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A PHYLOGENETIC HYPOTHESIS FOR SPECIES OF THE GENUS *TAENIA* (EUCESTODA: TAENIIDAE)

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ABSTRACT: Cladistic analysis of a numerical data matrix describing 27 characters for species of *Taenia* resulted in 4 most parsimonious phylogenetic trees (174 steps; consistency index = 0.28; homoplasy index = 0.72; retention index = 0.48). Monophyly for *Taenia* is diagnosed by the metacestode that is either a cysticercus or a form derived from a bladder-like larva; no other unequivocal synapomorphies are evident. Tree structure provides no support for recognition of a diversity of tribes or genera within the Taeniinae: Fimbriotaeniini and Taeniini have no phylogenetic basis. *Hydatigera*, *Fimbriotaenia*, *Fossor*, *Monordotaenia*, *Multiceps*, *Taeniarhynchus*, *Tetratirotaenia* must be subsumed within *Taenia* as synonyms. *Taenia saginata* and *Taenia asiatica* are sister species and distantly related to *Taenia solium*. Cospeciation with respect to carnivorous definitive hosts and *Taenia* appears to be limited. Although felids are putative ancestral hosts, contemporary associations appear to have resulted from extensive host-switching among felids, canids, hyaenids, and others. In contrast, relationships with herbivorous intermediate hosts are indicative of more pervasive coevolution; rodents as intermediate hosts are postulated as ancestral for the Taeniidae, *Taenia* + *Echinococcus*. Patterns appear consistent with rapid shifts between phylogenetically unrelated carnivores but among those that historically exploited a common prey resource within communities in specific biogeographic regions.

Cestodes of the genus *Taenia* Linnaeus, 1758 are of considerable medical and veterinary significance and, as a consequence studies at the species-level, have been focused and intensive (e.g., Abuladze, 1964; Verster, 1969; Rausch, 1994, 1997). There have been in excess of 70 nominal species described in the genus (Verster, 1969), but morphological limits among species are often problematic. Currently, approximately 35–40 species are recognized based on adult specimens, including those validated by Verster (1969) and additional species that were subsequently described (e.g., Jones and Khalil, 1984; Jones et al., 1988; Eom and Rim, 1993); many species continue to be established for metacestodes (e.g., Murai et al., 1993).

Although considerable taxonomic revision has been conducted, disagreements continue over both the number of genera in the family (2–13) and the number of species that are valid within *Taenia*, e.g., compare Abuladze (1964), Movsessian (1989), Bessonov et al. (1994), and Spasskii (1998) with Verster (1969), Schmidt (1986), and Rausch (1994). At 1 extreme of this continuum, the taxonomy proposed by Abuladze (1964) and adopted with some modifications by Bessonov et al. (1994) recognized 2 subfamilies with 12 or 13 genera: (1) Taeniinae Stiles, 1896 for *Taenia*, *Taeniarhynchus* Weinland, 1758, *Multiceps* Goeze, 1782, *Hydatigera* Lamarck, 1816, *Fossor* Honess, 1937, *Anoploaenia* Beddard, 1912, *Insinuarotaenia* Spasskii, 1948, *Tetratirotaenia* Abuladze, 1964, *Cladotaenia* Cohn, 1901 and *Paracladotaenia* Yamaguti, 1935; and (2) Echinococcinae Abuladze, 1960 for *Echinococcus* Rudolphi, 1801 and *Alveococcus* Abuladze, 1960. Taeniinae was partitioned into genera along 2 major ontogenetic paths; possession of fluid-filled metacestodes characterized *Taenia*, *Hydatigera*, *Multiceps*, and *Tae-*

niarhynchus; whereas a solid-bodied larva or armathyridium was regarded as typical of metacestodes in *Cladotaenia* and *Tetratirotaenia*. Subsequently, *Fimbriotaenia* Korniusshin and Sharpilo, 1986 was established for a unique, fimbriocercus larval form characteristic of a limited number of species formerly referred to *Taenia* (Korniusshin and Sharpilo, 1986).

In a further modification of this taxonomic framework, Spasskii (1998) recognized Taeniinae, Echinococcinae, and Anoploaeniinae Spasskii, 1990. In Taeniinae, he diagnosed 2 tribes: (1) Taeniini Rosmassler, 1832, for forms with a reticulate vitellarium, including *Taenia*, *Hydatigera*, *Multiceps*, and *Taeniarhynchus*; and (2) Fimbriotaeniini Spasskii, 1996 in which the vitellarium was compact or lobed, including *Fimbriotaenia*, *Insinuarotaenia*, *Monordotaenia* Little, 1967 and *Paracladotaenia*. In Anoploaeniinae, the tribes Dasyurotaeniini Spasskii, 1998 (for the rostellate and armed, *Dasyurotaenia*) and Anoploaeniini Spasskii, 1998 (for the arostellate and unarmed *Anoploaenia*) were established. Thus, a primary character of adult strobilate worms was used to justify the tribes, whereas a combination of morphological characters for adults or larvae or the range of intermediate and definitive hosts were employed to diagnose each of the genera. This proposal embodied much of the taxonomy outlined previously in the Russian literature where a number of genera, proposed for putative inclusive groups within *Taenia*, were based primarily on characteristics of larvae (e.g., Abuladze, 1964; Korniusshin and Sharpilo, 1986; Movsessian, 1989; Bessonov et al., 1994).

A contrasting view was outlined by Verster (1969) who diagnosed 2 major groups within *Taenia* based on the relative positions of the genital ducts and osmoregulatory canals in strobilate adults. In *Taenia*, Group I, the genital ducts pass between the osmoregulatory canals; in *Taenia*, Group II, they are ventral to the canals. Species referred to Group II were postulated to be relatively older or in relatively primitive carnivoran hosts. Verster (1969) relegated to synonymy with *Taenia* most of the genera of the Taeniinae regarded as valid in the taxonomy proposed by Abuladze (1964); she did not comment on *Anoploaenia*, *Dasyurotaenia*, *Cladotaenia*, or *Paracladotaenia*.

This concept for a reduced number of genera within the Taeniidae was supported by Rausch (1994, 1997), in part consistent

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with Verster (1969) and Schmidt (1986), who recognized 2 monotypic subfamilies: (1) Taeniinae for *Taenia* and (2) Echinococcinae for *Echinococcus* (with *Alveococcus* as a synonym). Such genera as *Hydatigera*, *Multiceps*, *Fossor*, *Monordotaenia*, *Taeniarhynchus*, *Tetratirotaenia*, and *Fimbriotaenia* were subsumed as synonyms of *Taenia*. Additionally, *Cladotaenia*, *Paracladotaenia* (earlier referred to Dilepididae by Freeman [1959] and Schmidt [1986]), *Anoplotaenia* (to Dilepididae by Schmidt [1986]), *Dasyurotaenia* (to Davaineidae by Schmidt [1986]), and *Insinuaroataenia* were excluded from the Taeniidae based on the contention that they were morphologically and ontogenetically incompatible (Rausch, 1994, 1997). Additionally, as Rausch (1994, 1997) indicated, divergent proposals for taxonomy within the Taeniinae stemmed from varying opinions about the significance of critical morphological characters for both strobilate adults and metacestodes.

Concepts for the structure of Taeniidae and Taeniinae are diverse, although most authorities considered, within the context of their respective studies, that each of the subfamilies, tribes, or genera that were diagnosed represented inclusive monophyletic groups within the family (e.g., Abuladze, 1964; Bessonov et al., 1994; Rausch, 1994; Spasskii, 1998). Monophyly for the Taeniidae has been generally accepted (e.g., Abuladze, 1964; Bessonov et al., 1994; Rausch, 1994, 1997; Spasskii, 1998) and corroborated by phylogenetic studies of the Eucestoda and Cyclophyllidea (Brooks et al., 1991; Hoberg et al., 1999). The Taeniidae is diagnosed as monophyletic within Cyclophyllidea, and as the putative sister-group of the Metadilepididae + Paruterinidae (see Hoberg et al., 1999), but phylogenetic relationships for species of *Taenia* remain largely unresolved. There was, however, no formal phylogenetic framework on which the taxonomic structure within Taeniidae was established; either Taeniinae was monotypic (e.g., Verster, 1969; Rausch, 1994, 1997) or relatively diverse, with a maximum of 8–10 genera (e.g., Bessonov et al., 1994; Spasskii, 1998).

These contrasting views of the taxonomic and genealogical diversity of *Taenia* have never been fully addressed within a phylogenetic context (see Okamoto et al., 1995; De Queiroz and Alkire, 1998). Thus, the degree to which Verster's groups or the array of genera that may be recognized within *Taenia* represent monophyletic taxa diagnosed by unequivocal characters remains to be evaluated. Attempts to resolve the current discordant taxonomy have relied thus far on distance methods lacking a phylogenetic context (e.g., Murai, et al., 1993; Gubányi, 1995). Indeed, Gubányi (1995) proposed that *Taenia* could be partitioned into several additional genera based on distance comparisons for morphometric characters of hooks; a phylogenetic basis for this proposal was not presented.

Knowledge of phylogenetic relationships is critical to inferring patterns of character evolution, diagnosis of monophyletic taxa, and elucidation of histories for host association and biogeography (Brooks and McLennan, 1991, 1993). Only 3 studies within *Taenia* have taken a phylogenetic approach, but these have examined relationships for a limited number of species in the genus (Moore and Brooks, 1987; Okamoto et al., 1995; De Queiroz and Alkire, 1998). Preliminary interpretation of the results of these investigations are consistent in suggesting that *Taenia* cannot be deconstructed if it is to represent a monophyletic taxon.

In the current study, we present the first comprehensive hypothesis for phylogeny of *Taenia* based on analysis of structural characters of adults and metacestodes within a comparative morphological context; this represents an extension of studies at the family level within the Cyclophyllidea (Hoberg et al., 1999). We do not examine here the larger issue of the placement of such genera as *Anoplotaenia*, *Dasyurotaenia*, or *Cladotaenia* but focus on phylogeny for species within the Taeniinae sensu stricto. Results of this analysis are applied to: (1) an examination of the taxonomic structure for the subfamily and genus; and (2) a discussion of putative relationships and coevolutionary history for species of *Taenia* in an array of herbivorous intermediate and carnivorous definitive hosts.

MATERIALS AND METHODS

Cladistic methods (Hennig, 1966) were applied to the development of an hypothesis for the phylogenetic relationships among species of *Taenia*. Species considered valid for this analysis were those listed by Verster (1969) and those that were subsequently described, primarily from African carnivores; species considered either as invalid or as inquirendae by Verster (1969) were excluded. In this initial analysis, character data were derived from Abuladze (1964), Verster (1969), original descriptions, and examination of specimens.

Monophyly for Taeniidae is consistent with results of phylogenetic analyses of the Cyclophyllidea (Hoberg et al., 1999), and this analysis forms the basis for outgroup comparisons in the current study. In the analysis of *Taenia* spp., there were 35 ingroup taxa. Among these species, transformation series were polarized by taxonomic outgroup criteria (Maddison et al., 1984) with reference to basal cyclophyllideans and particularly to *Echinococcus* that represents the putative sister-group for *Taenia* (e.g., Rausch, 1994; Okamoto et al., 1995). Characters 9 and 10 were evaluated with respect to a functional outgroup (Watrous and Wheeler, 1981) represented by the basal species of *Taenia*. Polymorphism for character 6 was evident in *Taenia acinonyxi*, *Taenia crocutae*, *Taenia laticollis*, *Taenia macrocystis*, *Taenia multiceps* and *Taenia taeniaeformis*; coding in the current study followed the most recent convention and was consistent with estimation of the ancestral condition (Kornet and Turner, 1999). A numerical matrix describing transformation series and characters for species of *Taenia* was developed from comparative morphological studies of adult and larval cestodes (Table I) and written with MacClade 3.05 (Maddison and Maddison, 1992).

Analysis was conducted with PAUP 3.1.1 (Swofford, 1993). The following parameters were specified: heuristic search (HS), ADD SEQ = simple, single tree held in stepwise addition, MULPARS, and BRANCH SWAPPING by tree bisection–reconnection (TBR); searches with other options yielded substantially longer trees. Bootstrap resampling with 100 replicates (with HS and TBR) was used to examine the relative strength of the phylogenetic hypothesis (see Swofford, 1993).

There were 27 binary and multistate characters in the analysis (Table I); multistate characters were run as unordered. Following development of the character matrix, 5 species, including *Taenia ingwei* Ortlepp, 1938, *T. laticollis* Rudolphi, 1819, *Taenia pseudolaticollis* Verster, 1969, *Taenia brachyacantha* Baer and Fain, 1951, and *Taenia dimniki* Jones and Khalil, 1984, all missing a block of data for metacestodes (characters 9–11), were excluded from the analysis. Relationships were examined for the following taxa: *T. solium* Linnaeus, 1758; *T. acinonyxi* Ortlepp, 1938; *Taenia crassiceps* (Zeder, 1800); *T. crocutae* Mettrick and Beverley-Burton, 1961; *Taenia endotheracicus* (Kirschenblatt, 1948); *Taenia gonyamai* Ortlepp, 1938; *Taenia hyaenae* Baer, 1926; *Taenia hydatigena* Pallas, 1766; *T. macrocystis* (Diesing, 1850); *T. multiceps* Leske, 1780; *Taenia omissa* Lühe, 1910; *Taenia ovis* (Cobbold, 1869) (including *Taenia krabbei* Moniez, 1879); *Taenia parenchymatosa* Pushmenkov, 1945; *Taenia pisiformis* (Bloch, 1780); *Taenia polyacantha* Leuckart, 1856; *Taenia regis* Baer, 1923; *Taenia rileyi* Loewen, 1929; *Taenia saginata* Goeze, 1782; *Taenia serialis* (Gervais, 1847); *T. taeniaeformis* (Batsch, 1786); *Taenia martis* Zeder, 1803; *Taenia mustelae* Gmelin, 1790; *Taenia parva* Baer, 1926; *Taenia selousi* Mettrick, 1962; *Taenia taxidiensis* Skinner, 1935; *Taenia twitchelli*, Schwartz, 1924; *Taenia asiatica* Eom and Rim, 1993; *Taenia madoquae*

TABLE I. Character matrix for phylogenetic analysis of *Taenia* spp.

Taxa	Characters																												
	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	26	27		
<i>Echinococcus*</i>	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	0	0	
<i>T. solium</i>	0	2	1	3	1	1	0	0	0	0	3	0	1	1	0	0	1	2	2	1	1	1	1	0	1	0	2	2	0
<i>T. acinonyxi</i>	0	0	1	2	1	0	0	0	0	0	3	0	1	0	0	1	0	1	1	1	1	0	1	0	1	1	1	1	
<i>T. crassiceps</i>	0	0	1	1	0	0	0	1	0	0	2	0	0	1	0	0	0	1	2	1	1	1	1	0	1	0	0	0	
<i>T. crocutae</i>	0	0	1	3	2	0	2	1	0	0	3	0	1	0	0	0	1	2	2	1	1	0	1	0	2	2	0	0	
<i>T. endotheracicus</i>	0	0	1	2	1	0	0	0	0	2	2	0	1	1	0	0	1	0	0	1	1	0	3	1	1	2	1	1	
<i>T. gonyamai</i>	0	0	1	4	1	1	2	1	0	0	3	0	1	0	0	0	0	2	0	1	1	0	1	0	1	2	1	1	
<i>T. hyaenae</i>	0	0	1	2	1	1	2	1	0	0	3	0	0	1	0	0	1	2	0	1	1	0	1	0	1	0	2	2	0
<i>T. hydatigena</i>	0	0	1	4	1	1	0	1	0	0	1	0	1	0	1	0	1	1	2	0	1	0	1	0	2	2	1	1	
<i>T. ingwei</i>	0	0	1	4	1	1	2	1	?†	? ?	? ?	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	1	1	
<i>T. laticollis</i>	0	0	1	2	0	0	0	1	? ?	? ?	? ?	0	1	1	0	0	1	1	0	1	1	0	3	1	1	1	0	0	
<i>T. macrocystis</i>	0	0	1	3	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	1	1	0	3	1	1	0	1	1	
<i>T. multiceps</i>	0	0	1	2	1	0	1	0	0	1	3	1	1	0	1	1	1	2	1	1	1	0	3	0	2	1	0	0	
<i>T. omisssa</i>	0	0	1	2	1	1	2	1	0	0	0	1	1	1	1	0	1	1	2	0	1	0	2	0	1	2	1	1	
<i>T. ovis</i>	0	0	1	4	2	1	2	0	0	0	3	0	1	0	1	1	0	1	1	0	0	1	1	0	2	2	1	1	
<i>T. parenchymatosa</i>	0	0	1	3	1	1	0	1	0	0	0	0	1	0	0	0	1	1	2	1	1	1	1	0	2	2	1	1	
<i>T. pisiformis</i>	0	0	1	4	0	1	0	0	0	0	1	0	0	0	0	1	1	2	1	1	0	0	2	0	2	1	0	0	
<i>T. polyacantha</i>	0	0	1	2	1	1	0	1	0	3	2	0	1	0	1	0	0	1	2	1	1	1	1	1	1	1	1	1	
<i>T. pseudolaticollis</i>	0	0	1	2	2	1	0	1	? ?	? ?	? ?	0	1	1	0	1	1	1	0	1	1	0	1	5	0	1	? ?	1	
<i>T. regis</i>	0	0	1	3	1	1	2	1	0	0	1	0	1	1	1	1	0	1	1	0	1	0	2	0	1	2	1	1	
<i>T. rileyi</i>	0	0	1	3	2	1	1	1	1	0	0	0	1	1	0	0	0	1	2	0	0	1	1	0	1	2	1	1	
<i>T. saginata</i>	1	3	1	5	2	1	2	1	0	0	3	0	1	0	0	0	1	2	1	0	1	0	4	2	2	2	1	1	
<i>T. serialis</i>	0	0	1	3	1	1	2	1	0	1	3	0	1	1	0	1	1	1	0	1	0	0	2	0	1	1	0	0	
<i>T. taeniaeformis</i>	0	0	0	3	0	0	2	1	1	0	0	0	0	1	0	0	0	0	2	1	1	2	3	0	1	2	1	1	
<i>T. brachyacantha</i>	0	0	0	1	0	1	0	0	? ?	? ?	? ?	0	1	1	0	1	1	0	2	1	1	0	0	1	0	0	0	? ?	
<i>T. martis</i>	0	0	0	1	1	1	0	1	0	3	2	0	0	1	0	1	1	1	2	0	0	1	1	0	0	0	1	1	
<i>T. mustelae</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	0	0	0	1	0	1	1	
<i>T. parva</i>	0	0	0	3	0	1	0	0	1	0	1	0	0	1	0	0	1	1	2	1	1	2	3	0	0	1	1	1	
<i>T. selousi</i>	0	0	0	2	0	1	0	0	0	2	1	0	1	1	0	0	0	1	2	1	0	2	2	1	1	0	0	0	
<i>T. taxidiensis</i>	0	1	0	1	1	1	0	1	0	0	3	0	0	1	0	0	0	1	2	0	0	1	1	0	1	1	1	1	
<i>T. twitchelli</i>	0	0	0	1	1	1	0	1	0	2	2	0	0	1	0	1	0	0	2	1	0	1	1	0	1	1	1	1	
<i>T. asiatica</i>	1	3	1	5	1	1	2	0	0	0	1	0	1	1	0	0	1	1	1	1	1	0	4	2	2	2	1	1	
<i>T. dinniki</i>	0	0	1	3	1	1	2	1	? ?	? ?	? ?	0	1	1	1	1	1	2	2	1	1	0	2	0	1	1	1	1	
<i>T. madoquae</i>	0	0	0	3	1	1	2	1	0	0	3	0	1	0	0	0	1	2	2	1	1	2	1	0	1	2	1	1	
<i>T. olngojinei</i>	0	0	0	3	1	1	0	0	0	0	3	1	1	0	1	0	1	1	2	1	1	1	3	0	1	1	0	0	
<i>T. simbae</i>	0	0	1	5	1	1	2	0	0	0	1	0	0	1	0	0	1	1	1	0	1	0	2	0	? ?	? ?	? ?	?	

* Outgroup and putative sister group for *Taenia*.
 † Missing data designated as “?”.

(Pellegrini, 1950); *Taenia olngojinei* Dinnik and Sachs, 1969; and *Taenia simbae* Dinnik and Sachs, 1972.

Results of the analyses are depicted as the most parsimonious phylogenetic tree(s) (MPTs) with associated statistics including the consistency index (CI), rescaled consistency index (RC), retention index (RI), and homoplasy index (HI) as defined in Swofford and Begle (1993). Consensus trees (50% majority rule) were used to examine relationships when more than a single MPT resulted from the analysis.

Host-parasite relationships and putative historical associations for parasites and hosts were examined by mapping extant host taxa (family level) onto the parasite tree. This was accomplished by using matrices for intermediate or definitive hosts (not shown) and optimizing these as characters on the parasite phylogeny with MacClade 3.05 (Maddison and Maddison, 1992). Data for life history and host distributions were derived primarily from Abuladze (1964), Sachs (1969), Verster (1969), Dinnik and Sachs (1969, 1972), Rausch (1977, 1981), and Jones et al. (1988).

RESULTS

Character descriptions for *Taenia* spp.

- 1. Hooks. 0 = present; 1 = absent.
- 2. Hooks. Number of rostellar hooks. Three states. 0 = 2 rows; 1 = 1 row; 2 = 3 rows; 3 = absent.

3. Position of genital ducts. In some species of *Taenia* and all *Echinococcus* the genital ducts pass outside the excretory canals. 0 = beyond the canals; 1 = between the canals.

4. Mean number of testes. Although the number of testes is difficult to determine, their mean value may reflect actual differences as discrete subsets. Most cyclophyllideans basal to the Taeniidae and the putative sister-group represented by the Metadilepididae + Paruterinidae have relatively few testes (Hoberg et al., 1999). 0 = ≤60; 1 = 100–200; 2 = 250≈350; 3 = ≈400 to ≤600; 4 = >600–700; 5 = >800.

5. Length of cirrus sac. The actual length of the cirrus sac is highly variable and often dependent on the age of the proglottid. Relative length (in relation to the position of the excretory canals), however, can be well defined, and an elongate cirrus sac is considered plesiomorphic. 0 = cirrus sac long (extending across canals); 1 = intermediate (extending to poral canals); 2 = short (not extending to canals).

6. Size of ovarian lobes. Lobation of the ovary is a synapomorphic condition in the Taeniidae. All species have 2 lobes

except *T. solium* that has 3. The relative size of the lobes appears to be species specific (Verster, 1969). Polymorphism is evident in *T. acinonyxi*, *T. crocutae*, *T. laticollis*, *T. macrocystis*, *T. multiceps*, and *T. taeniaeformis*, and these taxa are coded as plesiomorphic, consistent with the ancestral condition. 0 = lobes equal to subequal; 1 = antiporal lobe larger than poral lobe.

7. Vaginal sphincter. In many species a well developed vaginal sphincter is apparent, whereas in 2 species there is partial development of the sphincter. Presence of a sphincter is derived in *Taenia*. 0 = absent; 1 = incompletely developed; 2 = completely developed.

8. Vaginal dilatation. In some species the vagina has a characteristic dilatation proximal to the genital pore. This condition is not observed in species of *Echinococcus*. 0 = without dilatation; 1 = with dilatation.

9. Larval structure, mature metacestode strobilocercus. This character is considered for those species where the life cycle has been elucidated. The cysticercus and inclusive larval forms, represent a synapomorphy for *Taenia*. Coding for characters 9 and 10 is based on functional outgroup criteria, where the cysticercus is defined as plesiomorphic relative to the basal species of *Taenia* in preliminary analyses. The strobilocercus is considered to be derived from the cysticercus and is postulated as independent of other larval forms defined for species of *Taenia*. The strobilocercus, a strobilate metacestode with well developed scolex and prominent segmentation, is present in *T. taeniaeformis* and *T. parva*. The hemistrobilocysticercus, a larval form described for *T. rileyi* (see Rausch, 1981) is included here and is considered as intermediate to the cysticercus and strobilocercus. The coenurostrobilocercus larval form in *T. parva* is considered to be homologous with the strobilocercus (Murai et al., 1989). 0 = cysticercus; 1 = strobilocercus.

10. Larval structure, mature metacestode. The coenurus, polycephalic, and fimbriated larval forms are derived with respect to the cysticercus, but their ontogenetic relationships and homology are uncertain. Although both cysticercus and polycephalic larvae are known for *T. mustelae* (see Freeman, 1956), the former is postulated to be plesiomorphic (contrary to Crusz, 1948). Abuladze (1964) established *Tetratirotaenia* and defined the armatetrathyridium larva for *T. polyacantha*. Korniuschin and Sharpilo (1986) recognized the fimbriated form as characteristic of *T. martis*, *T. mustelae*, *T. twitchelli*, and *T. brachyacantha* and established *Fimbriotaenia*. In contrast, Rausch (1977) and Rausch and Fay (1988a, 1988b) considered the larval form defined for *T. polyacantha* to be similar to that of *T. martis* and that these differed substantially from the polycephalic metacestodes of *T. twitchelli*. 0 = cysticercus; 1 = coenurus (multiple scolices that develop by invagination into a central bladder—*T. serialis*, *T. multiceps*); 2 = polycephalic (protoscolices on elongate stalks that arise by exogenous budding from a central bladder that later regresses—*T. selousi*, *T. endothoracicus*, *T. twitchelli*); 3 = fimbriated (invaginated scolex, elongate, unsegmented larvae with characteristic folds—*T. martis*, *T. brachyacantha*, *T. polyacantha*).

11. Localization of the metacestode in the intermediate host. The site of larval development is generally species specific and without substantial variation. Several patterns of localization can be defined as follows and are related to where the hexacanth localizes with respect to the circulatory system of the inter-

mediate host: (a) hepatic, (b) peritoneal, (c) thoracic, and (d) systemic, usually intramuscular. 0 = hepatic; 1 = peritoneal; 2 = thoracic; 3 = systemic.

12. Testes, distribution and degree of confluence in anterior of proglottid. 0 = confluent; 1 = not confluent.

13. Testes, distribution and degree of confluence posterior to vitellaria. 0 = confluent; 1 = not confluent.

14. Testes, distribution and gap or discontinuity in field at level of the genital ducts. 0 = gap present; 1 = gap absent.

15. Testes distribution, fields disposed evenly or laterally. 0 = even; 1 = laterally.

16. Genital papilla. Two states. 0 = absent; 1 = present.

17. Uterine branches. 0 = lacking terminal bifurcation; 1 = with terminal bifurcation.

18. Genital pore, position on lateral margin of mature proglottid. 0 = anterior; 1 = median; 2 = posterior.

19. Vas deferens, route followed from cirrus sac relative to location of genital pore. 0 = anterior; 1 = median; 2 = posterior.

20. Testes, numbers of layers. 0 = 1; 1 = >2.

21. Vitellaria, shape of lobes. 0 = rounded; 1 = flattened.

22. Cirrus sac, shape. 0 = club or pear; 1 = ovoid; 2 = flask.

23. Large rostellar hooks, mean length. 0 = <50 μm ; 1 = 100–200; 2 = 250–300; 3 = >300.

24. Rostellar hooks, mean number. The number of rostellar hooks is usually distinctive, and 6 species have >54 hooks, whereas the remainder have 22–44. 0 = <44 hooks; 1 = >54 hooks.

25. Length of strobila (when gravid). 0 = small, <10 cm; 1 = medium, >10 cm to ≤ 75 cm; 2 = large, >1 m.

26. Width, maximum in gravid segments. 0 = 1–2 mm; 1 = 3–5 mm; 2 = >6 mm.

27. Mature proglottids, shape. 0 = longer than wide; 1 = wider than long.

Phylogeny for *Taenia* spp.

Analysis of a numerical data matrix describing characters for species of *Taenia* resulted in 4 MPTs (174 steps; CI = 0.28; HI = 0.72; RI = 0.48). Consensus trees (strict and 50% majority rule) are congruent) were used to summarize multiple, equal length trees (Fig. 1). Bootstrap resampling did not reveal strong support for any nodes. The 4 MPTs were largely congruent, differing only in relationships postulated within 3 derived subclades: (1) relationships for *T. twitchelli* or *T. taxiensis* as the sister species for *T. martis* within a *T. polyacantha* subclade; (2) the relationships among *T. ovis*, *T. hydatigena*, *T. omissa*, and *T. regis* as basal taxa within a *T. hydatigena* subclade that also contains *T. simbae* and *T. saginata* + *T. asiatica*; and (3) a basal polytomy in the *T. madoquae* subclade that also contains *T. solium*.

Monophyly for *Taenia* is diagnosed by the metacestode that is either a cysticercus or a form derived from a bladder-like larva. The genus is further diagnosed by a series of equivocal attributes that include characters influenced by homoplasy within the ingroup (apomorphic character states acquired basally, with either independent reversal or parallelism/convergence in crown taxa): (1) a high number of testes (character 4); (2) testes that are not confluent posterior to the vitelline gland (character

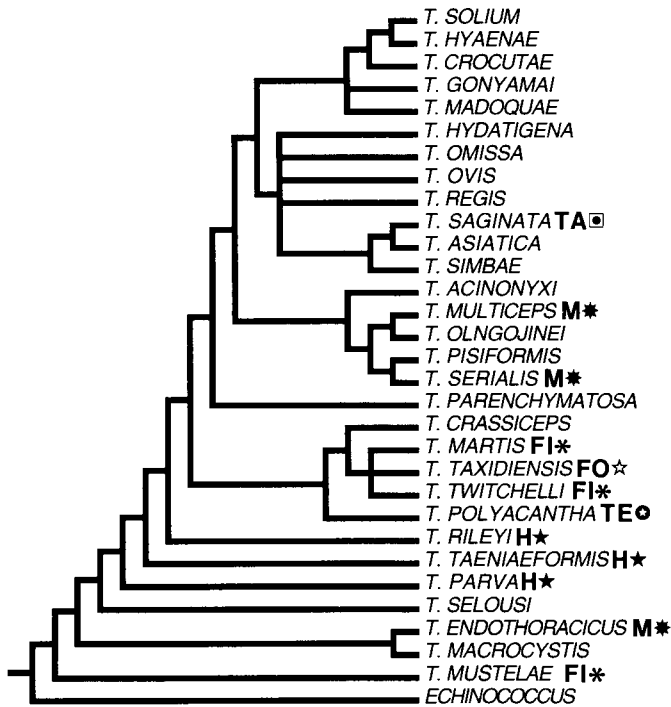


FIGURE 1. Phylogenetic hypothesis for species of *Taenia* based on analysis of comparative morphological data. Analysis resulted in 4 equal length trees (174 steps; CI = 0.28; HI = 0.72; RI = 0.48); shown is the 50% majority rule consensus tree (all nodes at 100%) derived from the 4 most parsimonious trees. Coding associated with terminal taxa indicates previous generic-level placement for respective species: FI = *Fimbriotaenia*; FO = *Fossor/Monordotaenia*; H = *Hydatigera*; M = *Multiceps*; TA = *Taeniarhynchus*; TE = *Tetratirotaenia*; repeated symbols indicate species referred to the same genus. Based on this hypothesis, these genera do not constitute inclusive monophyletic groups and should be subsumed as synonyms of the genus *Taenia*, consistent with Rausch (1994, 1997).

13); (3) a gap in the field of testes at the level of the genital ducts (character 14); (4) a median to posterior marginal genital pore (character 18); (5) flattened lobes of the vitelline gland (character 21); (6) generally medium to large strobila (character 25); and (7) mature proglottids that are often wider than long (character 27). These and other characters were mapped onto 1 of the MPTs in order to examine character evolution and support for the phylogenetic hypothesis for *Taenia* spp. (Fig. 2). Consistency indices for individual characters are summarized in Table II. Homoplasy was associated with 25 of 27 characters. Among these, 22 characters exhibited CIs substantially <0.50, further indicative of plasticity for structural, ontogenetic, and ecological attributes of *Taenia* spp.

Considering the overall topology for this hypothesis, *T. mustelae* is basal in the genus. There are 5 subclades within the largely resolved phylogeny, including: (1) *T. macrocystis* + *T. endothoracicus*; (2) *T. polyacantha* with *T. crassiceps* + *T. martis*, *T. twitchelli*, and *T. taxidiensis* in a polytomy; (3) *T. acinonyxi* with *T. multiceps* + *T. olngojinei* and *T. serialis* + *T. pisiformis*; (4) *T. hydatigena* in a polytomy with *T. omissa*, *T. ovis*, *T. regis*, and *T. simbae* + *T. asiatica* + *T. saginata*; and (5) *T. madoquae* in a polytomy with *T. gonyamai* and *T. crocutae* + *T. hyaenae* + *T. solium*. Notably, *T. solium* does not share a close common ancestor with *T. saginata*. Tree struc-

ture and partitioning of these subclades provides no support for recognition of a diversity of tribes or genera within Taeniinae (Fig. 1). The tribes, *Fimbriotaeniini* and *Taeniini* have no phylogenetic basis. *Hydatigera*, *Fimbriotaenia*, *Fossor*, *Monordotaenia*, *Multiceps*, *Taeniarhynchus*, and *Tetratirotaenia* must be subsumed within *Taenia*, as they do not represent discrete monophyletic taxa (Fig. 1).

Parasite–host relationships

Definitive and intermediate hosts for *Taenia* spp. were mapped onto the parasite phylogeny (Figs. 3, 4). Definitive hosts are represented by Viverridae, Mustelidae, Hyaenidae, Canidae, Felidae, and Hominidae; minimal consistency in host distribution is apparent (CI = 0.46, RI = 0.53; RC = 0.25) (Fig. 3). Felids may be ancestral definitive hosts for *Taenia*, and extensive colonization among a diverse assemblage of carnivores, particularly canids and felids, is postulated. Basal species are primarily found in felids and relatively derived species in canids as a subsequent source for cestodes in mustelids, some felids, and hyaenids. Limited cospeciation is postulated within the *T. polyacantha* subclade, for *T. twitchelli*, *T. taxidiensis*, and *T. martis* in mustelids and for *T. saginata* + *T. asiatica* in humans.

Intermediate hosts are represented by Rodentia, Artiodactyla (principally in Bovidae, Cervidae, Suidae), and rarely by Lagomorpha, Hyracoidea (Procaviidae), Canidae, and Primates (including Hominidae); a high consistency in host relationships is observed (CI = 0.89; RI = 0.85; RC = 0.75) (Fig. 4). Basal species and subclades are all associated with rodent intermediate hosts, except for *T. macrocystis*; and minimally, a single colonization of artiodactyls is postulated. Lagomorphs rarely occur as intermediate hosts (*T. macrocystis*, *T. serialis*, *T. pisiformis*), and the occurrence of *Taenia* in these mammals is compatible with 2 independent colonization events. Suid intermediate hosts are rare and associated typically with species that occur as adults in humans; e.g., *T. asiatica* and *T. solium*, and with putative host switches for *T. regis* and *T. acinonyxi*. Records for *T. multiceps* and *T. hydatigena* in domestic suids are likely incidental and were not included.

DISCUSSION

Contrasting phylogenetic hypotheses

The current analysis represents the first comprehensive and testable hypothesis for relationships for species in the genus *Taenia*. Conclusions and interpretations herein contrast with analyses presented by Moore and Brooks (1987), Okamoto et al. (1995), and De Queiroz and Alkire (1998). This may reflect uneven and incomplete sampling of taxa in these previous studies but also is indicative of some level of instability in the current tree(s), consistent with extensive levels of homoplasy for most structural attributes. Remarkable plasticity in morphology and ontogeny as documented in prior phylogenetic studies by Moore and Brooks (1987) is apparent (Table II; Fig. 2).

All available analyses place *T. mustelae* as the basal species in the genus (Moore and Brooks, 1987; Okamoto et al., 1995; De Queiroz and Alkire, 1998). Moore and Brooks (1987), evaluated relationships among 13 species of *Taenia* and in part

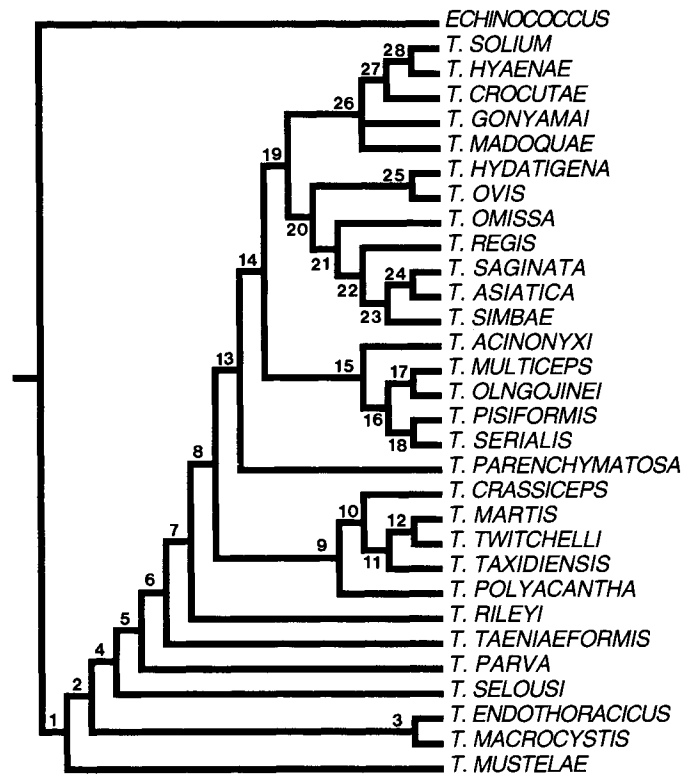


FIGURE 2. Phylogenetic hypothesis for species of *Taenia* based on analysis of comparative morphological data. Shown is 1 of 4 equal-length trees, largely congruent with the consensus tree (Fig. 1). Characters are mapped onto the tree and show the distribution of morphological attributes among terminal taxa and support for each node (numbered sequentially from the base of the tree); A = apomorphy, H = homoplasy as convergence or parallelism, R = reversal. Terminal taxa: *T. mustelae* (H: 16); *T. macrocystis* (H: 4, 12, 15); *T. endothoracicus* (A: 26; H: 5, 10, 11; R: 18); *T. selousi* (H: 10, 13, 27; R: 21); *T. parva* (H: 17; R: 25); *T. taeniaeformis* (H: 3; R: 6, 18); *T. rileyi* (H: 5, 7; R: 6, 18); *T. polyacantha* (H: 4, 10, 15, 24); *T. taxidiensis* (A: 2; H: 11); *T. twitchelli* (H: 20; R: 18); *T. martis* (H: 10, 17, 16; R: 25); *T. crassiceps* (H: 26, 27; R: 5, 6); *T. parenchymatosa* (H: 25); *T. serialis* (H: 7, 8, 10, 14, 19); *T. pisiformis* (H: 4, 18, 25; R: 5, 11, 13); *T. olngojinei* (H: 19; R: 3, 16, 22); *T. multiceps* (H: 4, 7, 10; 18; 25; R: 6); *T. acinonyxi* (H: 4; R: 6, 17); *T. simbae* (R: 1); *T. asiatica* (H: 20); *T. saginata* (H: 5, 8, 11, 18; R: 14); *T. regis* (H: 16; R: 17); *T. omissa* (H: 12; R: 4, 11); *T. ovis* (H: 5, 16, 19; R: 8, 11, 17, 21, 22); *T. hydatigena* (R: 7); *T. madoquae* (H: 22; R: 3); *T. gonyamai* (H: 4; R: 17, 19); *T. crocutae* (H: 4; R: 6); *T. hyaenae* (H: 4, 13, 19); *T. solium* (A: 2; R: 7, 8, 22). Internodes beginning basally are designated 1–28: 1: A: 4, 13, 14, 18, 21, 25, 27; 2: A: 11, 20, 23, 24; H: 4; 3: H: 3, 17; 4: A: 6, 19; H: 22; 5: A: 4, 9, 26; R: 13, 24; 6: A: 26; H: 8; R: 11; 7: A: 22, 23; H: 3, 5, 13; 8: R: 9, 14; 9: A: 11; H: 26; R: 4; 10: H: 14; R: 13; 11: R: 3, 20, 21; 12: H: 10, 16; 13: H: 17; 14: A: 11, 22; 15: H: 16, 19, 26; R: 8; 16: H: 23, 27; 17: A: 23; H: 12, 15; 18: R: 21; 19: H: 7; 20: A: 11; H: 15; R: 20; 21: H: 14, 23; 22: H: 19; 23: A: 4; R: 8, 15; 24: A: 1, 2, 23, 24; 25: H: 4, 25; 26: H: 18; 27: H: 25, 27; 28: H: 14.

consistent with the current study, placed *T. selousi*, *T. taxidiensis*, *T. martis*, *T. twitchelli*, and *T. crassiceps* as relatively basal and closely related; *T. pisiformis* and *T. serialis* were adjacent; and *T. ovis*, *T. hydatigena*, and *T. omissa* were placed near the crown of the tree. In contrast, Moore and Brooks (1987) placed *T. taeniaeformis* and *T. rileyi* in a polytomy with such derived taxa as *T. omissa* and *T. hydatigena*.

De Queiroz and Alkire (1998) evaluated molecular sequence

TABLE II. Consistency indices for individual characters used in analysis of *Taenia* spp.

Character no.	Character	CI
1	Hooks (presence)	1.000
2	Hooks (number)	1.000
3	Genital ducts	0.200
4	Testes (number)	0.357
5	Cirrus sac (length)	0.250
6	Ovarian lobes	0.167
7	Vaginal sphincter	0.286
8	Vaginal dilatation	0.143
9	Larva	0.500
10	Larva	0.429
11	Localization	0.273
12	Testes (distribution)	0.333
13	Testes (distribution)	0.143
14	Testes (distribution)	0.143
15	Testes (distribution)	0.200
16	Genital papilla	0.143
17	Uterine branches	0.125
18	Genital pore	0.250
19	Vas deferens	0.250
20	Testes (layers)	0.200
21	Vitellaria (shape)	0.167
22	Cirrus sac (shape)	0.286
23	Rostellar hooks (length)	0.571
24	Rostellar hooks (number)	0.500
25	Strobila (length)	0.222
26	Segment (gravid width)	0.286
27	Proglottid (shape)	0.200

data for 12 species of *Taenia*, including data from Okamoto et al. (1995). Consistent with the current analysis, *T. crassiceps* was relatively basal; *T. saginata* and *T. asiatica* are putative sister species; and *T. solium* does not share a very recent common ancestor with *T. saginata*. Congruence with the current hypothesis was otherwise limited.

De Queiroz and Alkire (1998) suggested that pending the evaluation of additional characters, both molecular and morphological, competing hypotheses for phylogenetic relationships among species of *Taenia* must be viewed with caution. The current study included 27 characters, in contrast to 19 applied in the analysis by Moore and Brooks (1987). Morphologically the group is relatively homogenous, and there are likely to be few additional attributes available from comparative morphology. Perhaps conclusions being drawn from multivariate analyses of morphometric data for hooks maybe applied to phylogenetic studies for *Taenia* (e.g., Murai et al., 1993; Gubányi, 1995). At present, however, representation and evaluation of multivariate data in a form suitable for phylogenetic systematics is problematic (Pimentel and Riggins, 1987).

Phylogeny and taxonomic structure

Diagnosis of a multitude of tribes or genera in the family Taeniidae and subfamily Taeniinae is not supported (e.g., consistent with Verster [1969] and Rausch [1994, 1997]). A reticulate versus compact or lobate vitellarium does not diagnose groups at the tribe level within Taeniinae; the tribes, Taeniini and Fimbriotaeniini recognized by Spasskii (1998) do not con-

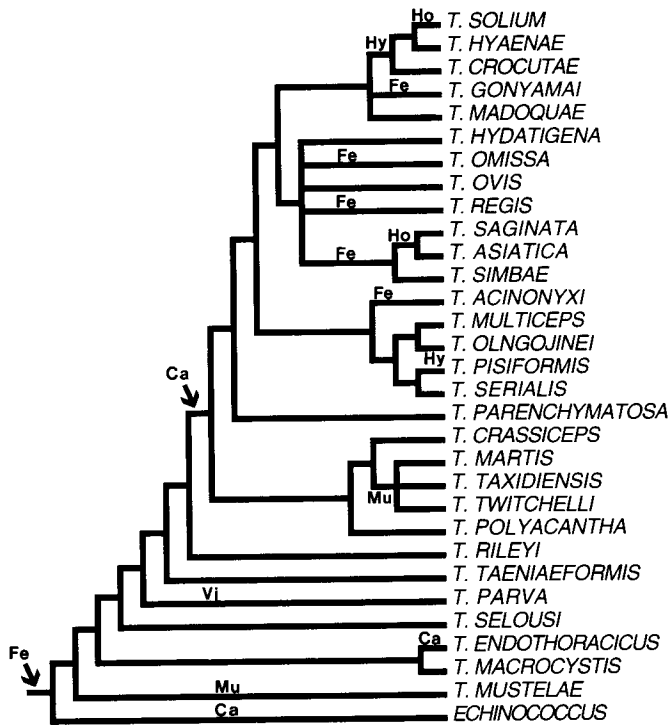


FIGURE 3. Phylogenetic hypothesis for species of *Taenia* showing distribution of definitive hosts mapped and optimized on the parasite cladogram (CI = 0.46; RI = 0.53; RC = 0.25). Definitive hosts are represented by Viverridae = Vi, Mustelidae = Mu, Hyaenidae = Hy, Canidae = Ca, Felidae = Fe, and Hominidae = Ho. Patterns are consistent with extensive levels of host-switching in the diversification of *Taenia* spp.

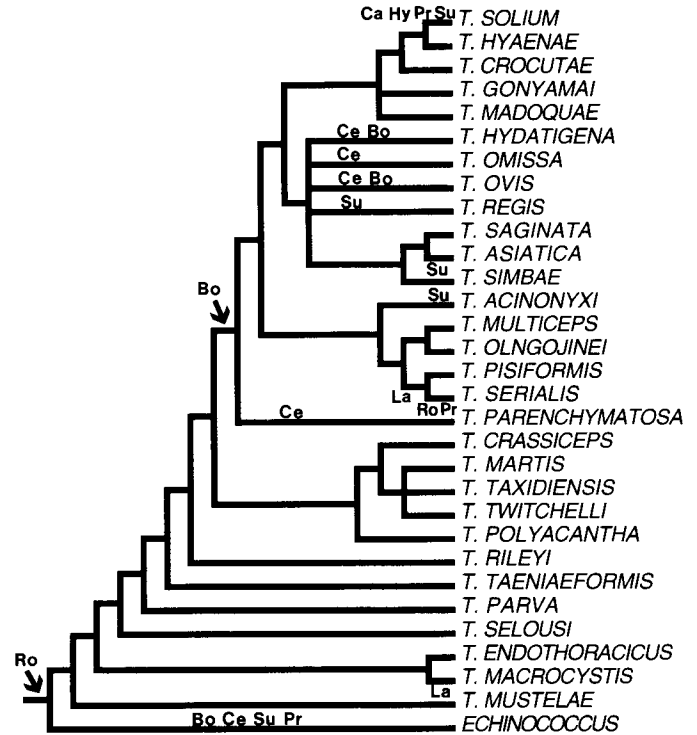


FIGURE 4. Phylogenetic hypothesis for species of *Taenia* showing distribution of herbivorous intermediate hosts mapped and optimized on the parasite cladogram (CI = 0.89; RI = 0.85; RC = 0.75). Intermediate hosts are represented by Rodentia = Ro, Bovidae = Bo, Cervidae = Ce, Suidae = Su, Lagomorpha (Leporidae) = La, Hyracoidea (Procaviidae) = Hy, Canidae = Ca and Primates (including Hominidae) = Pr. Patterns are consistent with stability in life history and transmission and relatively limited host-switching among rodent, leporid, and artiodactyl intermediates.

stitute inclusive monophyletic groups. Additionally, observations by one of us (A. Jones, unpubl. obs.) suggest that the reticulate vitellarium may be an artifact of fixation.

Interpretation of the current phylogenetic hypothesis is consistent with a restricted number of valid genera within the Taeniinae (Fig. 1). For example, even though *T. saginata* and *T. asiatica* are placed as sister species there remains no phylogenetic support for recognition of *Taeniarhynchus*. Although this genus has been defined primarily by the absence of a rostellum, its recognition would make *Taenia* paraphyletic. It is also apparent that the structure of larval parasites is inadequate for the delineation of genera. Thus, *Hydatigera* that was based on the presence of a strobilocercus larva (Abuladze, 1964; Movsesian, 1989; Bessonov et al., 1994) and included *T. taeniaeformis*, *T. parva*, and *T. rileyi*, and several other species, some of which are now either synonyms or species inquerendae (see Verster, 1969) cannot be justified. *Fimbriotaenia*, established for *T. martis*, *T. twitchelli*, *T. mustelae*, and *T. brachyacantha* is invalidated because the fimbriocercus larval form does not diagnose a group, and *T. mustelae* is not closely related to either *T. martis* or *T. twitchelli*. Additionally, the coenurus larva does not diagnose an inclusive group containing *T. serialis* and *T. multiceps*.

The following genera (inclusive with those listed by Rausch [1994]) become unequivocal synonyms of *Taenia*, consistent with monophyly for the genus (Fig. 1): (1) based on larvae, *Multiceps*, *Tetratirotaenia*, *Hydatigera*, and *Fimbriotaenia*; and

(2) based on the presence/absence of hooks, *Taeniarhynchus*, *Fossor*, and *Monordotaenia*. As Rausch (1994, 1997) has outlined, recognition of these genera would result in a number of often monotypic taxa, for many based solely on characteristics of the metacestodes. That these concepts for a diversity of discrete genera within *Taenia* are refuted is indicated by the phylogenetic relationships postulated for this group in which recognition of any of these would result in paraphyly for *Taenia* (Fig. 1).

Diagnosis for Group I and Group II within *Taenia* as proposed by Verster (1969) is equivocal. The relative position of the genital ducts and osmoregulatory canals (character 3) exhibits extensive parallelism and reversal within the genus; CI = 0.20 for this character (Fig. 2).

Phylogenetic studies of the Cyclophyllidae indicate a close relationship for Taeniidae and *Dasyurotaenia*, but inclusion along with *Anoploaenia* in the Taeniidae remains equivocal. For the latter, this contention appears to be refuted by the structure of the metacestode (Beveridge et al., 1975; Hoberg et al., 1999). The placement of *Insinuatoaenia* also remains ambiguous, pending description of metacestodes and elucidation of the life cycle (Rausch, 1994, 1997).

Phylogeny and morphogenesis of metacestodes

Asexual development and multiplication of metacestodes is widespread among species of *Taenia* (e.g., Freeman, 1956;

Abuladze, 1964; Moore and Brooks, 1987); however, morphogenesis by proliferative budding leading to discrete cysticerci appears relatively rare and is observed primarily in *T. crassiceps* and *T. polyacantha*. Rausch and Fay (1988a, 1988b) indicated that morphogenesis by proliferative budding in early metacestodes of these species was independently derived. The close relationship postulated, however, suggests that such proliferative morphogenesis may be homologous. Interestingly, there are also reports of proliferative budding for *T. pisiformis* (Crusz, 1948; Opuni, 1970), placed in the *T. acinonyxi* subclade and as the sister species of *T. serialis*. In this situation, however, the transverse fission described for *T. pisiformis* does not appear homologous to the ontogeny of metacestodes in *T. crassiceps* or *T. polyacantha* nor to development of the coenurus and other polycephalic forms.

Polycephalic larvae (excluding the coenurus) are primarily characteristic of basal species in the genus, including *T. mustelae*, *T. selousi*, *T. twitchelli*, and *T. endothoracicus*. The diversity of proliferative forms, and their distribution among often phylogenetically unrelated species of *Taenia* is consistent with the contention by Moore and Brooks (1987) for multiple and independent origins of asexual reproduction.

Rausch (1981) postulated that the hemistrobilocercus larva of *T. rileyi* was intermediate in form to the strobilocercus and cysticercus. The relative relationships for *T. taeniaeformis* (possessing a strobilocercus), *T. parva* (polycephalic strobilocercus), and *T. rileyi* corroborate homology for development and structure of metacestodes (character 9) among these species.

Parasite–host cospeciation

Verster (1969) in recognizing 2 groups within *Taenia* postulated that Group I included those species in humans and all in canines and felids (except *T. taeniaeformis*); Group II included *T. taeniaeformis* in addition to those cestodes in mustelids and viverrids. Based on the current study, 2 groups of *Taenia* are not demonstrated, and basal species are represented broadly among mustelids, viverrids, felids, and canids (Fig. 3). Results of analyses by Moore and Brooks (1987), Okamoto et al. (1995), and De Queiroz and Alkire (1998) were largely incongruent with host relationships, refuting an hypothesis for extensive cospeciation between *Taenia* spp. and either their intermediate or definitive hosts.

Examined at the level of order or family for hosts, the results of the current study in part corroborate these latter conclusions. Coevolution (encompassing cospeciation and coadaptation; Brooks and McLennan, 1991; Hoberg et al., 1997) with respect to carnivorous definitive hosts and *Taenia* appears to be limited. Although felids are putative ancestral hosts, contemporary associations appear to have resulted from extensive host-switching among felids, canids, hyaenids, and others (Fig. 3).

In contrast, relationships with herbivorous intermediate hosts are indicative of more pervasive coevolution (Fig. 4). It is postulated that rodents as intermediate hosts were ancestral for the Taeniidae, *Taenia* + *Echinococcus*. This is also compatible with a sister-group relationship between the Taeniidae and the Paruterinidae + Metadilepididae (Hoberg et al., 1999). Basal intermediate hosts for species of *Taenia* are rodents and early diversification within the genus, except for *T. macrocystis*, appears associated with these mammals; acquisition of ruminant

or lagomorph intermediates occurred independently (Fig. 4) and for the latter is represented by multiple events of colonization. Additionally, ruminants were independently colonized by both *Taenia* and *Echinococcus* subsequent to the divergence of these taxa. Minimally, artiodactyls (particularly bovids) may have been colonized once by *Taenia* (Fig. 4), but the occurrence of some cervids and suids as intermediate hosts may be explained by independent host-switching, e.g., *T. parenchymatosa* and *T. omissa* in cervids; *T. hydatigena* and *T. ovis* in bovids and cervids; *T. solium* and *T. asiatica* in suids; and *T. acinonyxi* and *T. regis* in suids.

We can further examine the putative relationships among *Taenia* and their hosts based on mapping and optimization of host taxa onto the parasite phylogeny (Figs. 3, 4). It is apparent that intermediate hosts (CI = 0.89) are evolutionarily conservative for *Taenia*, in contrast to definitive hosts (CI = 0.46) that appear to be more contingent. Acquisition of novel definitive hosts occurred more often in the evolution of this group in contrast to shifts among alternative intermediate hosts that are intimately involved in the maintenance of cycles. Life history then must be viewed as evolutionarily conservative with respect to diversification within this clade; host-switching occurred as a stochastic process but within the context of paleo-guilds, or guilds, linked to specific trophic associations. Thus, shifts between definitive hosts were facilitated, whereas those between intermediate hosts were moderated, particularly if such would remove a parasite from a particular guild assemblage and result in a discontinuity in transmission (consider the contrasting micro- versus macroevolutionary implications).

We would predict that ecological stability and continuity is linked to intermediate hosts and transmission dynamics in this assemblage, which is otherwise driven and defined by predator–prey associations. This suggests that selection is for continuity in transmission rather than for association with a particular definitive host group. Consequently, speciation is likely to be driven by definitive hosts, whereas ecological continuity and predictability are limited by transmission dynamics linked to the intermediate hosts (Hoberg et al., 1999). This observation and prediction parallels that developed for patterns and processes of speciation within the marine assemblage represented by tetrabothriid cestodes of the genus *Anophryocephalus* and their pinniped hosts (see Hoberg, 1992, 1995, 1997).

These observations are compatible with relatively low levels of apparent cospeciation between *Taenia* and their definitive hosts, e.g., in mustelids, in some hyaenids, and possibly to a limited extent among some large felids, canids, and humans (Fig. 3). Otherwise, patterns appear consistent with rapid shifts between phylogenetically unrelated carnivores but among those that historically exploited a common prey resource in communities that occupied a specific biogeographic region. Such is particularly evident with respect to the distribution of *Taenia* spp. among large felids, hyaenids, some canids, and humans in Africa, e.g., *T. madoquae*, *T. gonyamai*, *T. crocutae*, *T. hyaenae*, and *T. solium*.

As adults, species of *Taenia* are characteristic parasites in carnivore definitive hosts; only 3 species (*T. saginata*, *T. asiatica*, and *T. solium*) occur in humans (Eom and Rim, 1993; Bowles and McManus, 1994; Fan et al., 1995). Consistent with De Queiroz and Alkire (1998), results of the current analysis

indicate that *T. saginata* + *T. asiatica* are putative sister species and that they are distantly related to *T. solium* (Fig. 1).

Although these species may be of substantial economic significance (e.g., Fan and Chung, 1995), there have been few prior hypotheses for the relationships of *Taenia* spp. in humans. Origins of *Taenia* in humans were considered to have been coincidental with the domestication of bovid and suid hosts and colonization of humans by cestodes associated with companion carnivores in which a synanthropic cycle was characteristic (conventional wisdom outlined by Cameron [1956]). Baer (1940), however, articulated a more detailed hypothesis for the relationships of these species. He considered that *T. saginata* and *T. solium* were not closely related and had been acquired by humans via colonization along 2 separate routes. For *T. solium*, this would have predated the domestication of suid hosts, with colonization of hominids by a *Taenia* possibly circulating in wild suids such as warthogs (*Phacochoerus aethiopicus* [Pallas]) or bush pigs (*Potamochoerus porcus* [Linnaeus]) and large felids. Secondarily, synanthropic maintenance of this association would have involved human definitive and canid and suid intermediate hosts, including *Sus scrofa* Linnaeus. In contrast, the origin of *T. saginata* was linked to domestication of bovinds by modern humans. This latter point is of interest with respect to the putative dates of domestication for bovinds and cattle in particular at a minimum of 8,000–10,000 yr, and the possibility of independent centers of domestication for cattle of Asia, Europe, and Africa that could be substantially older (Epstein and Mason, 1984; Bradley et al., 1996). Hypotheses for the diversification of *Taenia* spp. in human hosts will be examined in detail elsewhere.

Species of *Taenia* are important parasites and pathogens and have considerable veterinary and medical significance (Abuladze, 1964; Rausch, 1994, 1997). Knowledge of phylogenetic relationships for this complex genus will enhance our ability to predict and understand life history, geographic distribution, and the zoonotic potential for a diversity of species. Although deferred to a future analysis, resolution of the coevolutionary and biogeographic history for this assemblage will result from: (1) refinement of this initial hypothesis for phylogeny of *Taenia*; (2) a phylogenetic context for relationships of families and genera of terrestrial mammals serving as intermediate and definitive hosts; and (3) examination of the geographic ranges for the diversity of *Taenia* spp.

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