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Origins of social parasitism: The importance of divergence ages in phylogenetic studies

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Abstract

Phylogenetic studies on insect social parasites have found very close host-parasite relationships, and these have often been interpreted as providing evidence for sympatric speciation. However, such phylogenetic inferences are problematic because events occurring after the origin of parasitism, such as extinction, host switching and subsequent speciation, or an incomplete sampling of taxa, could all confound the interpretation of phylogenetic relationships. Using a tribe of bees where social parasitism has repeatedly evolved over a wide timescale, we show the problems associated with phylogenetic inference of sympatric speciation. Host-parasite relationships of more ancient species appear to support sympatric speciation, whereas in a case where parasitism has evolved very recently, sympatric speciation can be ruled out. However, in this latter case, a single extinction event would have lead to relationships that support sympatric speciation, indicating the importance of considering divergence ages when analysing the modes of social parasite evolution.

Keywords: Social parasite; Sympatric speciation; Allodapine bees

1. Introduction

Social parasitism is a relationship between two species, with one being parasitically dependent on the other. The parasite benefits from their host in many ways, including brood care and exploitation of other socially managed resources, generally at the expense of the host colony (Schmid-Hempel, 1998). Social parasitism occurs in a wide variety of insects and, for the most part, socially parasitic species are closely allied to their hosts, a relationship known as Emery's Rule (Wilson, 1971). Emery's rule can be divided into two forms: the strict form, that states parasites are the closest relatives of their hosts, and the loose form, that states a parasite, or a group of parasites, are only closely related to their hosts. Recent molecular phylogenetic studies have revealed a mixture of these two forms in various ant and wasp groups (Savolainen and Vepsäläinen, 2003; Sumner et al., 2004) and the existence of sister-species relationships between hosts and parasites has been used to infer sympatric speciation (Buschinger, 1990; Bourke and Franks, 1991). At the same time, it is recognised that such inferential approaches can be problematic and further empirical evidence is required to more firmly distinguish between allopatric and sympatric hypotheses (Berlocher, 2003; Coyne and Orr, 2004).

Acquiring firm phylogenetic evidence for or against sympatric speciation is difficult because multiple factors, such as extinction and host switching (see Fig. 1), as well as incomplete taxon sampling can all confound the interpretation of phylogenetic relationships. Phylogenetic

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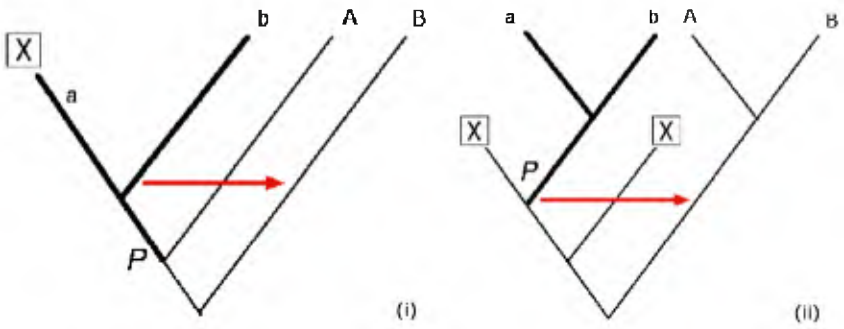

Fig. 1. How extinction and host switching events can distort evidence for sympatric or allopatric origins of social parasitism. 'P' indicates an origin of social parasitism, bolded lines indicate parasite species and thin line indicate social species, red (horizontal) arrows indicate host switching, 'X' indicates an extinction event, and upper and lower case letters indicate hosts and their parasites respectively. (i) A sympatric origin followed by host switching and then extinction of the original parasite—a sympatric origin would then appear to be an allopatric origin. (ii) An allopatric origin followed by co-speciation of hosts and parasites with the extinction of the closest relatives to the parasite lineage—an allopatric origin would then appear as a sympatric origin.

evidence therefore needs to be interpreted cautiously as the information obtained from present day species may not be an accurate representation of past events (Barraclough et al., 1998). Furthermore, these confounding factors would become increasingly more likely over time (Hey, 1992; Nee et al., 1994; Barraclough et al., 1998), so that phylogenetic approaches to the origin of social parasitism would be most effective when based on evolutionarily very recent origins (Parker and Rissing, 2002; Sumner et al., 2003; Sumner et al., 2004).

The majority of molecular phylogenetic studies on the relationships of insect social parasites to their hosts have been based on ants, with fewer studies on wasps, and corbiculate and halictine bees. However, there have been almost no studies on parasitic allodapine bees, even though they show at least eleven independent origins of social parasitism (Michener, 1970; Smith and Schwarz, 2006a). This number of origins could be due to the nature of allodapines, where brood are not enclosed within cells and multi-female nesting is ubiquitous (Schwarz et al., 1998). These characteristics are believed to provide a large exploitation potential for parasitic strategies (Smith and Schwarz, 2006b). The lack of research on allodapine bee parasites is therefore surprising, especially considering that 7.9% of the currently described species have been determined to be social parasites, which compares to only 1.7% for all known ant species (Brandt et al., 2005).

The socially parasitic allodapines exhibit a diverse range of morphological adaptations, with some species only distinguishable from their hosts by minor differences, such as slightly reduced scopae, while other species are extremely modified, with characteristics such as greatly reduced mouthparts, unique head and tergite projections, and a complete lack of functioning scopae (Michener, 1970). This range in the degree of adaptation to social parasitism is reflected in taxonomic structure, with some parasites accorded generic status, and others being placed in the same genus as their hosts. It seems likely that the extent of morphological adaptation to a parasitic lifestyle is at least partly correlated with the length of time since parasitism evolved (Savolainen and Vepsäläinen, 2003) and, if so, suggests a wide variation in the age of these parasitic allodapine lineages.

Here, we use molecular tools to explore phylogenetic relationships and divergence dates for a variety of allodapine social parasites and hosts (Table 1). These host-parasite relationships are analysed to examine evidence for and against sympatric speciation origins of social parasitism.

2. Materials and methods

2.1. DNA extraction, amplification and sequencing

DNA extraction, purification and amplification techniques were as previously described (Bull et al., 2003; Schwarz et al., 2003; Schwarz et al., 2004). Three gene fragments, from two mitochondrial and one nuclear gene were sequenced, COI, cytb and the F2 copy of EF-1α using described primers (Bull et al., 2003; Schwarz et al., 2003; Danforth et al., 2004; Schwarz et al., 2004). Most of the taxa used in these analyses have been presented in previous studies, and the GenBank accession numbers of these species can be found in Schwarz et al. (2003, 2004)); Bull et al. (2003) and Cronin (2004). Additional sequences for newly added taxa (Table 1) have GenBank Accession Nos. EF103589-EF103603 and EF190092-EF190112.

2.2. Phylogenetic techniques

Maximum parsimony (MP) analyses were carried out using PAUP* b4.10 (Swofford, 2002). Heuristic searches were undertaken using 50 random addition sequences of taxa, keeping only the best trees, holding 3 trees at each step, and using tree bisection and reconnection (TBR) swapping on all trees. The same searching protocol was used for bootstrap analyses, with support based on 500 bootstrap pseudoreplicates. Previous studies (Schwarz et al., 2003; Schwarz et al., 2004) on allodapines have shown extreme saturation problems for 3rd mitochondrial codon positions and they were therefore omitted from these parsimony analyses.

Table 1
Ingroup taxa used in this study, with the collecting locality and nesting strategy (host/parasite/non-host) included for each species

Genus	Species	Collecting locality	Host/ parasite[a]
Ceratina	*japonica*	Hokkaido, Japan	Non-host
Macrogalea	*zanzibarica*	Jambiani, Zanzibar Island, Tanzania	Non-host
	candida	Meru National Park, Kenya	Non-host
	magenge	Pemba Island, Tanzania	Non-host
	Malawi sp[b]	Mangochi, Malawi	Non-host
	antanosy	Fort Dauphin, **Madagascar**	**Host**[1]
	ellioti[b]	Toliara, **Madagascar**	**Host**[2]
	ellioti Moro[b]	Morondava, Madagascar	Host
	ellioti B[b]	Avenue du Baobabs, **Madagascar**	**Host**[2]
	maizina[b]	Fort Dauphin, **Madagascar**	**Parasite**[1]
	berentyensis[b]	Toliara, **Madagascar**	**Parasite**[2]
	berentyensis B[b]	Avenue du Baobabs, **Madagascar**	**Parasite**[2]
	infernalis[b]	Avenue du Baobabs, Madagascar	Non-host
	scaevolae[b]	Isle St. Marie, Madagascar	Non-host
	Ramena sp[b]	Ramena, Madagascar	Non-host
Brevineura	*xanthoclypeata*	Cobboboonee State Forest, Victoria, Australia	Non-host
	elongata	Great Sandy National Park, Queensland, Australia	Non-host
Exoneurella	*tridentata*	Lake Gilles, South Australia, Australia	Non-host
	setosa	Semaphore, South Australia, Australia	Non-host
Inquilina	***excavata***	Dandenong Ranges, Victoria, **Australia**	**Parasite**[3]
	schwarzi	Dandenong Ranges, Victoria, **Australia**	**Parasite**[4]
	Adelaide sp	Bridgewater, South Australia, **Australia**	**Parasite**[5]
Exoneura	***angophorae***	Dandenong Ranges, Victoria, **Australia**	**Host**[3]
	robusta	Dandenong Ranges, Victoria, **Australia**	**Host**[4]
	nigrescens	Cobboboonee State Forest, Victoria Australia	Non-host
	Adelaide sp	Bridgewater, South Australia, **Australia**	**Host**[5]
Halterapis	*seyrigi*	Ifaty, Madagascar	Non-host
	minuta	Anakao, Madagascar	Non-host
Compsomelissa	*borneri*	Meru National Park, Kenya	Non-host
Halterapis	*nigrinervis*	Beaufort, Cape Province, South Africa	Non-host
Allodapula	*empeyi*	Cape St. Francis, Cape Province, South Africa	Non-host
	melanopus	Wilderness, Cape Province, South Africa	Non-host
Allodape	*exoloma*	Cape St. Francis, Cape Province, South Africa	Non-host
	mucronata	Kleinmond, Cape Province, South Africa	Non-host
Braunsapis	*trochanterata*	Matemwe, Zanzibar Island, Tanzania	Non-host
	pictarsis	Nilgiri Hills, Tamil Nadu, India	Non-host
	KoChang sp	Ao Khlong Proa, Ko Chang Island, Thailand	Non-host
	Pilbara sp	Pilbara, Western Australia, Australia	Non-host
	unicolor	Lake Gilles, South Australia, **Australia**	**Host**[6]
	falcata	Lake Gilles, South Australia, **Australia**	**Parasite**[6]
	leptozonia[b]	Nelspruit, South Africa	Non-host
	paradoxa	Cape St. Francis, Cape Province, South Africa	parasite
	foveate[b]	Nelspruit, South Africa	Non-host
	Kenya sp	Meru National Park, Kenya	Non-host
Nasutapis	**Nasutapis sp**	Mangochi, Malawi, **Africa**	**Parasite**[7]
Braunsapis	*bouyssoui*	Soutpansberg Range, South Africa	Non-host
	Nasutapis host	Mangochi, Malawi, **Africa**	**Host**[7]
	vitrea	Soutpansberg Range, South Africa	Non-host
	otavica	Soutpansberg Range, South Africa	Non-host
	albipennis	Soutpansberg Range, South Africa	Non-host

The host and parasite species are in bold.
[a] The superscript numbers after host and parasite correspond to the host–parasite pairs in this study.
[b] These species have not been presented in previous studies and have GenBank accession numbers EF103589-EF103603 and EF190092-EF190112.

Bayesian analyses provide large advantages over MP and maximum likelihood analyses as they can accommodate different substitutional models for separate partitions (Huelsenbeck and Ronquist, 2001). Data were divided into six partitions: 1st, 2nd and 3rd codon positions for the combined mitochondrial (mt) genes and for EF-1α, based on recommendations of previous studies of allodapine bees (Schwarz et al., 2003; Schwarz et al., 2004). A General Time Reversible (GTR) + Gamma shape (Γ) model was used for all partitions with Invariant sites (I) assumed for 1st and 2nd positions but not for 3rd positions. Rates, substitution matrices, base compositions, proportion of invariant sites and Γ-shapes were estimated separately for each partition by unlinking these estimates across partitions.

Analyses were started using default priors from MrBayes 3.0b4 (Huelsenbeck and Ronquist, 2001). Analyses were run for 3 million generations, sampling every 500th generation. Log likelihood values were examined to detect stationarity, and a burnin of 1.5 million generations (3000 trees) was used, which was well after stationarity of the model parameters was reached. Three runs, each using three cold and one hot chain, were used to check that the priors used did not lead to different stationarity parameters.

2.3. Estimating divergence ages

Bayesian dating analyses were not used because the two available techniques were not suitable for our data. For Mutlidivtime (Thorne et al., 1998) the most complex substitutional model that can be enabled is F84, and rates matrices for allodapine mitochondrial regions clearly contradict this assumption (Schwarz et al., 2004 and rates matrices estimated here but not shown). In PhyBayes (Aris-Brosou and Yang, 2002) missing characters are excluded list-wise and the absence of any gene fragment for any of the included taxa would have lead to a greatly diminished data set. We therefore produced chronograms using Sanderson's penalised likelihood (PL) method, enabled in the program r8s (Sanderson, 2002). Branch lengths from phylograms were used to provide estimates of divergence times by adjusting the branch lengths so that they were more likely to correspond to periods of evolutionary time, rather than only evolutionary change, with evolutionary rates being able to vary between branches. Local transformations in rates were smoothed, using the assumption that evolutionary rates are temporally autocorrelated, with this autocorrelation placing a limit on the speed at which any rate can change from an ancestral to a descendant lineage (Sanderson, 1997). Point estimates of node divergence times were based on a consensus phylogram from a randomly chosen Bayesian run (see above) and 95% central distribution limits were calculated using a method outlined by Schwarz et al., 2006). This involved filtering all sampled post-burnin runs from the three replicate Bayesian analyses according to the consensus cladogram and then subjecting each of the retained phylograms to PL analysis. For the nodes of interest the top and bottom 2.5% divergence-age tails were then removed. The resulting trimmed ranges were used as the 95% central distribution limits for each node of interest.

There are no known fossil allodapines, so that nodes within the Allodapini could not be used as calibrating points. Instead, several other non-allodapine bees were included to enable deeper-level calibration points, as has been done previously (Fuller et al., 2005; Schwarz et al., 2006). The extinct fossil tribe Boreallodapini from Baltic amber is the sister tribe to the allodapines and three *Boreallodape* species are reliably dated at 44.1 million years ago (MYA; Engel, 2001). Ceratinini is the extant sister clade to Boreallapini + Allodapini (Engel, 2001), and therefore 45 MYA is believed to be an extremely conservative estimate of the minimum divergence time between Ceratinini and Allodapini. There is strong indirect evidence that the monophyletic corbiculate bees had evolved by at least 90 MYA because of a dated fossil angiosperm group, Clusiaceae, whose floral morphology is tightly linked to the corbiculates (Crepet and Nixon, 1998). The oldest fossil bee, *Cretotrigona prisca*, belongs to a highly derived clade in the extant Meliponini and is dated from the Maastrichtian (Engel, 2001), so that an origin of the corbiculates by 90 MYA does not seem unreasonable. The most basal divergence within the Apidae is between the lineages leading to the corbiculates and the allodapines, so this node was set at 90 MYA. In order to root this node, *Lasioglossum lanarium* and *Agapostemon tyleri*, two halictid bee species, were used as a monophyletic outgroup.

3. Results

Phylogenetic relationships among the major allodapine bee groups were well resolved with the Bayesian analyses (Fig. 2) with the exception of the Australian 'exoneurine' genera (*Brevineura*, *Exoneura* and *Exoneurella*), which are thought to comprise either a hard polytomy or two very rapid bifurcations (Schwarz et al., 2006). In contrast, the MP analyses obtained relationships with very low bootstrap support, as has been shown in previous allodapine studies (Fuller et al., 2005), although the topology obtained was almost identical to that shown in Fig. 2, with the only difference being the basal relationships among the 'exoneurine' genera and *Braunsapis trochanterata*, which was recovered as sister group to the African species rather than the Australia/Asian species, but whose position also had low support in the Bayesian analysis. Neither of these differences between the MP and Bayesian topologies effect the conclusions made concerning the allodapine social parasites.

The analyses included seven parasitic species, four from Australia, two from Madagascar and one from Africa, with four independent origins of social parasitism among these taxa (Fig. 2), two from Australia (*Inquilina* and *B. falcata*), one from Madagascar (*Macrogalea*) and one from Africa (an undescribed *Nasutapis* sp). The analyses also indicated subsequent speciation following the parasitic origin for both *Inquilina* and *Macrogalea*.

The four independent origins of social parasitism indicated various host-parasite relationships. The parasitic clade, *Inquilina*, was the sister group to the clade containing their host species, *Exoneura*, while *B. falcata*, was the closest relative to its host species, *B. unicolor*, and *Nasutapis*, was most closely related to a clade of free-living species that contained its host, an undescribed *Braunsapis* species (*Braunsapis Nasutapis* host). However, the parasitic clade, comprising *Macrogalea maizina* and *M. berentyensis*, was the sister group to a clade of free-living *Macrogalea* species that are not their hosts.

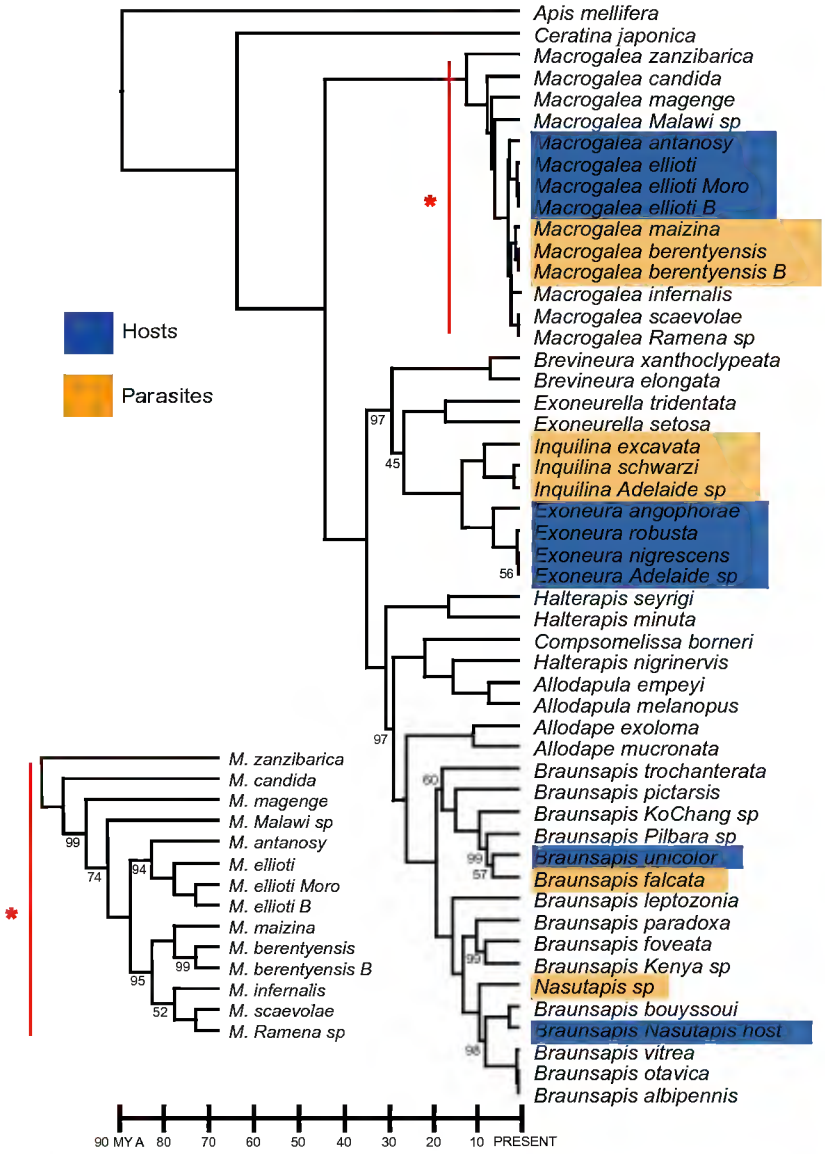

Fig. 2. Chronogram of allodapine species based on a penalised likelihood transformed Bayesian consensus phylogram. The insert shows an enlarged view of the chronogram for the *Macrogalea* species, whose divergences are very recent. The divergence ages of the parasitic lineages are indicated with the scale, and any posterior probability support values less than 100 are shown (these values are indicated on the enlarged view of the chronogram for *Macrogalea*). Host species are indicated with a superimposed blue box, while the corresponding parasite species are shown with an orange box. (For interpretation of the references in colour in this figure legend, the reader is referred to the web version of this article.)

The socially parasitic lineages have varying ages of divergence from non-parasitic sister groups. The chronogram (Fig. 2) indicates that *Inquilina* diverged from its host clade 12.88 MYA (95% central distribution limits (CDL) between 10.42 and 12.25 MYA), *Braunsapis falcata* diverged from its host clade 5.80 MYA (95% CDL between 4.38 and 7.73 MYA), *Nasutapis* diverged 9.51 MYA (95% CDL between 7.21 and 11.74), and the parasitic *Macrogalea* clade diverged from their host clade 2.01 MYA (95% CDL between 0.97 and 2.48 MYA). The ages of divergence from hosts are therefore related to the extent of morphological adaptations associated with parasitism, with *Inquilina* and *Nasutapis* having extreme parasitic adaptations (Michener, 1970; Michener, 2000). In contrast, the parasitic *Macrogalea* have barely recognisable parasitic adaptations (Pauly et al., 2001) and appear able to still collect pollen and rear brood in the absence of a host (Smith and Schwarz, 2006a).

4. Discussion

The host-parasite relationships observed for *Inquilina*, *B. falcata* and *Nasutapis* all conform to either the strict or loose form of Emery's rule, and as such, are compatible with previous studies that have suggested social parasites evolved via sympatric speciation (Savolainen and Vepsäläinen, 2003; Sumner et al., 2004). However, the host-parasite relationships observed for the *Macrogalea* social parasites

are not consistent with an intra-specific origin via sympatric speciation. These different host-parasite clade relationships may be associated with the divergence ages of the parasites, with the more anciently derived parasite species having a close relationship to their hosts, and the much more recent parasitic clade from Madagascar being the only group not to indicate a sister clade relationship between hosts and parasites.

These different host-parasite relationships illustrate some of the potential problems associated with using phylogenetic analyses to assess speciation. If the Malagasy social parasites had not been included in this investigation, the results could be seen as providing further support for a sympatric origin of parasitism within allodapines. However, the phylogenetic relationships observed between the Malagasy hosts and parasites could not have occurred via sympatric speciation and due to their relatively recent origin, the Malagasy clade would provide a more accurate representation of speciation events, as the likelihood of confounding events, such as extinction and host switching, would be lower for these relationships.

The phylogeny of the Malagasy species also provide another important example, namely that if a single extinction event had occurred, the loss of the lineage leading to *M. infernalis*, *M. scaevolae* and *M. Ramena* sp., before those species had diverged, the resulting phylogeny would have shown a sister group relationship between host and parasite lineages. Such clade extinctions would be impossible to detect within the information obtained from present day species, since no genetic record of the clade would exist, and this phylogeny therefore indicates how easy an allopatric origin of social parasitism could become distorted to appear as support for an origin via sympatric speciation.

It has been suggested that the idea of sympatric speciation, for explaining the evolution of social parasitism, has been too easily accepted, and that such theory needs to be re-evaluated (Ward, 1996). Allopatric speciation is considered to be the most likely hypothesis, as sympatric speciation appears to require quite an improbable sequence of events (Wilson, 1971) and rejecting any alternative hypotheses has proven to be difficult (Coyne and Orr, 2004). Continued research may be able to more firmly distinguish between the opposing allopatric and sympatric hypothesis for social parasite evolution, but there are always going to be problems associated with the indirect methods available to analyse these theories.

The recent research on the phylogenetic relationships of social parasites with their hosts has produced many different results, some seeming to show strong support for sympatric speciation (Savolainen and Vepsäläinen, 2003; Sumner et al., 2004), while others appear to provide evidence against a sympatric origin of social parasites (Carpenter et al., 1993; Choudhary et al., 1994; Ward, 1996; Steiner et al., 2006). It may very well be that the different relationships obtained are due to the different divergence dates of the parasitic species used in each of these studies. We believe such information to be a critical inclusion in all future studies, to correctly use phylogenetic relationships to determine speciation events. The use of divergence dates will allow more recently evolved parasite species to be identified, and will therefore allow more confident conclusions to be made about the phylogenetic relationships found.

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