

Phylogeny of *Taenia*: Species definitions and origins of human parasites

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Abstract

Phylogeny is fundamental as it constrains explanations about history and forms our foundation for recognizing and diagnosing species. In the absence of such a framework taxonomists historically relied on intuitive processes, personal judgment and authority, often embracing a typological view of species that disregarded otherwise unequivocal historical and biological criteria. Species of *Taenia* are among the most characteristic tapeworms infecting carnivores and humans as definitive hosts and indeed Taeniidae is unique among the Eucestoda in requiring 2 obligate mammalian hosts for transmission; a high percentage (>80%) of life cycles have been completely elucidated among the approximately 45 species and nominal subspecies of *Taenia*. Until recently there had been no comprehensive attempts at reconstruction of a phylogeny among these important parasites. Such analyses have allowed us to explore the origins and evolution of those independent species of *Taenia* that occur in humans (*T. saginata*, *T. asiatica*, and *T. solium*) and to understand the ecological and historical processes serving as determinants of biogeography and host-association. These studies supported the status of *T. asiatica* as a valid species and diagnosed a relationship as the sister-species of *T. saginata*. These conclusions contrasted with a diversity of opinions that would subsume *T. asiatica* as a subspecies. Recognition of a species constitutes a specific and testable hypothesis, is not an arbitrary decision and is most appropriately assessed in the context of phylogenetic or historical data. Considering macrospecies, a process has been outlined by Brooks and McLennan [Brooks DR, McLennan DA. The nature of diversity: an evolutionary voyage of discovery. University of Chicago Press: Chicago; 2002] as follows: (1) *Discovery*: a systematist describes the species; (2) Phylogenetic reconstruction; (3) *Evaluation I*: do sister-species show geographical overlap—are they sympatric or allopatric (use phylogeny+geographical distributions)? (4) *Evaluation II*: are sister-species reproductively isolated based on information from natural history, ecology and reproductive biology? Species may be viewed in the context of microevolutionary and macroevolutionary processes. For instance, microspecies are defined in ecological time and involve populations and contemporary process that are potentially reversible (reticulate). In contrast, macrospecies as exemplified by *T. saginata* and *T. asiatica* are divergent lineages resulting from processes in evolutionary time where an ancestor has undergone a permanent split that is non-reversible (non-reticulate). Applying these criteria in evaluation of *T. saginata* and *T. asiatica*, it becomes clear that in evolutionary time these represent historical lineages with independent spatial and temporal trajectories, having separated from a common ancestor near 0.78 to 1.71 MYBP in Africa, or Eurasia. In ecological time, sympatry, reproductive isolation, and differences in life history evident for *T. saginata* and *T. asiatica* as observed in China, and perhaps other regions of Southeast Asia, further serve to validate these taeniids. Published by Elsevier Ireland Ltd.

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1. Introduction

Globally, taeniid tapeworms (Eucestoda: Cyclophyllidea: Taeniidae: species of *Taenia* and *Echinococcus*) are among the most characteristic parasites in an array of carnivore definitive hosts, and are among a typical and host-specific cestode fauna in humans. [1–3]. Species of *Taenia* were among the earliest recognized helminths in humans, with written records of

their occurrence extending into antiquity. In terms of ontogeny, life-history and ecology, species of *Taenia* have received considerable attention and are the best understood of any of the eucestodes. Contemporary studies of this group, however, are driven by substantial challenges for public health, food safety, human and animal health, and globally by the consequences of economic impacts that dampen socioeconomic development [4,5].

Taenia is a relatively large genus containing approximately 42 valid species and 3 subspecies (in part based on Loos-Frank [3]), and continuing discoveries broaden our concepts for

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diversity in this group (e.g., Rausch [6]). Patterns of life history are unique for *Taenia* where transmission is ecologically based and life cycles are dependent on specific predator–prey associations among mammalian definitive and intermediate hosts [1]. Diversification or speciation within *Taenia* thus appears to have been driven primarily by host-switching among carnivorous definitive hosts, and only limited evidence of cospeciation is postulated [7]. Patterns of host association are consistent with shifts among phylogenetically unrelated carnivores such as mustelids, felids, procyonids, canids and hyaenids in the biological context of foraging guilds delimited by specific biogeographical regions [7,8]. Consequently, the host distribution for species of *Taenia* in both carnivores and in humans is a function of historical ecology and food habits within foraging guilds in contrast to cospeciation. *Taenia* represents a unique model system among the eucestodes for elucidating the evolution of life history where >80% of life cycles are completely known; in conjunction with parasite phylogeny it is possible to delineate the relative contribution of definitive hosts and intermediate hosts in parasite diversification [8]. In this regard, phylogenetic studies are important, serving as constraints on hypotheses about processes for speciation within *Taenia* and also contributing to our concepts for species-level diversity.

Although species diversity, taxonomy and ecology among species of *Taenia* has often received exhaustive treatment [1–3], there have been limited attempts to explore phylogenetic relationships [7–12]; few recent studies represent comprehensive treatments of the genus [7,8]. Phylogenetic studies inform us about the origins of species diversity, the history of host association and geographic distribution for complex assemblages, and are the foundation for classification and predictions about parasite behavior and biology [13–15]. Phylogenetic insights have also become a standard component of both (1) explicit species concepts and (2) detailed methodologies and approaches for delimiting species [16–20].

Recognition of species has great practical value in providing a highly refined understanding of patterns and processes involved in origins of global biodiversity, as a basis for exploring the historical associations and biogeographical distributions of parasites and their hosts, and in developing robust predictions about emerging and re-emerging pathogens and disease on regional and global scales [15,21]. In the absence of accurate limits for species, our understanding of disease-processes is confounded by erroneous “knowledge” for parasite life history, behavior and distribution [4]. Such is exemplified by the controversy about the status of certain species of *Taenia* in humans (*T. saginata* and *T. asiatica*). Conflict resides at the interface for a typological and phylogenetic universe where taxa are either defined in a “limited” comparative context [22–26] or are evaluated relative to explicit hypotheses derived from historical data [7,8,11]. In the former there is ample latitude for alternative but not always comparable opinions based on experience, special knowledge of morphology or molecular data including genetic yardsticks, and taxonomic intuition, whereas in the later explicit hypotheses and methods irrespective of data serve as constraints on taxonomic decisions in delimiting species [19,20].

In this review, I explore current ideas for origins and diversification of human-*Taenia* (*T. saginata* + *T. asiatica* and *T. solium*) in a framework derived from historical studies. I examine the status and validity of *Taenia saginata* and *Taenia asiatica* based on inference from phylogenetic and historical data. Concepts and methods for delimitation of phylogenetic species [18–20] are discussed and applied to these taxa of tapeworms among human definitive hosts. More generally an argument is articulated for an explicit historical foundation and methodology in species-level taxonomy and systematics of helminth parasites such as the taeniids of vertebrates.

2. *Taenia* phylogeny, life history, and historical ecology

Phylogenetic relationships among species of *Taenia* have been analyzed in a limited fashion with both morphological and molecular data [7–11]. Further progress in delineating robust relationships will likely be derived from multi-locus approaches using analyses of nuclear and mitochondrial DNA [12], a goal that may be limited by access to suitable specimens representing sufficient diversity in the genus. Studies to date agree on several points: (1) monophyly for *Taenia* as the sister-group of *Echinococcus* in the Taeniidae; (2) a basal position for *T. mustelae*; and (3) divergent histories for *T. solium* and the sister-species *T. saginata* + *T. asiatica* [7,8,11]. Incomplete taxon sampling and availability of comparable data sets have likely influenced the structure of trees derived in these prior analyses.

Near-comprehensive analyses of relationships among *Taenia*, including those species with complete life cycle information, have provided an opportunity to examine the evolution of life history and host associations (Figs. 1 and 2) [7]. Included are 35 species (with 3 subspecies) for which complete life history and morphological data are available for adults and metacystodes; *Taenia pencei* is placed in this tree based on structural characters indicating relationship to a putative subclade of cestodes in mustelids [6]. Excluded from these analyses are 5 species with incomplete life cycle data (*T. brachyacantha*, *T. dinniki*, *T. ingwei*, *T. jaipurensis*, and *T. pseudolaticollis*) and 5 species where both life history data and comparative morphology for adult strobilate worms is absent or incomplete (*T. kotlani*, *T. krepkogorski*, *T. laticollis*, *T. retracta*, and *T. saigoni*).

A pervasive history of host-switching for *Taenia* is evident among carnivores, and only minimal associations by cospeciation are apparent among definitive hosts; e.g., among the mustelids, hyaenids and hominids (Fig. 1). Events of colonization explain in excess of 50–60% of associations among *Taenia* and carnivore definitive hosts [7]. In contrast minimal colonization has characterized associations among intermediate hosts where rodents are basal and ungulates appear linked to a single event of host-switching; events of colonization explain approximately 20–30% of associations among herbivores and *Taenia* [7] (Fig. 2). A primary conclusion suggests that acquisition of novel definitive hosts occurred more often in the diversification of *Taenia* than did shifts among alternative intermediate hosts. Evolution of *Taenia* is consistent with a growing body of evidence that host-switching occurs most often within guilds and that diversification proceeds through

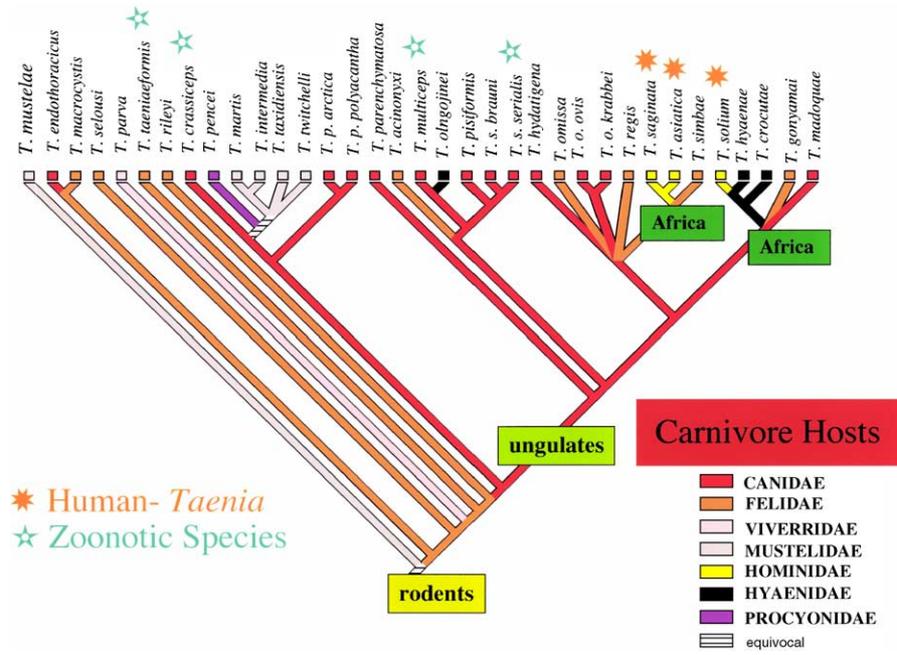


Fig. 1. Phylogeny and host associations for species of *Taenia*, adopted modified from Hoberg and others [7]. Taxonomy in part is based on decisions by Loos-Frank [3] for species and subspecies of *Taenia* and by Rausch [6] for *Taenia* in mustelid hosts. Phylogenetic hypotheses constrain explanations about host associations and history of parasite species. Demonstrated here is the importance of foraging guilds and pervasive host-switching among carnivore definitive hosts and hominids in the diversification of *Taenia*; host-switching among rodents and ungulates, the primary intermediate hosts, for *Taenia* has been minimal (see Fig. 2) [7,8]. Those species that are specific parasites in human definitive hosts, *T. saginata*, *T. asiatica*, and *T. solium* (denoted by stars) represent discrete historical or evolutionary lineages with independent biological, temporal and spatial trajectories [8,11]. Among these macrospecies, *T. saginata* and *T. asiatica* are sister-species and share a relationship with *T. simbae* a parasite circulating in lions and antelopes in Africa. In contrast, *T. solium* represents a discrete lineage and is the putative sister-species of *T. hyaena* a parasite in hyena, African hunting dogs and ungulates in Africa. Phylogenetic information supports origins in Africa for the species of *Taenia* now in humans and is consistent with divergence for *T. asiatica* + *T. saginata* between 0.78 and 1.71 MYBP in Africa or Eurasia [8]. In this tree, the position of *T. pencei* is consistent with comparative morphological characters as outlined by Rausch [6].

colonization and radiation among definitive hosts within such assemblages [27]. Thus, it is historically continuous trophic associations within guilds and ecosystems that serve as a

foundation for predictability in life history and the dynamics of transmission. *Taenia* falls within the groups of helminths that may be defined by “context-based specificity” which has a

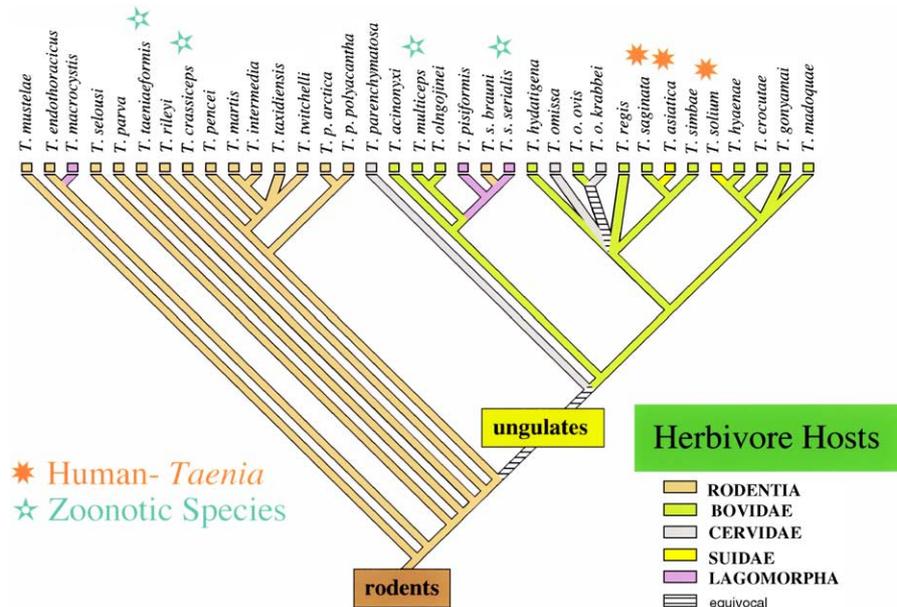


Fig. 2. Phylogeny and host associations for species of *Taenia*, adopted from Hoberg and others [7]. The distribution of *Taenia* among herbivore intermediate hosts is associated with minimal host-switching. Rodents are regarded as basal intermediate hosts, and inference of a single colonization event among ungulates is evident; minimally, Suidae was colonized from humans on 2–3 occasions and is consistent with the host distributions for *T. solium* and *T. asiatica*. Among species of *Taenia*, guild-dynamics define ecologically conservative patterns of transmission, and diversification is associated with colonization among carnivores exploiting a common prey resource in contrast to an extended coevolutionary history for this host–parasite assemblage.

strong ecological and geographical basis, where associations are determined regionally, and are influenced by extrinsic factors beyond coevolution. Secondly, “non-contextual specificity” and relatively narrow distributions for some species of *Taenia* and their carnivore hosts [3] has resulted from microevolutionary processes that may be physiological, immunological, or intrinsically phylogenetic.

In this sense, life history for *Taenia* is evolutionarily conservative where shifts by parasites (with or without subsequent speciation) among definitive hosts are facilitated by guild structure, whereas those among potential intermediate hosts (between or among guilds) are moderated; selection is the driver for such continuity in transmission. The latter is particularly apparent in instances where switching among potential intermediate hosts could remove parasites from specific guild-associations resulting in discontinuity for transmission [7,21,27]. Among *Taenia* and perhaps other host-parasite assemblages, transmission is phylogenetically conservative and ecologically constrained, where there is selection and fidelity linked to guild dynamics rather than to a host species or host-clade in a framework for cospeciation.

Patterns of host association are consistent with shifts and radiation of *Taenia* among phylogenetically disparate carnivores such as mustelids, felids, procyonids, canids, hyaenids, and hominids in the biological context of foraging guilds and common prey resources for communities delimited by specific biogeographical regions (Figs. 1 and 2) [7,8]. For example, origins of an array of closely related *Taenia*-species in Africa (*T. madoquae*, *T. gonyamai*, *T. crocutae*, *T. hyaenae* and *T. solium*) were historically associated with a paleoguild of medium and large apex carnivores and scavengers (felids, canids, hyaenids and hominids) that foraged on antelopes and other bovid prey [7,8,28]. This generality for colonization and radiation among *Taenia* further applies to the history of associations for those species, *T. solium* and *T. asiatica* + *T. saginata* that are now host-specific parasites in humans.

3. Origins of *Taenia* in humans

Origins of *Taenia* in humans have traditionally been associated with domestication of either cattle (*T. saginata*) or swine (*T. solium*) concurrent with modern *Homo sapiens* acquiring their now host-specific fauna and adaptation of synanthropic cycles during the past 10,000 years [29,30]. Phylogenetic resolution for human-*Taenia* indicated independent origins for *T. solium* and *T. asiatica* + *T. saginata* suggesting a more complex picture for faunal diversification [11]. Historical analyses exploring biogeography and host associations for carnivores and herbivores was consistent with a deeper temporal relationship for hominids and *Taenia* established on the savannahs of sub-Saharan Africa during the past 1–2.5 MYBP [7,8]. Host-switching by *Taenia* among felid, canid, and hyaenid carnivores and ancestors of *Homo sapiens* was driven by guild associations established over the exploitation of bovid prey species serving as intermediate hosts under a regime of changing climatological and ecological conditions near the Pliocene–Pleistocene transition [28,

31–34]. The occurrence of *Taenia* in humans minimally represents 2 independent events of host-switching from felids (*T. saginata* + *T. asiatica*) and hyaenids (*T. solium*) substantially prior to the advent of animal husbandry.

The estimated age for divergence of *T. saginata* and *T. asiatica* at 0.78–1.71 MYBP [8] is consistent with acquisition of *Taenia* by hominids coincidental with a shift in diet from herbivory to omnivory and facultative carnivory near 2.0–2.5 MYBP [35]; the ancestor of *T. asiatica* + *T. saginata* is inferred to have already been a parasite in hominid hosts. Subsequent biotic expansion from Africa into Eurasia for this assemblage of hosts and parasites may have resulted in the isolation and later divergence of *T. asiatica* in Asia [36]. Estimates for the timing of separation of *T. solium* from its sister, *T. hyaenae* have not been established [12]. Ecological conditions and guild associations, however, surrounding scavenging or direct predation of bovid prey by hominids have also been postulated in the origin of *T. solium* [8]. Maintenance of *T. solium* within populations of *Homo* may have further been facilitated by cannibalism [37] in a unique “human–human cycle” [8,12,29]. A clear implication of these analyses is that colonization of hominids such as *H. erectus* and the occurrence of *Taenia* in humans predate the domestication of primary food animals and the origins of agricultural systems [8].

In contrast to these archaic origins, secondary acquisition of *Taenia* from humans by domesticated ungulates appears coincidental with the advent of animal husbandry and the inception and maintenance of synanthropic cycles [8]. Multiple events for domestication in lineages of cattle [38] and swine [39,40] are recognized during the past 8000–10,000 years establishing a time frame for putative colonization events by respective species of *Taenia* from humans to cattle (1 event for *T. saginata*) and to swine (1 for *T. asiatica*; 2 for *T. solium*).

Occurrence of *T. asiatica* and *T. solium* in domestic swine may be linked to a minimum of 3 independent events of host-switching from humans to *Sus scrofa* prior to establishment of synanthropic cycles for these taeniids [8, 12]. For *T. asiatica* an association with pigs may have been established in Asia following divergence of host populations that later expanded into Europe [40]; consistent with an apparently limited distribution of this taeniid in Asia, Taiwan and China [25,41]. In contrast, *T. solium* is associated with pigs representing independent centers of domestication in both Europe and Asia. Such would be consistent with documented genetic variation and differentiation of *T. solium* populations in Asia and those in Central and South America + Africa [12] and within Mexico [42]. Patterns of human mediated dispersal are evident for *T. solium* and swine, perhaps emanating from these independent centers of regional domestication with range expansion across Europe and North Africa and from SE Asia into Near Oceania ensuing during the past 9000–10,000 years BP [39,40]. Later with initiation of European contact in North America over 500 years ago, the host–parasite assemblage was introduced from heterogeneous sources in the Palearctic and established in the Western Hemisphere [12,40,42]; a

similar history of geographic colonization and translocation with humans and domestic cattle is evident for *T. saginata*. Thus, *T. solium* and *T. asiatica*+*T. saginata* are clearly differentiated macrospecies with divergent histories, and each is further partitioned at the level of microspecies and populations [43].

4. Species of *Taenia*—spatial, temporal and historical attributes and criteria in evolutionary and ecological time

Species are among the most important and basic units of evolution, where speciation resulting from cladogenesis (creation of new lineages by splitting) produces monophyletic and irreversible lineages in space and time [18–20,44]. There has been considerable controversy and discussion about the reality of species, and the processes and mechanisms associated with their origins, but such arguments are not simply arcane [44,45]. As Nadler [20] has stated, with relevance to parasitology: “This problem has far-reaching consequences for biological research, because conclusions about patterns and process in nature often depend on understanding how many species are present in a biological system.” The species problem to some extent resides at the nexus of the need for discrimination between natural variation within species and patterns of variation between species [20]. In an operational sense, however, there has been little consensus in how we might discover, recognize and delimit species [19,44] although evolutionary or phylogenetic–historical concepts and approaches are in apparent ascendancy [18,19].

Over the past 200 years a certain consistency has existed in how taxonomists have come to recognize and describe and delimit species. Concepts for species go unrecognized, and methods have been predominantly “typological” emphasizing distinctiveness and differences among taxa. Such comparative methods have relied on experience, depth of knowledge, a certain taxonomic intuition and authority, where interpretations were most often conducted within an historical vacuum [20]. Even with the advent of phylogenetic methods comparisons typically remained limited to application of molecular data and assessments based on narrowly established criteria such as pairwise comparisons of sequence divergence for single loci (genetic yardsticks) [20,46]. Significantly little has changed in an operational sense over the past centuries, and according to Nadler [20] and Adams [18]: “. . .no explicit methodology is used to reach the conclusion that a taxon merits recognition as a distinct species, and there is no indication of how observed differences relate to an underlying concept of what species are.” Species-decisions among *Taenia*, provide a clear example of the current challenges [4].

Although competing concepts for species represent a diverse array of proposals, they generally fall into 2 broad categories: (1) “Non-dimensional” or “relational” concepts emphasize reproductive (e.g., Biological Species Concept or BSC of Mayr [47]) and ecological factors (e.g., Ecological Species Concept of Van Valen [48]) that make species distinct and isolated or contrasting mechanisms that promote cohesion [19]; and (2) “Historical or evolutionary concepts,” incorporating the views

of Simpson [49] and Wiley [50] as the basis for recognizing phylogenetic species. Brooks and McLennan [19] provided an extensive review of phylogenetic species concepts, and these form the focus for the following discussion of a process for the discovery and evaluation of species that is appropriate in evaluations among species of *Taenia*.

There has been a need to articulate a concept for species and then to specify an explicit methodology to test such hypotheses [18–20]. Such may be accomplished in the following manner by employing: (1) a process of discovery derived from phylogenetic reconstruction—which establishes pattern, and identifies putative species (phylogenetic species concept); and (2) a process of evaluation or studies of process that allow testing of species-hypotheses (derived from non-dimensional definitions).

The process has been succinctly summarized by Brooks and McLennan [19].

- 1) Discovery I: A systematist describes the species.
- 2) Discovery II: Phylogeny construction using morphology or molecular criteria.
- 3) Evaluation I: Do sister species show geographical overlap across a continuum from sympatry to allopatry? Integrate data for phylogeny+geographical distributions.
- 4) Evaluation II: Are the sister species reproductively isolated? Employ data from natural history, reproductive biology, ecology, experimental evidence from cross-breeding, genetics, morphology, behavior and biogeography (hosts and geography).

Thus, phylogenies become the fundamental tools needed to discover species, whereas the BSC and other non-dimensional concepts provide the basis for their evaluation. Non-dimensional concepts are insufficient by themselves to allow recognition of species, but the absence of reproductive isolation is sufficient to falsify a hypothesis for distinct species [19]. Phylogenetically based approaches integrate a concise and unambiguous concept for species with methods to provide unequivocal evaluation of such hypotheses [20].

Phylogenetic inference also promotes an exploration of the linkages between macroevolutionary and microevolutionary processes in operation at the level of species and populations [43]. Thus, we can discover macrospecies which represent independent and divergent lineages resulting from a permanent split that is irreversible (non-reticulate) in evolutionary time [18,19]. Such contrast with microspecies that constitute closely related historical lineages (populations, geographical races, subspecies) in which divergence is reversible (reticulate) resulting from temporally shallow processes in ecological time; microspecies are the focus of evaluation in phylogeography [43]. Defined in another manner by Brooks and McLennan [19]: “Microspecies represent the realm of what is happening right now and the realm of possibilities for what might happen in the future.” This conceptual universe provides the requisite tools to explore the relationship between *T. saginata* and *T. asiatica* in evolutionary and ecological time.

5. *Taenia asiatica* a valid species

Field-based investigations by Fan [51,52] established the existence of an apparently unique *Taenia* circulating among humans and swine in Taiwan, and adjacent areas of SE Asia. Initial studies were based on comparative morphology, epidemiology and elucidation of the life cycle for what was designated as “Taiwan” or “Asian” *Taenia*, a taxon of uncertain affinities that was not formally named in these early reports; also tentatively referred to as *T. saginata taiwanensis* [53], Recognizing the unique biology for this taeniid (circulating in pig intermediate hosts with cysticerci in the liver and visceral organs), distinct structural characters relative to *T. saginata* and a broader distribution in Asia led Eom and Rim [22] to formally name, describe and provide a differential diagnosis for *T. asiatica*. Over the past 15 years, controversy has attended decisions about the status and validity of *T. asiatica* as an independent species (see reviews [4,26,41]).

Comparative morphological, molecular, ontogenetic, life history and epidemiological data have been applied in delving into the status of *T. asiatica*, which Eom and Rim [22] correctly regarded as a valid species. The initial complete description of *T. asiatica*, and most subsequent treatments, have been deficient in being devoid of references to any explicit concept for species and in not testing explicit hypotheses derived from phylogenetic inference [22–26]. A series of arbitrary decisions in the absence of clearly defined concepts and methodology have subsumed *T. asiatica* as a subspecies of *T. saginata*, a conclusion that is considered to be lacking in support [4,41].

A short history, discussed in the context of concepts for species outlined in the prior section, is required to understand why *T. asiatica* cannot be relegated to the status of subspecies. *Taenia asiatica* was established in a limited comparative universe [22] where species status was based on perceived degrees of difference and the required amount of distinction necessary to recognize a species varied according to authority; this practice has been common and continues throughout parasitology [20].

In this strictly comparative universe exploring overall similarity, Bowles and McManus [23] applied pair-wise comparisons of gene sequences and genetic yardsticks to justify a subspecies status for *T. asiatica*. Thus, *T. asiatica* was considered to be less distinct from *T. saginata*, relative to differences established among other “related” species of *Taenia*. Such comparisons, however, have limited value and are strongly confounded by heterogeneity in rates of substitution and are not based on an explicit phylogenetic context incorporating total diversity for a group [20].

Fan et al. [24] redescribed *T. asiatica* and reported considerable variation in structural attributes used in the original description to differentiate specimens of this taxon from *T. saginata* in Asia. They concluded that variation in morphology and lack of strongly distinct partitions in genetic sequence data precluded recognition of a species. Interestingly, although it was clear that these taxa could be separated based on an array of morphological and molecular data [22,23,54] and strong evidence for sympatry of *T. saginata*, *T. asiatica*

and *T. solium* across Asia was apparent, the former were relegated to subspecies status [24,25].

Phylogenetic and historical approaches to this problem were introduced by de Quieroz and Alkire [11] who firmly established a sister-species status for *T. saginata* and *T. asiatica* and indicated that these taxa were only distantly related to *T. solium*; these conclusions were confirmed by Hoberg et al. [7,8] in more comprehensive studies of *Taenia*. Established was an historical–phylogenetic context for *T. saginata* and *T. asiatica*, indicating that they represented taxa with distinct and divergent evolutionary and historical trajectories as independent species that diverged from a common ancestor 0.78–1.71 MYA [4,7,8].

Eom et al. [41] conclusively supported the argument for species status of *T. asiatica* by demonstrating sympatry with *T. saginata* and *T. solium* in China. Thus, all major criteria in the process for establishing species-status have been reconciled for *T. asiatica*. In the discovery process: (1) *Taenia asiatica* was completely described, and although morphological characters are distinct such were also poorly resolved relative to *T. saginata* [22] as might be predicted in species that have diverged relatively recently in the Pleistocene; (2) molecular characters are also distinct, particularly where phylogenetic analyses of complete sequences from ITS-2 of rDNA indicated reciprocal monophyly for multiple isolates of putative *T. asiatica* and *T. saginata* [41]; and (3) phylogenetic analysis established the sister-species status for *T. asiatica* and *T. saginata* [7,8,11]. In the evaluation process: (1) *T. asiatica* and *T. saginata* represent distinct biological entities that are reproductively isolated when in sympatry [41]; and (2) *T. asiatica* is further distinguished from its sister *T. saginata* by epidemiological, biological, and historical criteria and a series of attributes including differences in life history and localization in the intermediate host [24,25,41].

Both *T. saginata* and *T. asiatica* are valid macrospecies with intraspecific partitioning demonstrated among microspecies representing historical but reversible lineages in space and time [41]. In this regard, both are similar to *T. solium* where genetic differentiation is partitioned historically and geographically [12,42]. Sympatry with *T. saginata* and *T. solium* in China without evidence of hybrids is an indicator of reproductive isolation, and a primary criterion that should be satisfied in evaluation of species [19].

6. Conclusions

Establishing hypotheses for species and a capacity to apply a uniform methodology to establish their limits is fundamental in parasitology and all disciplines of biology [18–20]. Accurate recognition of species serves as a basis for studies of diversity and host–parasite assemblages across a continuum from biotic survey and inventory to epidemiology and is a first line of response in diagnostics and medicine [15]. Recognition of species-status implies historical independence and refines our ability to understand patterns and processes at the host–parasite interface, parameters of life history and the distribution of diseases attributable to parasites. In the absence of such

information, and interpretations derived from phylogeny, we may tend to extrapolate incorrect biological information from unrelated species and compound errors in identification, diagnosis and regimes for treatment [4]. Current studies among *Taenia*, and particularly the controversy over *T. saginata* and *T. asiatica* further emphasize the need for specific testable hypotheses designed to explore the history of diversification for parasitic groups [18,19].

A generality appears to be that diversification for *Taenia* has been driven by switching among carnivore definitive hosts; essentially there has been an ecological rather than phylogenetic (coevolutionary) basis for radiation. Such observations continue to underscore the complexity involved in the evolution of host–parasite systems, and serve to recognize the importance of colonization in the origins and subsequent development of faunal diversity in evolutionary time [27]. Diversification for *Taenia* has also been a history for associations among carnivores, bovids and foraging guilds under a prevailing influence from climatological and ecological perturbation in evolutionary time, particularly for events in Africa during the Pliocene and Pleistocene [8]. Lessons are apparent in the context of ecological time, in that habitat and faunal disruption may be the driver for bouts of host-switching in contemporary systems, and may be expected to increasingly control the geographic and host distributions for pathogenic parasites and emergence of associated diseases in the future [21,55].

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