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HOST SPECIFICITY AMONG *UNIONICOLA* SPP. (ACARI: UNIONICOLIDAE) PARASITIZING FRESHWATER MUSSELS

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ABSTRACT: Water mites of *Unionicola* spp. are common parasites of freshwater mussels as adults, living on the gills, or mantle and foot of their hosts and using these tissues as sites of oviposition. The present study addresses specialization among North American *Unionicola* mussel-mites using 2 measures of host specificity: (1) the number of host species used by a species of mite; and (2) a measure that considers the taxonomic distinctness of the hosts utilized by mites, weighted for their prevalence in the different hosts. Results of this study indicate the *Unionicola* spp. mussel-mites are highly host specific, with most species occurring in association with 1 or 2 species of hosts. If 2 or more host species are utilized, they are typically members of the same genus. These data are consistent with studies examining the dispersal abilities and host recognition behavior for members of the group. When the average values of host specificity for *Unionicola* subgenera were mapped on a phylogenetic tree for these taxa, a clade comprised of gill mites appeared to be more host specific than a clade consisting of mantle mites. There were, however, no apparent patterns of host specificity within each of the clades. Differences in specificity between the 2 lineages may reflect either a long evolutionary history that gill mites have had with host mussels or the intense competition among gill mites for oviposition sites within unionid mussels, leading to increased host specialization.

Host specificity is a fundamental property of parasites and is an important measurement in the study of parasite evolutionary ecology. The degree to which a parasite species is host specific can, however, be influenced by the manner in which host specificity is measured, leading to discrepancies in the reported specialization for a given parasite taxon (Poulin and Mouillot, 2003; Krasnov et al., 2005) or difficulties in making meaningful comparisons of host specificity among different parasite taxa (Poulin and Mouillot, 2003). Specialization among parasitic organisms traditionally has been based on the number of host species used by a species of parasite. This measurement may be a misleading indicator of host specificity because it implies that a parasite exploits all of its recorded hosts equally. Moreover, it fails to take into account the taxonomic relationships among the host species that are utilized (Poulin and Mouillot, 2003). Two species of parasites may infect the same number of host species, but differ in their patterns of host use depending on the taxonomic relationships of those hosts. For example, a parasite that exploits 4 species of hosts from the same genus would exhibit a higher degree of host specificity than a parasite that utilized the same number of host species from 4 distinctly different genera.

There have been a number of attempts to provide more instructive measures of specialization by parasites. For example, Rohde (1980, 1993) developed host specificity indices that accounted for either or both the prevalence or the intensity of infection of a parasite in all of its reported hosts. Poulin and Mouillot (2003) proposed an index of specificity that incorporated the average taxonomic (or phylogenetic) distance between pairs of host species exploited by a parasite. More recently, Poulin and Mouillot (2005) developed a comprehensive index of host specificity that combined measures of either or both the prevalence or intensity of infection of a parasite among its hosts with measures of taxonomic (or phylogenetic) distinctiveness of the set of host species used by a parasite. A better understanding of specialization for a parasite taxon also can benefit from an assessment of patterns of host specificity for the group using phylogenetic analyses (Brooks and McLennan, 1993; Thompson, 1994, 2005). For some parasite clades, host specificity increases during the evolutionary history of the group, a pattern that is consistent with hypotheses of progressive specialization in host-parasite lineages (Brooks and McLennan, 1993). However, analyses of the phylogenetic specificity for many parasite lineages have revealed no emerging patterns of specialization during the evolutionary history of these clades and suggest that specialization is not a causal component of parasite diversification (Brooks and McLennan, 1993).

Water mites of *Unionicola* spp. (Acari: Unionicolidae) commonly occur in parasitic association with freshwater sponges or mollusks during 1 of more stages of their life cycle. More than half of the described species of *Unionicola* parasitize freshwater mussels, living on the gills or mantle and foot of their hosts, and using these tissues as sites of oviposition (Vidrine, 1996a). There are approximately 70 described species of *Unionicola* from North America in some 19 subgenera (Vidrine, 1996a). Our understanding of the host specificity for this assemblage of mites is rather limited. Two surveys of the *Unionicola* spp. fauna among North American mollusks indicate that these mites exhibit highly variable patterns of host specificity, with some species occurring in association with a long list of host species and others utilizing 1 or at most a few species of hosts (Dobson, 1966; Vidrine, 1996a). Unfortunately, analyses of the host specificity among North American *Unionicola* spp. that take into account either or both the prevalence or abundance of infection or the taxonomic structure of the hosts used by mite species of this genus are lacking. Behavioral studies of *Unionicola* spp. mussel-mites also suggest that these mites are differentially host specific. While some species are capable of distinguishing between host and nonhost mussels (LaRochelle and Dimock, 1981; Edwards and Dimock, 1995), others fail to discriminate among potential hosts (Downes, 1986, 1989) when presented with a choice. Although an examination of the host recognition behavior of North American *Unionicola* spp. has proven to be useful in elucidating the degree of specialization among members of the group, behavioral data for this assemblage have been limited to studies from 6 species of mussel-mites.

The present study addresses specialization among *Unionicola* of North America that occur in parasitic association with freshwater mussels using 2 indices of host specificity: (1) the number

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of host species used by a species of *Unionicola*, and (2) a measure of specificity that considers the taxonomic distinctness of the hosts utilized by unionicolid mites and their prevalence in the different hosts (Poulin and Mouillot, 2005). Host specificity measurements that were generated for individual species were also used to estimate the average values of host specificity for their designated subgenera. These indices were then mapped on a phylogeny that was constructed for the mussel-mite subgenera to assess phylogenetic patterns of specialization for the group.

MATERIALS AND METHODS

Measures of host specificity

The data used for this analysis were obtained from a list of host records for North American *Unionicola* species in which 22,231 individuals representing 212 species of mussels were examined for mites (Vidrine, 1996b). This data set is amenable to analysis of host specificity because it represents a single published record for the occurrence of unionicolid mites from freshwater mussels of North America and thus minimizes concerns about the relationship between the number of host species recorded for a species and study effort (Poulin, 1992). Furthermore, there was no significant correlation between the number of individuals that were sampled for a given species of host and the number of mite species associated with that host ($F_{1,114} = 0.18$, $P = 0.67$), suggesting that host affiliations for North American *Unionicola* species were not influenced by sampling effort.

For each species of mite, we recorded the number of host species with which it occurred. Because a number of the mussels that are listed includes hosts for various species of *Unionicola* that are regarded as incidental records (Vidrine, 1996b), we decided to include a mussel as a host for a mite if it was found in a minimum of 10 hosts and its prevalence (= the proportion of host mussels harboring a species of mite) was greater than 10%. Also, this arbitrary cutoff reduced the possibility of generating estimates of prevalence for small sample sizes (<10 hosts). Abundance of infection, another good indicator of infection levels among hosts, was not included in the present analysis because these data were not provided in Vidrine's (1996b) data set.

Host specificity for each species of mite was also determined using the specificity index, S_{TD}* proposed by Poulin and Mouillot (2005). This index measures the average taxonomic distinctness among the host species used by a mite, weighted by the product of a mite's prevalence in the various hosts (Poulin and Mouillot, 2005). Taxonomic distinctness for each species of mite represents the mean number of steps up the taxonomic hierarchy that are required to reach a taxon that is common to 2 host species when computed for all possible pairs of hosts that are utilized by that species. The taxonomic classification schemes presented by Roe and Hoeh (2003) and Graf and Cummings (in press) were used as a basis for evaluating the taxonomic distinctness between 2 hosts used by a species of mite. The mussel taxonomies proposed by these authors were based on phylogenetic relationships of mussel taxa using morphological and DNA sequence data. All mussels included in this study were members of the Unionoida (Unionidae and Mycetopodidae). Mussel genera of the Unionidae were assigned to 1 of 3 subfamilies. Thus, if 2 host species were assigned to the same genus, then 1 step would be required to reach a node in the hierarchy that is common to both species. Hosts that belong to different genera of the same subfamily would require 2 steps to reach a common node in the taxonomic tree. If 2 species of hosts belonged to genera from different subfamilies, then 3 steps would be required to reach a common node in the hierarchical taxonomic tree. A taxonomic distinctness value of 0 was assigned to those species of mites that occurred in association with a single host species, as recommended by Poulin and Mouillot (2004). Microsoft Excel was used to create the formulae that were needed to compute S_{TD}* for each species of mussel-mite.

Host specificity and mite phylogeny

The morphological and life history characters (Table I) that were used to construct a phylogenetic hypothesis for North American *Unionicola* subgenera parasitizing freshwater mussels were obtained from the paper by Vidrine (1996a). Species of *Neumania*, a distinctly different taxon of sponge-associated mites that are closely related to mites from *Unionicola* spp. (Proctor and Wilkinson, 2001), was designated as the outgroup. Derived character states related to egg deposition (characters 20 to 27) and spinous extensions on female genital plates (characters 29 to 32) represent multistate transformation series (e.g., characters with a plesiomorphic character and more than 2 apomorphic characters that are not related to each other in a linear fashion). Nonadditive binary coding procedures were used to code these characters as outlined by Wiley et al. (1991). Morphological and life history character states for *Neumania* spp. were obtained from the paper by Cook (1974). The character state matrix for the characters described in Table I is presented in Table II.

Phylogenetic analyses of the character matrix was performed using maximum-parsimony (MP) search criteria in PAUP*4.0b10 (Swofford, 2002). MP analysis was performed using heuristic searches with tree-bisection reconnection branch swapping algorithms and MAXTREES set to 100. The shortest trees that were recovered were pooled and used to generate strict consensus trees with the majority-rule option set at 50%. Statistical support for trees generated by the analysis was estimated by 100 bootstrap iterations on the original data matrix.

To assess patterns in the evolution of host specialization among mussel-mite subgenera, the average values of the 2 measures of host specificity (number of host species and S_{TD}*) for species within each subgenus were mapped on the phylogeny of *Unionicola* subgenera. Three subgenera (*Clarkatax*, *Causeyatax*, and *Pentatax*) were represented by 1 species in North America. In these cases, host specificity measures for a single species were used to characterize the degree of specialization for each subgenus.

RESULTS

Measures of host specificity

Forty-seven of 55 species of *Unionicola* mussel-mites were found in a minimum of 10 host mussels and had a prevalence that was greater than 10%. The distribution of numbers of host species among these 47 species of mites was skewed, with most mites parasitizing 1 or 2 species of hosts (Fig. 1). The mean number of hosts for North American mussel-mites was 4.1 (± 0.93 SE, median = 2.0, range = 1–35).

Twenty of 47 species of *Unionicola* were recorded from 1 host species and were assigned an S_{TD}* value of 0. The distribution of S_{TD}* values among *Unionicola* spp. mussel-mites revealed that most species had values of 0 or 1 (Fig. 2). The average value of S_{TD}* across all species of mites parasitizing mussels was 0.95 (±0.12 SE, median = 1.0, range = 0–2.73). These data indicate that most species of *Unionicola* parasitize mussels within a single genus.

Host specificity and mite phylogeny

MP analysis of morphological and life history data for representative subgenera of North American *Unionicola* revealed 23 parsimony informative characters. Heuristic searches yielded 3 equally parsimonious trees with a tree length of 50 steps (CI = 0.76). A 50% majority rule consensus for the 3 trees is presented in Figure 3a. Bootstrap analysis (100 pseudoreplicates) provided statistical support for most relationships presented in the tree (Fig. 3a).

The typology of the MP tree indicates 2 major clades, with subgenera that occur in association with a host's mantle tissues (*Pentatax*, *Anodontinatax*, *Neoatax*, *Causeyatax*, and *Clarkatax*) forming 1 clade and subgenera that reside in a host's gills (*Unionicolides*, *Berezatax*, *Atacella*, *Parasitatax*, *Wolcottatax*, and *Dimockatax*) forming the other. Although the analysis did not resolve relationships among all taxa from the former clade, members of the latter clade clearly resolved into 2 branches, 1

TABLE I. List of morphological and life history character and character states for *Unionicola* spp. mussel-mites of North America.

Character No.	Character description	Character states
1	Female genital plates	0 = 2 plates; 1 = 4 plates
2	Number of pairs of genital acetabula	0 = more than 6 pairs; 1 = 6 pairs or less
3	Genital seta	0 = absent; 1 = present, centrally located; 2 = present, posteriorly located
4	Pedipalps	0 = ventrally sclerotized; 1 = not ventrally sclerotized (dorsoventrally flat)
5	Pedipalp tarsus	0 = tapered distally; 1 = not tapered distally
6	Blunt spines on leg I	0 = present; 1 = absent
7	Distal spatulate seta over tarsal claws of walking legs	0 = absent; 1 = present, extending beyond length of tarsal claws; 2 = present, not extending beyond length of tarsal claws
8	Clumps of modified seta on Genu of male leg IV	0 = absent; 1 = present, serrated; 2 = present, spinous
9	Modified seta on tibia of male leg IV	0 = absent; 1 = present, numerous serrated; 2 = present, 1 or 2 spinous
10	Body reticulate	0 = no; 1 = yes
11	Female genital plates separate	0 = yes; 1 = no
12	Length of palp tarsus clawlet less than basal width of palp tarsus	0 = yes; 1 = no
13	Length of palp tarsus clawlet less than length of palp tarsus	0 = yes; 1 = no
14	Posterior glandularia	0 = present; 1 = absent
15	Posterior apodeme on coxal plate IV	0 = present; 1 = absent
16	Biogeographic distribution	0 = global; 1 = North America; 2 = North America and Eurasia; 3 = North America and South America; 4 = South America
17	Size of genital acetabula	0 = uniform; 1 = variable (e.g., there are at least 2 large acetabula forming a distinct group in the genital field)
18	Seta on leg I on raised cuplike structures	0 = yes; 1 = no
19	Lifestyle	0 = sponge-associated mite; 1 = not a sponge mite
20	Egg deposition	0 = eggs not deposited in mussel mantle tissue; 1 = eggs deposited in mussel mantle tissue
21	Egg deposition	0 = eggs not deposited in labial palps of mussels; 1 = eggs deposited in labial palps of mussels
22	Egg deposition	0 = eggs not deposited throughout the mantle and foot tissues of mussels; 1 = eggs deposited throughout the mantle and foot tissues of mussels
23	Egg deposition	0 = eggs not deposited in mantle siphonal tissue of mussels; 1 = eggs deposited in mantle siphonal tissue of mussels
24	Egg deposition	0 = eggs not deposited in gills of mussel host; 1 = eggs deposited in gills of mussel host
25	Egg deposition	0 = eggs not deposited in the water tubes of mussels gill tissue; 1 = eggs deposited in the water tubes of mussels gill tissue
26	Egg deposition	0 = eggs not deposited along the ventral margins of the gills in the water tubes of mussels; 1 = eggs deposited along the ventral marginsof the gills in the water tubes of mussels
27	Egg deposition	0 = eggs not deposited in the water tubes along the lateral length of the gills in mussel hosts; 1 = eggs deposited in the water tubes along the lateral length of the gills in mussel hosts
28	Spinous extensions of female genital plate	0 = absent; 1 = present
29	Females with two pairs of genital plates and spinous extensions	0 = no; 1 = yes
30	Females with one pair of genital plates and spinous extensions	0 = no; 1 = yes
31	Females with one pair of genital plates with flaplike spines extending posteriorly past genital plates	0 = no; 1 = yes
32	Females with one pair of genital plates, with spines forming a flaplike thickened region	0 = no; 1 = yes

with the subgenera *Parasitatax*, *Wolcottatax*, and *Dimockatax*, and the other with *Unionicolides*, *Berezatax*, and *Atacella*.

The average number of hosts and average values of S_{TD}* for the subgenera of *Unionicola* mussel-mites are mapped on the phylogeny presented in Figure 3b. With the exception of the low mean values of host specificity for the subgenus *Andontinatax*, the clade consisting of gill mites had relatively fewer host species and lower S_{TD}* values than the clade containing mantle mites. However, there were no apparent regularities in the patterns of host specificity within a given clade.

TABLE II. Character state matrix of 32 morphological and life history characters for *Unionicola* spp. mussel-mites of North America. The outgroup (*Neumania*) is listed first. The numbered characters correspond to characters and character states listed in Table I.

Mite taxon	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	28	29	30	31	32
Neumania	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	0	0	0	0
Pentatax	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	1	1	0	1	1	0	0	0	0	1	1	0	0	0
Anodontinatax	1	1	1	0	0	0	0	1	1	0	1	1	0	1	0	2	0	1	1	1	0	1	0	0	0	0	0	1	1	0	0	0
Unionicolides	0	1	1	0	0	1	1	0	0	0	1	0	0	1	0	3	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0
Berezatax	0	1	1	1	1	1	1	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0
Atacella	0	1	2	1	1	1	1	0	0	0	1	0	0	1	0	3	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0
Neoatax	1	1	1	0	1	0	0	2	2	0	1	1	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	1	1	0	0	0
Causeyatax	1	1	1	0	1	1	0	2	0	0	1	1	0	1	1	1	0	1	1	1	0	1	0	0	0	0	0	1	1	0	0	0
Clarkatax	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0
Parasitatax	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	2	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0
Wolcottatax	0	0	1	0	0	1	2	0	0	0	1	0	0	1	1	2	1	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0
Dimockatax	0	0	1	0	0	1	2	0	0	1	1	0	0	1	1	2	1	1	1	0	0	0	0	1	1	0	1	1	0	1	0	1

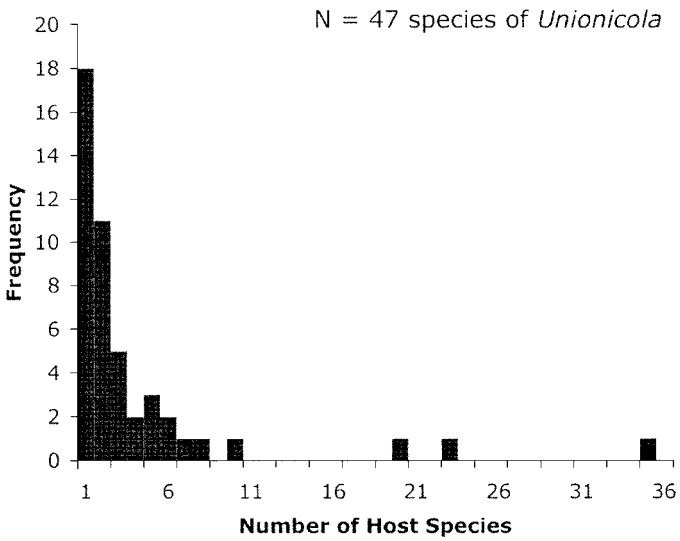

FIGURE 1. Frequency distribution of the number of species of hosts among North American *Unionicola* spp. that occur in parasitic association with freshwater mussels. Data were obtained for those mussel-mites found in a minimum of 10 host mussels with a prevalence greater than 10%.

Of the 47 species of *Unionicola* that were included in the analysis, 37 species were from subgenera recognized as gill mites and 10 species were from subgenera identified as mantle mites. Although gill mites occurred in association with a fewer species of mussels than mantle mites (Table III, Fig. 3b), there was no significant difference in the number of host species utilized by the two groups ($U = 220.5$, $P = 0.24$). There was, however, a significant difference in the S_{TD}* index ($U = 257.5$, $P = 0.05$) when the values for gill mites and mantle mites (Table III) were compared.

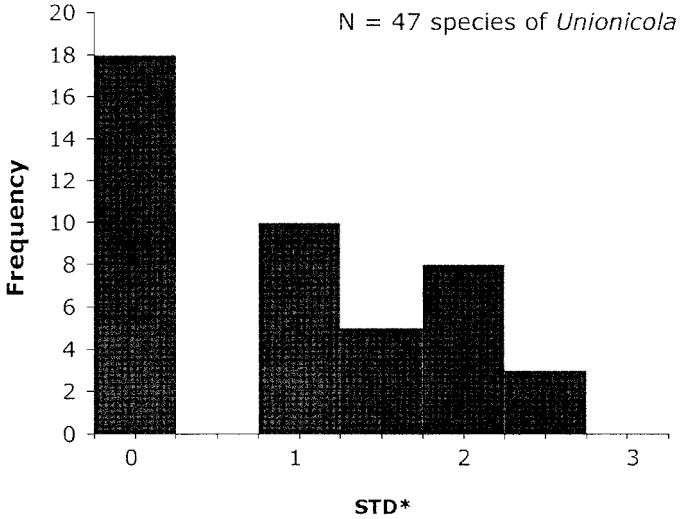

FIGURE 2. Frequency distribution of the S_{TD}* index among species of North American *Unionicola* spp. that occur in parasitic association with freshwater mussels. Data were obtained for those mussel-mites found in a minimum of 10 host mussels with a prevalence greater than 10%.

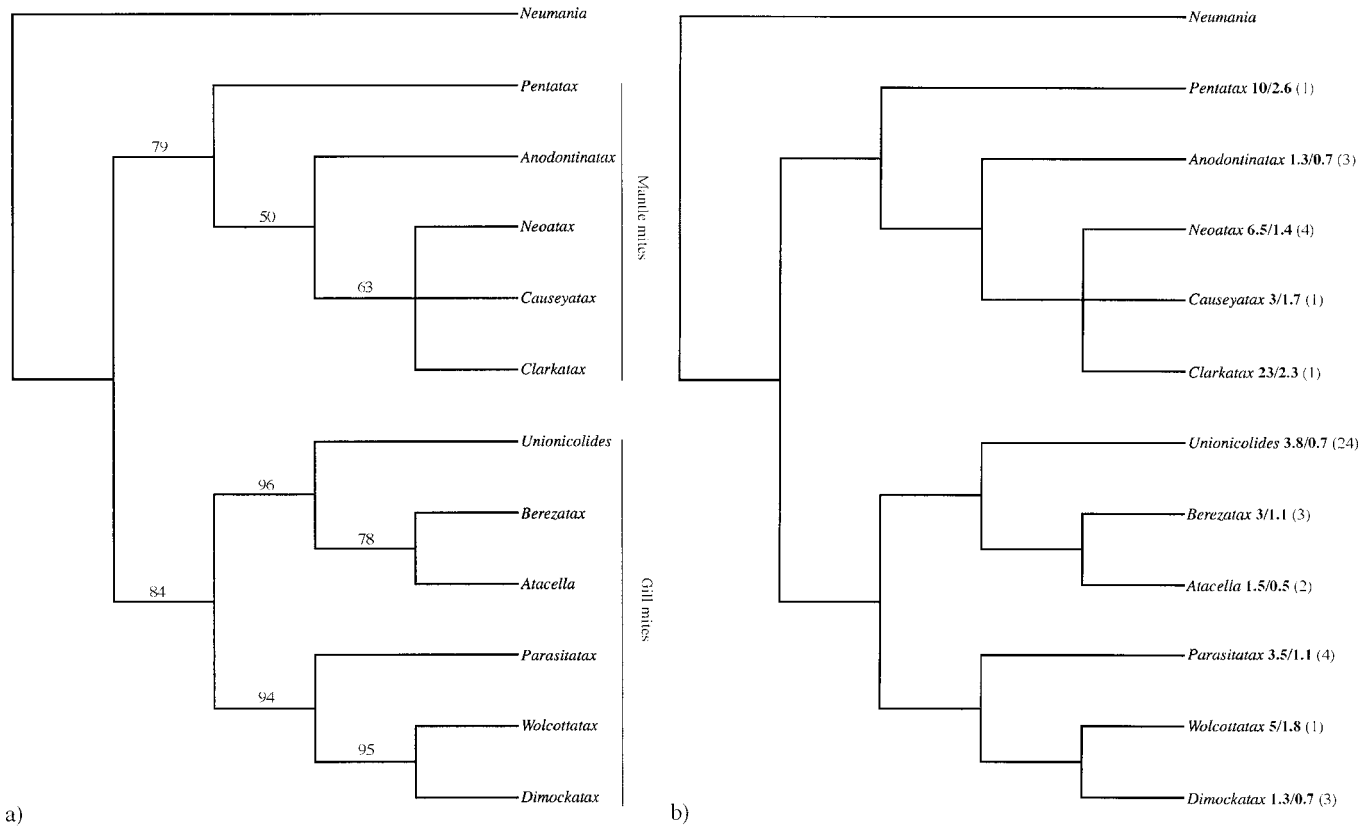

FIGURE 3. Maximum-parsimony (MP) tree showing phylogenetic relationships among subgenera of *Unionicola* spp. from North America that parasitize freshwater mussels based on morphological and life history characters. **(a)** Bootstrap support values >50% from MP analysis reported above the branches; **(b)** average number of host species (values on the left) and S_{TD}* values (values on the right) mapped on the phylogeny. Values in parentheses indicate the number of species of mites included for each subgenus.

DISCUSSION

The results of this study indicate that while a few species of North American *Unionicola* mussel-mites occur in association with a broad array of host species, most are restricted to 1 or 2 species of hosts. The low S_{TD}* values (0 or 1) reported for most species indicate that if *Unionicola* spp. mussel-mites are associated with more than 1 species of mussel, they are likely to be a congeners rather than a species belonging to a different genus or family of hosts. These results support the general conclusions of Vidrine (1996b), who suggested without providing quantitative evidence, that most species North American *Unionicola* were host specific.

The results of this investigation also support studies examining the dispersal abilities and host recognition behavior of *Unionicola* spp. mussel-mites. Mites that are poor dispersers and exhibit species-specific behaviors toward host mussels appear to be more specialized than mites that have good dispersal abilities and no apparent patterns in their behavioral responses toward mussels. For example, an examination of the specificity of the photoresponse for several species of mussel-mites by Downes (1989) revealed that *U. abnormipes* did not preferentially respond to chemical signals from host mussels. Results of the present study indicate that *U. abnormipes* occurs in association with 20 species of unionid mussels and has a relatively high (1.78) S_{TD}* value. Downes (1989) also observed that while *U. serrata* exhibited negative phototaxis in water modified by mussels, its response was not specific, given that the host-induced behavior was elicited in the presence of mussels they did not inhabit naturally. *Unionicola serrata* is one of the least specialized mussel-mites, exploiting 23 species of mussels and having the third highest (2.27) S_{TD}* value. Because *U. abnormipes* and *U. serrata* are relatively good swimmers (Downes, 1989), they are hypothesized to have good dispersal abilities and thus able to locate and colonize a broad range of host species. Conversely, 2 species of *Unionicola* from the subgenus *Parasitatax* (*U. formosa* and *U. foili*) with relatively poor swimming abilities (D. Edwards, pers. obs.) have been shown to exhibit highly species-specific behaviors toward host mussels (Edwards et al., 1998). Results from this study also indicate that 1 of the 2 species (*U. foili*) is highly host specific, parasitizing 2 species of mussels and reporting an S_{TD}* of 1.0. Although the measures of host specificity calculated for *U. for-*

TABLE III. The mean (±SE) values for 2 measures of host specificity for 2 lineages of *Unionicola* spp. mussel-mites from North America. Median values appear in parentheses.

Lineage of *Unionicola*	No. host species	S_{TD}*	Sample size
Gill mites	3.4 ± 1.0 (2.0)	0.8 ± 0.1 (1.0)	37
Mantle mites	6.6 ± 2.0 (2.5)	1.4 ± 0.3 (1.7)	10

mosa (number of hosts = 6; S_{TD}* = 1.70) do not appear to be consistent with a species of mite with poor dispersal ability and a high degree of behavioral specificity, they may be a reflection of the hidden patterns of specialization that are characteristic for this species. An examination of the genetic structure of *U. formosa* from 3 host genera (Edwards et al., 1998) revealed that several host-associated populations were highly genetically differentiated and comprised reproductively isolated sibling species. Thus, what has traditionally been regarded as 1 species of mite occurring in parasitic association with a diverse array of mussels may instead represent 2 or more highly specialized cryptic species of *Unionicola*.

A comparison of host specificity between the 2 major clades of mussel-mites (gill mites vs. mantle mites) revealed that gill mites parasitized a taxonomically narrower range of hosts than did mantle mites. The 1 exception to this general pattern was the host specificity values obtained for mites of the subgenus *Anodontinatax*. There was, however, a high degree of variability in the S_{TD}* values among species of this subgenus (*U. belli* = 0, *U. smithae* = 0, *U. wolcotti* = 2), making general comments regarding host specificity for *Anodontinatax* inconclusive. Behavioral studies of *U. intermedia*, a European mite, *Anodontinatax* sp., indicate that although this species can occur in association with the mussels *Anodonta cygnea* and *A. anatina*, it is, interestingly, excluded from the former species by *U. ypsilophora* (Davids et al., 1988). *Unionicola intermedia* is believed to be restricted to the host mussel *A. anatina* because of competitive exclusion. Whether or not exclusion accounts for the high levels of host specificity reported for *U. belli* and *U. smithae* from North America has not been investigated. With the exception of differences in host specificity among gill mites and mantle mites, there were no emerging patterns of host specificity within each of these clades. These results are consistent with phylogenetic patterns of host specificity observed for many parasite taxa (Brooks and McLennan, 1993) and suggest that host specificity among *Unionicola* spp. mussel-mites is not causally linked to their diversification.

The reasons for the differences in the patterns of host specificity between gill mites and mantle mites are uncertain. It would be interesting to compare the host recognition behavior and swimming abilities of representative species from the 2 clades to determine whether there is a relationship between dispersal ability and host specificity as suggested by Downes (1989). Differences in specificity between these groups may reflect the long evolutionary history gill mites have had with host mussels (Vidrine et al., 2005) or intense competition among gill mites for oviposition sites within unionid mussels (Mitchell, 1965; Downes, 1995), leading to increased host specialization.

The present study represents the first time that ecological and phylogenetic information have been integrated to assess host specificity among parasitic water mites of the *Unionicola*. This type of analysis undoubtedly provides more meaningful information regarding specialization than can be gained from merely listing the number of host species used by species of *Unionicola* and should be useful in addressing patterns of host specificity among unionicolid water mites that utilize mussels, gastropods, and sponges, both in North America and throughout the world. Once patterns of host specificity for species and subgenera of this taxon have been characterized, the mechanisms responsible for mediating those patterns, including the effects of dispersal capacity by parasites (Downes, 1989; Giorgi et al., 2004), competitive exclusion (Davids et al., 1988; Adamson and Noble, 1993), behavioral specificity (Soneshine et al., 1986; Edwards and Dimock, 1995), and host compatibility (Preston and Southgate, 1994; Combes, 2001) can be elucidated. Furthermore, an analysis of host specificity among *Unionicola* spp. mussel-mites would not be complete without examining the interrelationships between the geographic distributions of the mites, their hosts, and variations in host use. Thompson (1994) indicated that while most species of parasites are extremely specialized, there are distinct geographic differences in specialization, owing to factors such as ecological opportunity (e.g., when a preferred host is not available) and genetic constraints (e.g., the inability to recognize a species as a good host). An accurate assessment of host specificity among *Unionicola* will be instrumental to addressing questions related to the nature of coevolutionary relationships among water mites and their host mussels (Edwards et al., 1998) and the relationship between specialization by water mites and the potential risk of extinction (Poulin, 1998). The latter question may be of heightened interest given the imperiled state of North America's freshwater mussel fauna (Ricciardi and Rasmussen, 1999).

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