternating.
12. GENITAL PORE. 2 states. 0 = alternating irregularly; 1 = unilateral.
15. TEGUMENTAL WRINKLES (transverse). 2 states. 0 = absent; 1 = present.
16. METASCOLEX. 2 states. 0 = absent; 1 = present.
18. SUCKERS. 2 states. 0 = spherical; 1 = alternative structures.
19. SUCKERS (appendages, auricular, papilla-like). 2 states. 0 = absent; 1 = present.
20. SUCKERS (distal sphincter). 2 states. 0 = present; 1 = absent.
23. LONGITUDINAL MUSCULATURE (arrangement). 2 states. 0 = isolated fibres; 1 = fibres organized in discrete bundles.
24. CIRRUS (spination). 2 states. 0 = present; 1 = absent.
25. SUCKERS (spination). 2 states. 0 = absent; 1 = present.
27. TEGUMENTAL WRINKLES (longitudinal). 2 states. 0 = absent; 1 = present.

Appendix 12.2 Continued.

Order Pseudophyllidea including Bothriocephalidae, Triaenophoridae and Diphyllobothriidae.

11 characters (characters 1205–1215 for comprehensive matrix). Corresponding to Bray *et al.* (1999). Numbers correspond to those for characters in original papers. Polarity is discussed and defined in Rego *et al.* (1998), Bray *et al.* (1999), and Hoberg *et al.* (1997c, 1999a,b).

3. SEGMENTATION (external). 3 states. 0 = absent; 1 = incomplete; 2 = present.
7. GENITAL PORE. 3 states. 0 = single; 1 = double; 2 = multiple.
8. GENITAL PORE (when median). 2 states. 0 = dorsal; 1 = ventral.
15. BOTHRIA (shape). 2 states. 0 = elongate slit; 1 = tiny slit.
21. APICAL DISC. 2 states. 0 = absent; 1 = present.
23. APICAL DISC (armature). 2 states. 0 = unarmed; 1 = armed.
27. OSMOREGULATORY CANALS. 2 states. 0 = four; 1 = many.
28. OSMOREGULATORY CANALS. 2 states. 0 = medullary; 1 = cortical.
37. VAGINA (sphincter). 2 states. 0 = absent; 1 = present.
39. UTERUS (shape, structure). 4 states. 0 = sigmoid, sinuous; 1 = saccular; 2 = diverticulate; 3 = Y-shaped.
40. UTERINE PORE. 2 states. 0 = median; 1 = submedian.

'Comprehensive' matrix for morphological characters. Characters 1–113. Complete listing of species-level taxa is found in Mariaux (1998). Uniformity in characters for spermatozoa and spermiogenesis is assumed within families; data for spermatozoa and spermiogenesis in Nematotaeniidae (*Distoichometra*) are for *Nematotaenia chantale* summarized in Miquel *et al.* (1999). Codes: [n] = polymorphism; '?' = missing/unknown; '9' = inapplicable character.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Gyrodactylus	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schizochoerus	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Caryophyllaeus	0	0	0	0	1	[01]	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	[01]	0
Cyathocephalus	0	0	0	0	1	0	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Molluscotaenia	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Hepatocestus	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Neogryporhynchus	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Paricterotaenia	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Trichocephaloidis	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Wardium	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Vigisolepis	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Vampirolepis	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Diploposthe b	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Diploposthe l	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Diorchis	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Passerilepis	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Rodentolepis	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Staphylocystis	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Anoplocephaloides	3	3	3	1	2	2	2	3	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	0
Catenotaenia	3	3	3	0	2	2	2	3	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	2	0
Tatria	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Raillietina	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Ophryocotyle	3	3	3	0	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Skrjabinoporus	3	3	3	1	2	2	2	3	0	1	0	0	0	1	3	0	0	1	1	1	1	1	1	2	0
Mesocestoides	1	3	3	0	1	2	2	3	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	0
Distoichometra	3	3	3	?	2	2	2	3	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	0
Choanoscolex	2	3	1	0	2	2	2	3	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
Spatuliferm	2	3	1	0	2	2	2	3	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	1
Nomimoscolex	2	3	1	0	2	2	2	3	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
Spatulifer	2	3	1	0	2	2	2	3	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	0
Proteocephalusp	2	3	1	0	2	2	2	3	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
Proteocephaluss	2	3	1	0	2	2	2	3	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
Ophiotaenia	2	3	1	0	2	2	2	3	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	2	0
Eubothrium	0	1	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Triaenophorus	0	1	0	0	2	2	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1
Abothrium	0	1	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Bothriocephalus	0	1	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Schistocephalus	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Diphyllobothrium	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tetrabothrius	2	2	2	1	2	2	2	4	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	0
Echeneibothrium	1	2	1	0	2	2	2	1	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0
Phyllobothrium	1	2	1	0	2	2	2	2	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0
Calliobothrium	1	2	1	0	2	2	2	2	0	0	2	0	1	0	2	1	1	0	1	1	1	1	1	1	0
Litobothrium	1	2	?	0	2	1	0	9	0	0	0	0	0	0	0	?	0	0	1	1	?	?	?	?	?
Echinobothrium	1	1	3	0	1	1	1	1	0	0	1	0	2	1	1	0	1	0	0	1	?	?	?	1	0
Gilquinia	1	2	3	0	2	2	2	1	0	0	2	1	0	0	2	0	1	0	0	[01]	0	0	1	1	1
Grillotia	1	2	1	0	2	2	2	1	0	0	2	1	0	0	2	0	1	0	0	[01]	0	0	1	0	1
Amurotaenia	1	2	3	0	2	2	0	9	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
Eniochobothrium	1	2	1	0	2	2	2	3	1	0	0	0	0	[01]	0	0	0	0	1	1	1	1	1	1	0
Haplobothrium	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Gyrodactylus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schizochoerus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caryophyllaeus	1	0	[01]	0	0	0	0	0	0	0	0	1	3	1	1	0	1	0	1	0	0	0	0	0	0
Cyathocephalus	1	0	0	0	0	0	1	0	0	0	0	1	3	1	?	0	?	0	?	0	0	?	?	?	0
Molluscotaenia	1	0	1	2	2	1	1	2	1	1	0	1	2	?	?	?	?	?	?	0	0	?	?	?	0
Hepatocestus	1	0	1	2	2	1	1	2	1	1	0	1	2	?	?	?	?	?	?	0	0	?	?	?	0
Neogryporhynchus	1	0	1	2	2	1	1	2	1	1	0	1	2	?	?	?	?	?	?	0	0	?	?	?	0
Paricterotaenia	1	0	1	2	2	1	1	2	1	1	0	1	2	?	?	?	?	?	?	0	0	?	?	?	0
Trichocephaloidis	1	0	1	2	2	1	1	2	1	1	0	1	2	?	?	?	?	?	?	0	0	?	?	?	0
Wardium	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	3	0	2	0	0	1	1	0	0
Vigisolepis	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	3	0	2	0	0	1	1	0	0
Vampirolepis	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	3	0	2	0	0	1	1	0	0
Diplopostheb	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	3	0	2	0	0	1	1	0	0
Diplopostheb	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	3	0	2	0	0	1	1	0	0
Diorchis	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	3	0	2	0	0	1	1	0	0
Passerilepis	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	3	0	2	0	0	1	1	0	0
Rodentolepis	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	3	0	2	0	0	1	1	0	0
Staphylocystis	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	3	0	2	0	0	1	1	0	0
Anoplocephaloides	1	0	1	2	2	1	1	2	1	1	0	1	2	1	1	1	3	1	2	0	0	1	1	0	0
Catenotaenia	1	0	1	2	2	1	1	1	1	1	0	0	2	1	1	1	2	1	2	1	0	1	?	0	0
Tatria	1	0	1	2	2	1	1	2	1	1	1	1	2	?	?	?	?	?	?	0	0	?	?	?	0
Raillietina	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	2	1	2	0	0	1	1	0	0
Ophryocotyle	1	0	1	2	2	1	1	2	1	1	1	1	2	1	1	1	2	1	2	0	0	1	1	0	0
Skrjabinoporus	1	0	1	2	2	1	1	2	1	1	0	1	2	?	?	?	?	?	?	0	0	?	?	?	0
Mesocestoides	1	0	1	2	2	1	1	2	1	1	0	1	2	1	1	0	1	?	1	0	0	0	0	0	0
Distoichometra	1	0	1	2	2	1	1	1	1	1	0	1	2	1	1	1	2	?	2	0	0	1	1	0	0
Choanoscolex	1	0	0	0	0	1	1	1	0	?	0	?	2	1	1	?	?	0	?	0	0	0	?	0	0
Spatuliferm	1	0	0	0	0	1	1	1	0	0	0	?	2	1	1	?	?	0	?	0	0	0	?	0	0
Nomimoscolex	1	0	0	0	0	1	1	2	1	?	0	?	2	1	1	0	0	0	0	0	1	0	0	0	0
Spatulifer	1	0	0	0	0	1	1	1	1	0	0	?	2	1	1	?	?	0	?	0	0	0	?	0	0
Proteocephalusp	1	0	2	0	0	1	1	1	1	[01]	0	[01]	2	1	1	0	0	0	0	0	[012]	0	0	0	0
Proteocephaluss	1	0	2	0	0	1	1	1	1	[01]	0	[01]	2	1	1	0	0	0	0	0	[012]	0	0	0	0
Ophiotaenia	1	0	2	0	0	1	1	1	1	1	0	0	2	1	1	?	?	0	?	0	[012]	0	?	0	0
Eubothrium	1	0	0	0	0	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Triaenophorus	1	0	0	0	0	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Abothrium	1	0	0	0	0	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Bothriocephalus	1	0	0	0	0	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Schistocephalus	1	0	0	0	0	1	1	2	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Diphyllobothrium	1	0	0	0	0	1	1	2	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Tetrabothrius	1	0	1	1	2	1	1	2	1	0	0	0	5	1	1	1	1	1	1	1	1	0	1	0	0
Echeneibothrium	1	1	1	0	0	1	1	[12]	1	0	0	[01]	5	1	1	0	1	0	1	0	1	0	0	1	0
Phyllobothrium	1	[01]	1	0	0	1	1	[12]	1	0	0	[01]	5	1	1	0	1	0	1	0	1	0	0	1	0
Calliobothrium	1	0	1	0	0	1	1	2	1	0	0	0	5	1	1	0	0	0	0	1	1	0	0	1	0
Litobothrium	1	[01]	1	0	0	1	1	2	1	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0
Echinobothrium	1	0	0	0	0	1	1	1	1	0	?	?	?	1	1	0	[01]	0	[01]	0	0	0	0	0	1
Gilquinia	1	0	0	0	0	1	1	1	1	0	0	1	4	1	?	0	0	?	0	0	0	0	0	0	1
Grillotia	1	0	0	0	0	1	1	1	1	0	0	1	4	1	?	0	0	?	0	0	0	0	0	0	1
Amurotaenia	1	0	1	1	1	1	1	1	1	0	0	0	2	1	?	0	?	0	1	0	0	?	?	?	0
Eniochobothrium	1	0	1	0	0	1	1	1	1	0	0	1	5	1	1	0	1	0	1	0	0	0	0	1	0
Haplobothrium	1	0	1	0	0	1	1	1	1	0	0	1	1	1	?	0	0	0	0	0	0	0	0	0	0

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Gyrodactylus	0	0	0	9	9	0	0	9	0	0	0	0	9	9	0	9	0	9	9	9	9	9	9	9	9
Schizochoerus	0	0	0	9	9	0	0	9	0	0	0	0	9	9	0	9	0	9	9	9	9	9	9	9	9
Caryophyllaeus	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Cyathocephalus	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Molluscotaenia	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	3	1
Hepatocestus	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	5	0	0	0	0	0	0	0	3	1
Neogryporhynchus	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	3	0
Paricterotaenia	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	3	1
Trichocephaloidis	0	0	0	0	1	0	0	[01]	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	3	1
Wardium	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	3	0	0	0	0	[01]	0	0	3	1
Vigisolepis	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	3	0	0	0	0	0	0	0	3	1
Vampirolepis	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	2	0	0	0	0	0	0	0	3	1
Diploposthe b	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	2	0	0	0	0	0	0	0	3	1
Diploposthel	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	2	0	0	0	0	0	0	0	3	1
Diorchis	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	3	0	0	0	0	1	0	0	3	1
Passerilepis	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	3	0	0	0	0	[01]	0	0	3	1
Rodentolepis	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	5	0	0	0	0	0	0	0	3	1
Staphylocystis	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	3	0	0	0	0	0	0	0	3	1
Anoplocephaloides	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	2	0	0	0	1	0	0	0	0	0
Catenotaenia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Tatria	0	0	0	0	1	0	1	0	1	1	1	0	0	1	0	3	0	0	0	0	[01]	0	0	3	0
Raillietina	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	3	1	0	0	0	0	0	1	4	0
Ophryocotyle	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	4	0
Skrjabinoporus	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	3	0	0	0	0	0	0	0	1	0
Mesocestoides	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Distoichometra	0	1	0	1	0	0	0	1	0	0	0	0	0	1	?	3	1	1	0	0	0	0	0	0	0
Choanoscolex	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Spatuliferm	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Nomimoscolex	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Spatulifer	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Proteocephalusp	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Proteocephaluss	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Ophiotaenia	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Eubothrium	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Triaenophorus	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Abothrium	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Bothriocephalus	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Schistocephalus	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Diphyllobothrium	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Tetrabothrius	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Echeneibothrium	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Phyllobothrium	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Calliobothrium	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Litobothrium	?	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Echinobothrium	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Gilquinia	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Grillotia	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Amurotaenia	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Eniochobothrium	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Haplobothrium	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Gyrodactylus	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Schizochoerus	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Caryophyllaeus	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Cyathocephalus	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Molluscotaenia	1	2	0	0	0	0	1	1	1	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Hepatocestus	1	2	0	0	0	0	1	1	1	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Neogryporhynchus	1	2	0	0	0	0	0	1	0	1	?	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Paricterotaenia	1	1	0	0	0	0	1	1	1	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Trichocephaloidis	1	1	0	0	0	0	1	1	1	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Wardium	1	1	0	0	0	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Vigisolepis	1	1	0	0	0	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Vampirolepis	1	1	0	0	0	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Diplopostheb	1	1	0	0	0	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Diplopostheł	1	1	0	0	0	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Diorchis	1	1	0	0	[01]	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Passerilepis	1	1	0	0	0	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Rodentolepis	1	1	0	0	0	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Staphylocystis	1	1	0	0	0	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Anoplocephaloides	0	0	0	0	0	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Catenotaenia	0	0	0	0	0	0	1	1	0	0	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Tatria	1	1	0	0	[01]	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Raillietina	1	2	1	0	1	0	1	1	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Ophryocotyle	1	2	1	0	1	?	1	?	?	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Skrjabinoporus	1	[12]	0	1	0	?	1	?	?	1	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Mesocestoides	0	0	0	0	0	0	0	0	0	1	0	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Distoichometra	0	0	0	0	0	?	?	0	1	1	?	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Choanoscolex	9	9	9	9	9	9	9	9	9	9	9	2	0	1	2	0	1	0	1	1	1	0	0	0	1
Spatuliferm	9	9	9	9	9	9	9	9	9	9	9	1	0	0	0	1	2	0	1	1	0	0	0	0	1
Nomimoscolex	9	9	9	9	9	9	9	9	9	9	9	1	2	2	0	0	2	1	1	1	1	1	1	1	0
Spatulifer	9	9	9	9	9	9	9	9	9	9	9	1	0	0	0	1	2	0	1	1	0	0	0	0	1
Proteocephalusp	9	9	9	9	9	9	9	9	9	9	9	0	1	0	[01]	0	2	0	0	0	1	0	0	1	1
Proteocephaluss	9	9	9	9	9	9	9	9	9	9	9	0	1	0	[01]	0	2	0	0	0	1	0	0	1	1
Ophiotaenia	9	9	9	9	9	9	9	9	9	9	9	0	1	0	[01]	0	2	0	0	0	1	0	0	1	1
Eubothrium	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Triaenophorus	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Abothrium	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Bothriocephalus	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Schistocephalus	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Diphyllobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Tetrabothrius	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Echeneibothrium	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Phyllobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Calliobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Litobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Echinobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Gilquinia	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Grillotia	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Amurotaenia	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Eniochobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Haplobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9

	101	102	103	104	105	106	107	108	109	110	111	112	113
Gyrodactylus	9	9	9	9	9	9	9	9	9	9	9	9	9
Schizochoerus	9	9	9	9	9	9	9	9	9	9	9	9	9
Caryophyllaeus	9	9	9	9	9	9	9	9	9	9	9	9	9
Cyathocephalus	9	9	9	9	9	9	9	9	9	9	9	9	9
Molluscotaenia	9	9	9	9	9	9	9	9	9	9	9	9	9
Hepatocestus	9	9	9	9	9	9	9	9	9	9	9	9	9
Neogryporhynchus	9	9	9	9	9	9	9	9	9	9	9	9	9
Paricterotaenia	9	9	9	9	9	9	9	9	9	9	9	9	9
Trichocephaloidis	9	9	9	9	9	9	9	9	9	9	9	9	9
Wardium	9	9	9	9	9	9	9	9	9	9	9	9	9
Vigisolepis	9	9	9	9	9	9	9	9	9	9	9	9	9
Vampirolepis	9	9	9	9	9	9	9	9	9	9	9	9	9
Diplopostheb	9	9	9	9	9	9	9	9	9	9	9	9	9
Diplopostheb	9	9	9	9	9	9	9	9	9	9	9	9	9
Diorchis	9	9	9	9	9	9	9	9	9	9	9	9	9
Passerilepis	9	9	9	9	9	9	9	9	9	9	9	9	9
Rodentolepis	9	9	9	9	9	9	9	9	9	9	9	9	9
Staphylocystis	9	9	9	9	9	9	9	9	9	9	9	9	9
Anoplocephaloides	9	9	9	9	9	9	9	9	9	9	9	9	9
Catenotaenia	9	9	9	9	9	9	9	9	9	9	9	9	9
Tatria	9	9	9	9	9	9	9	9	9	9	9	9	9
Raillietina	9	9	9	9	9	9	9	9	9	9	9	9	9
Ophryocotyle	9	9	9	9	9	9	9	9	9	9	9	9	9
Skrjabinoporus	9	9	9	9	9	9	9	9	9	9	9	9	9
Mesocestoides	9	9	9	9	9	9	9	9	9	9	9	9	9
Distoichometra	9	9	9	9	9	9	9	9	9	9	9	9	9
Choanoscolex	0	1	9	9	9	9	9	9	9	9	9	9	9
Spatuliferm	0	0	9	9	9	9	9	9	9	9	9	9	9
Nomimoscolex	1	1	9	9	9	9	9	9	9	9	9	9	9
Spatulifer	0	0	9	9	9	9	9	9	9	9	9	9	9
Proteocephalusp	1	1	9	9	9	9	9	9	9	9	9	9	9
Proteocephaluss	1	1	9	9	9	9	9	9	9	9	9	9	9
Ophiotaenia	1	1	9	9	9	9	9	9	9	9	9	9	9
Eubothrium	9	9	0	2	9	0	1	1	?	?	1	1	1
Triaenophorus	9	9	0	2	9	0	1	1	?	?	1	1	1
Abothrium	9	9	0	2	9	0	1	1	?	?	1	1	1
Bothriocephalus	9	9	2	0	0	0	1	0	0	0	0	1	0
Schistocephalus	9	9	2	0	1	1	0	9	1	0	0	0	0
Diphyllobothrium	9	9	2	0	1	0	0	9	1	1	1	0	0
Tetrabothrius	9	9	9	9	9	9	9	9	9	9	9	9	9
Echeneibothrium	9	9	9	9	9	9	9	9	9	9	9	9	9
Phyllobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9
Calliobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9
Litobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9
Echinobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9
Gilquinia	9	9	9	9	9	9	9	9	9	9	9	9	9
Grillotia	9	9	9	9	9	9	9	9	9	9	9	9	9
Amurotaenia	9	9	9	9	9	9	9	9	9	9	9	9	9
Eniochobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9
Haplobothrium	9	9	9	9	9	9	9	9	9	9	9	9	9