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129TH ANNUAL ACADEMY MEETING[1]

Presidential Address by Dale D. Edwards[2]

"Let's Talk Science—Mites of Freshwater Mollusks"

ACADEMY MEETING WELCOME

Welcome to the 129th Annual Academy Meeting!

The Indiana Academy of Science has had the privilege of serving Indiana scientists from industry and academia, Indiana science educators, and Indiana graduate and undergraduate science students, as well as aspiring young future scientists and the Indiana general public since 1885. With the mission of promoting scientific research, diffusing scientific information, improving education in the sciences, and encouraging communication and cooperation between Indiana scientists, the Academy hosted its first Annual Academy Meeting in Indianapolis in 1885, at the Marion County Courthouse. From this historic, yet humble beginning a proud academy was built. There are many leading scientists in our membership, and many who have made the difference in science as we know it here in Indiana.

We have a wonderful Annual Meeting planned for you today, resulting in large part from the generosity of Eli Lilly and Company Foundation, the W.K. Kellogg Foundation, Subaru of America, and the White River State Park. Today, 160 of you, researchers from the State of Indiana, will be presenting science in both oral and poster presentations. Nationally recognized guest speakers Dr. James Bing, a Global Trait Introgression Leader at Dow AgroSciences, and Johannah Barry, President of the Galapagos Conservancy, will be adding to our science conversation. Hot topics will be delivered by those on the cutting edge of much of the conversation of those topics. Workshops will also be offered for your professional development, and for the first time this year, with the approval of the Department of Education, professional education credits will be granted for our Indiana science teachers participating in today's meeting. We are also very happy to have a handful of young high school science students with us today. I encourage you to take time to get to know these young people as they move about the meeting.

At our Luncheon today, in addition to hearing from our guest speaker Dr. Jim Bing, we will introduce our Academy leadership, welcome our new Academy Fellows, and applaud our 2014 Awardees. Immediately following lunch, our poster presenters will be standing aside their posters in Grand Ballroom 1-4 to talk with you about their research. Though their posters will be up for you to view all day, we will be dedicating our attention to their presentations from 2:00 to 3:10 p.m. We are also truly looking forward to hearing Johannah Barry's Plenary Address this afternoon, regarding the ongoing conservation efforts in the Galapagos Islands.

Following Ms. Barry's Plenary, we will hold a brief, but very important Academy Membership Meeting. At this meeting, we will hear from our Section leadership who will be meeting with you this morning (check for the room number of your section meeting in the program book). We will also take a few minutes to vote on recommended adjustments to our Bylaws, and welcome in the incoming Academy President, and the newly elected officers and committee members, who will officially take on their new responsibility June 1. Be sure to join us for desserts, soft drinks, coffee, tea, wine, and beer to wrap up our meeting this year.

Earlier this year, Delores Brown, Executive Director of the Academy, thought it would be a good idea to reinstate an old tradition at the annual meeting. One in which the Academy President opened the meeting by talking about science. In this case, she asked if I would be willing to talk about my research. I thought it was a great idea and was happy to oblige. So without further ado, let's talk science!

MITES OF FRESHWATER MOLLUSKS

What I want to do this morning is give you an overview of some research that I have

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been doing for the past twenty years or so involving the ecology and evolution of water mites of the genus *Unionicola* that live in symbiotic association with freshwater mussels and snails.

The primary objectives of this talk are as follows: 1) to put the genus *Unionicola* into taxonomic perspective; 2) to provide you with a general life cycle of these water mites; 3) to characterize the precise nature of the symbiotic association between these mites and their molluscan hosts; 4) to discuss some of my behavioral research involving *Unionicola* mites and how these studies have changed our perception about what it means to be a species in the context of these mites; 5) to provide you with a framework regarding the phylogenetic systematics and biogeography of *Unionicola* mites; and 6) to leave you with insights regarding future directions of my research program involving these mites.

PUTTING *UNIONICOLA* MITES INTO TAXONOMIC PERSPECTIVE

Mites, or taxonomically speaking the Acari, represent a diverse and variable group of arthropods. Three major lineages or superorders of mites are currently recognized: Opilioacariformes, Parasitiformes, and Acariformes. The Acariformes (the mite-like mites) contains over 300 families and over 30,000 described species. Two major lineages of Acariformes are recognized, the Sarcoptiformes (Oribatida and Astigmata) and Trombidiformes (Prostigmata). The Trombidiformes represents a diverse assemblage of mites. The largest and most spectacular lineage within Trombidiformes is Parasitengona, with over 7000 described species of terrestrial and aquatic mites. Mites belonging to several unrelated groups are commonly found in freshwater habitats. However, the true water mites (Acariformes: Trombiformes: Parasitengona) or Hydrachnida (= Hydrachnellae, Hydracarina, and Hydrachnidia) represent a series of extensive adaptive radiations occurring mostly in freshwater habitats. Well over 5000 species of water mites are recognized worldwide, representing more than 300 genera and subgenera in over 100 families and subfamilies.

Water mites of the genus *Unionicola* (Acari: Hydrachnida: Unionicolidae) represent a diverse collection of more than 250 species in some 57 subgenera (Edwards & Vidrine 2013) distributed in freshwater habitats around the world. More than half of the described species are symbionts of freshwater mussels and snails. Indeed, the Latin name *Unionicola* literally means 'living within mussels'—since 'cola' or 'icola' mean 'to live within' and 'unio' is a name for mussels.

UNIONICOLA LIFE CYCLE

The life cycle of water mites is complex and includes the egg, larva, protonymph, deutonymph, tritonymph, and adult. Larvae, deutonymphs, and adults are motile, whereas protonymphs and tritonymphs are quiescent, transformational stages of the life cycle. The adults and deutonymphs of most water mite species are free-living predators. However, there are species from the Pionidae and Unionicolidae that are symbiotic with freshwater gastropods, mussels, and sponges (Mitchell 1955). Although some species of *Unionicola* are free-living predators as nymphs and adults and depend on hosts only for sites of oviposition and post-larval resting stages, most species are obligate symbionts of their hosts. Among those species living within mollusks, the females deposit eggs in specific tissues (gills or mantle or foot) of the hosts, with larvae emerging in late spring and summer. The larvae of most water mites parasitize aquatic insects and in so doing acquire nutrition for larval development and a primary mechanism for dispersal. Larval mites of the genus *Unionicola* utilize chironomids and generally locate these insect hosts during the pupal phase of development (Fig. 1), but the mechanisms of host location are not well understood. The larvae eventually reinvade a host mussel, embed in host tissue, and enter a transformational stage from which the sexually immature nymph emerges (Fig. 1). The nymph subsequently enters a transformational stage from which the sexually mature adult emerges.

NATURE OF THE SYMBIOTIC ASSOCIATION BETWEEN *UNIONICOLA* MITES AND MOLLUSKS

Although *Unionicola* mollusk mites have been traditionally recognized as parasites, there is little known about the nutritional dependence of these mites on their hosts or the impact that unionicolids may have on the hosts with which they are associated. Baker (1976, 1977) provided evidence that *U. intermedia* from *Anodonta anatina* is capable of piercing

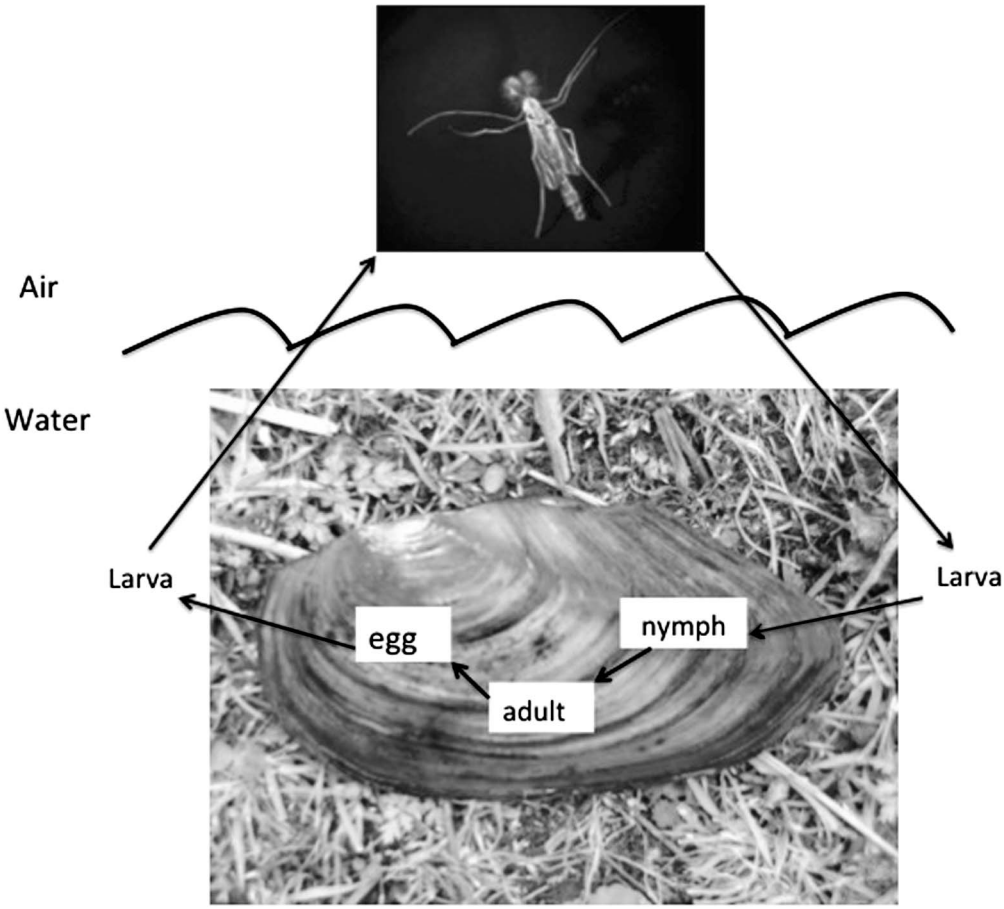

Figure 1.—Generalized life cycle of *Unionicola*.

the gills of host mussels with their pedipalps, allowing them to feed on hemolymph and mucus. Extensive infiltration of hemocytes into the damaged regions of the host's tissue may provide these mites with an additional nutritional source (Baker 1976). Observations by LaRochelle & Dimock (1981) of *U. foili* from *Utterbackia imbecillis* indicated that these mites would occasionally penetrate the gills of their host using their pedipalps. However, histological examination of the midgut of these animals could not definitely conclude that they were feeding on host tissues. More recently (Fisher et al. 2000) used both histochemical approaches and immunological assays to confirm that *U. formosa,* a sibling species of *U. foili,* does indeed ingest mucus and hemolymph from its mussel host, *Pyganodon cataracta*.

Although it is becoming increasingly apparent that *Unionicola* mollusk mites are utilizing host mucus, gill tissue, or hemolymph for at least part of their nutrition, the effects that these mites have on a host has not yet been examined in any detail. Laboratory experiments by MacArthur (1989) indicated that long-term exposure of *P. cataracta* to *U. formosa* did not significantly alter the host's shell morphology and composition, or soft-tissue mass and biochemical composition. In addition, there was no evidence that short-term exposure of *P. cataracta* to these mites significantly altered their ability to move water or filter particles.

THE POPULATION BIOLOGY OF ADULT MITES

A polygynous mating system.—One of the main reasons I became interested in studying *Unionicola* mites was because of their peculiar population structure. While examining the pop-

ulation dynamics of *U. foili* (formerly identified as *U. formosa*) from the mussel *Utterbackia imbecilis*, my PhD advisor, Ron Dimock, discovered that the density (number of mites/mussel) of female mites was positively correlated with host size. Male *U. foili* were, on the other hand, under dispersed among their hosts, with most mussels harboring a single male. This drastic difference in the density of male and female mites was reported for every month of the year, with the mean sex ratio during a two-year study period being close to 30 females:1 male (Dimock 1985).

The persistent female-biased sex ratio reported by my advisor, fit together with other work (Dimock 1983, Edwards & Dimock 1991) indicating that male mites are territorial and aggressive to other males. The behavior by males was characterized as being consistent with those of a female-defense polygynous mating system. Although a female-biased sex ratio appears to be typical for many species of *Unionicola* (Mitchell 1965; Davids 1973; Baker 1987), there is little known about the impact of this population structure on the reproductive biology of *Unionicola* mollusk mites. Because fertilization among these mites most likely occurs within the confines of a host mussel (Hevers 1978), then establishing and maintaining this territory would dramatically increase a male's reproductive success. Unfortunately, we know next to nothing regarding the structure (e.g., can resident males successfully inseminate all females residing inside the mantle cavity of a host mussel?) and dynamics (e.g., how often are males displaced by other males during the mating season?) of the mating system for *Unionicola* mollusk mites, making further comments about male mating success speculative at best (Edwards et al. 2004).

Behavioral specificity.—Symbiotic relationships between *Unionicola* mites and their molluscan hosts are characterized by a diversity of host-influenced behaviors by the mites (Dimock 1988). The first experiments to examine and document these behaviors in some detail were performed by Welsh (1930, 1931). Welsh's (1930) paper reported that the mite *U. ypsilophora* (probably *U. formosa*) was positively phototactic in the absence of any chemical influence of its host mussel, *Anodonta* (now *Pyganodon*) *cataracta,* but exhibited negative phototaxis when tested in water containing extract of host gill tissue or in water from the mantle cavity of the host. Since the pioneering work of Welsh (1930, 1931), other studies have found that the response to light by several additional species of unionicolid mites is influenced by the chemistry of the water in which they were examined (e.g., mites are positively phototactic when tested in water that is free of any chemical influence from a host, but in the presence of extracts from its host, the sign of their response reverses to negative; Roberts et al. 1978).

Host-specific behavior by *Unionicola* mussel mites is also evident from studies examining the recolonization of mussel hosts. For example, when either *U. formosa* (from the mussel *Pyganodon cataracta*) or its sibling species *U. foili* (from the mussel *Utterbackia imbecillis*) are removed from a mussel and presented with a choice between *P. cataracta* and *U. imbecillis,* I found that adult mites would preferentially reenter the host species from which they had initially been collected (Edwards 1988). The mechanisms by which *Unionicola* mussel mites discriminate among host mussels are not known. The behavioral studies of LaRochelle & Dimock (1981) and Werner (1983) emphasize the role of contact chemoreceptors in mediating host recognition. However, the findings of LaRochelle & Dimock (1981) and the fact that the induction of mite negative phototaxis can occur in water modified by mussels clearly suggest that it can be mediated by distance chemoreception as well.

Although most studies regarding the specificity of the host recognition behavior of *Unionicola* mussel mites have involved adults, there have been few attempts to characterize the behavioral specificity during other stages (nymphal and larval) of the life cycle. Because it is the larvae that initiate an association with a host mussel (Fig. 1), characterizing the behavior of this stage of the life cycle was critical in documenting the nature of host specificity of these mites. When I examined the behavior of larval *U. foili* from *Utterbackia imbecillis* and *U. formosa* from *Pyganodon cataracta,* (what was then thought to be one species of mite from two different species of host mussels), I found that they preferentially responded to chemical signals from their respective host mussels, but the pattern of their responses changed during larval ontogeny (Edwards & Dimock 1995). For example, larvae emerging from *U. imbecillis* that had

completed their parasitic phase with chironomids (what I referred to as post-chironomid larvae) exhibited negative phototaxis only in the presence of water that had been modified by *U. imbecillis.* The host-influenced behavior exhibited by these larvae was absent among mite larvae prior to parasitizing chironomids (what I referred to as pre-chironomid larvae). The changes in the behavior of pre-chironomid and post-chironomid larvae probably reflected major differences in the life history strategies of these developmental stages. For example, post-chironomid larvae represent the invasive stage of the mussel-mite symbiosis. A preferential response to a host chemical factor would, therefore, be expected, especially if it increased the likelihood of locating a host.

Cryptic species of molluscan symbionts.—I was intrigued by the specificity of host discrimination behavior by larval mites between the host mussels *U. imbecillis* and *P. cataracta,* because these findings, coupled to the fact that fertilization among these mussel-mites occurs only within the confines of a host mussel (Hevers 1978), suggested that specific behavioral responses to mussels could maintain reproductive isolation between mites occurring with different host species. An examination of the genetic structure of populations of mites from *U. imbecillis* and *P. cataracta* using allozyme electrophoresis (Edwards & Dimock 1997) revealed a high degree of genetic differentiation between these host-associated populations, including mites from the two species of hosts being fixed for different alleles at three loci. Edwards & Dimock (1997) concluded that mites from these two species of mussels were reproductively isolated and thus constituted good biological species. Mites from *P. cataracta* were recognized as *U. formosa* sensu stricto, whereas mites from *U. imbecillis* were identified as a new sibling species, *U. foili.* Since this work was published, genetic studies in my lab, including allozyme analysis (Edwards et al. 1998, Edwards & Labhart 2000) and DNA sequence comparisons (Ernsting et al. 2006, Ernsting et al. 2008), have been helpful in delineating additional species of *Unionicola* that were, on the basis of traditional anatomical criteria, morphologically indistinguishable.

Interestingly, North American *Unionicola* mussels-mites are known to exhibit highly variable patterns of host specificity, with some species occurring in association with a long list of host species and others utilizing one or at most a few species of hosts (Edwards & Vidrine 2006). An examination of both interspecific and intraspecific genetic diversity among host-associated populations of these mites undoubtedly will play a valuable role in testing hypotheses about current species designations and potentially uncover sibling species of *Unionicola* mussel-mites. Results of some recent molecular genetic work in my laboratory are beginning to bear witness to the predication. A comparison of partial COI sequences between host-associated populations of *U. hoesei*, a mite that is known to occur in association with many species of host mussels throughout North America, has revealed a high degree of genetic differentiation. Moreover, these differences are within range of the genetic differentiation that has been observed among previously recognized sibling species of *Unionicola*, including those in which morphological differences among species are relatively minor (Ernsting et al. 2008) and those that appear to be morphologically indistinguishable (Ernsting et al. 2006). The discovery of cryptic species of *Unionicola* mites based on molecular sequence data has obvious implications regarding estimates of biodiversity within this taxon. A failure to recognize cryptic species among unionicolid mites would also have important implications for anyone trying to unravel the nature of co-evolutionary relationships among *Unionicola* mites and their hosts.

A PHYLOGENETIC BLANK SLATE

Our understanding of the evolutionary relationships among *Unionicola* water mites is limited and has largely been derived from morphology-based classifications among members that comprise the group. For example, Vidrine (1996) and Wu et al. (2009) suggested that sponge-associated mites of the subgenus *Hexatax* (formerly *Unionicola*) represent the least-derived taxon within the genus. Morphologically, these mites closely resemble species of free-swimming mites from the genus *Neumania* (Unionicolidae: Piontacinae). Vidrine (1996) subsequently identified 20 groupings of *Unionicola* subgenera based on sets of shared morphological and life-history characters. Despite these rather broad assessments of unionicolid systematics, the evolutionary history of the genus has not been adequately tested using phylogenetic approaches.

A number of recent studies have attempted to reconstruct evolutionary relationships among a limited number of mussel-mite taxa based on morphological characteristics (Edwards & Vidrine 2006, Wu et al. 2009) and molecular data sets (Edwards et al. 2010, Wu et al. 2012). The topologies of trees generated by these analyses are congruent in that they suggest that mites that live in the gills of host mussels (= gill mites) are monophyletic. This hypothesis is consistent with that of Vidrine et al. (2007) who suggested a shared evolutionary history among the gill mites based upon a number of anatomical similarities. These studies, however, have revealed conflicting hypotheses regarding relationships among *Unionicola* mites that live in the mantle and foot area of host mussels (= mantle mites). While morphologically-based trees recognize mantle mites as a distinct monophyletic grouping (Edwards & Vidrine 2006), molecular phylogenies suggest that these mites are part of a paraphyletic grade that includes gill mite taxa (Edwards et al. 2010). Thus, although the gill mites represent a monophyletic clade (Edwards & Vidrine 2006, Vidrine et al. 2007, Wu et al. 2009, Edwards et al. 2010), the relationship between gill mites and other species of *Unionicola* remains unclear. The mantle mites appear to be a conglomerate of diverse taxa at the subgeneric level, with some subgenera having morphological affiliations with sponge mites, and others sharing morphological similarities with gill mites (Vidrine 1996, Edwards et al. 2010).

One major caveat of this previous work is that both the morphological and molecular phylogenetic studies were limited in their geographical scope (e.g., limited to one continent) and in their sampling of taxa. Furthermore, the trees generated by these studies were based on a relatively small number of characters. For example, the morphologically-based phylogeny of Edwards & Vidrine (2006) was constructed using 32 characters. The gene tree generated by my colleagues and I (Edwards et al., 2010) was based on 664 bp from the cytochrome oxidase subunit I gene. Clearly, a more robust phylogenetic hypothesis of the genus *Unionicola* would require broader taxon sampling (both in terms of geographic distribution and sample size) and the incorporation of a substantially larger number of characters into the analysis.

A phylogenetic analysis of *Unionicola* mites based on molecular sequence data would undoubtedly be the best approach to resolving evolutionary relationships among taxa that comprise the genus. There are, however, at least two compelling reasons why generating a molecular phylogeny for the group could be problematic and thus warrant reconstructing the evolution history among these mites based on morphological data. First, many of the mollusk mites that have been identified and described were collected long ago and would be difficult to relocate primarily due to host extinction and habitat destruction. Second, holotypes and representative paratypes of described species have been preserved in solutions that have invariably damaged the quality and integrity of their DNA. In short, a phylogenetic analysis of *Unionicola* mites based on non-molecular data would presumably allow for greater taxon sampling.

Addressing evolutionary relationships among *Unionicola* mites based on morphological criteria is not without its challenges, given that so few characters historically have been used to diagnose the genus and its subgenera (Cook 1974). Moreover, a cursory glance at the taxonomic studies involving *Unionicola* mites suggests that a limited number of characters are available for phylogenetic inference. Despite the apparent pitfalls of using morphological data to reconstruct the phylogeny of unionicolid mites, Malcolm Vidrine, a colleague of mine from Louisiana, and I revisited the taxonomic literature for the group and generated 158 characters that could be used to estimate evolutionary relationships among most of the currently named subgenera that comprise the genus, including relationships between free-swimming taxa and those that have adopted symbiotic lifestyles (Edwards & Vidrine 2013). We subsequently identified 139 characters that could be used to reassess and potentially resolve conflicting hypotheses regarding the phylogeny of *Unionicola* mites that occur in association with mollusks (molluscan gill mites and mantle mites).

A tree based on the Bayesian inference of morphological data for *Unionicola* mites (e.g., representative species from 53 subgenera that comprise the genus) is presented in Fig. 2. The Bayesian tree suggests that most of the free-swimming *Unionicola* subgenera are a distinct radiation (see node labeled A). Although the tree recognizes multiple clades of free-

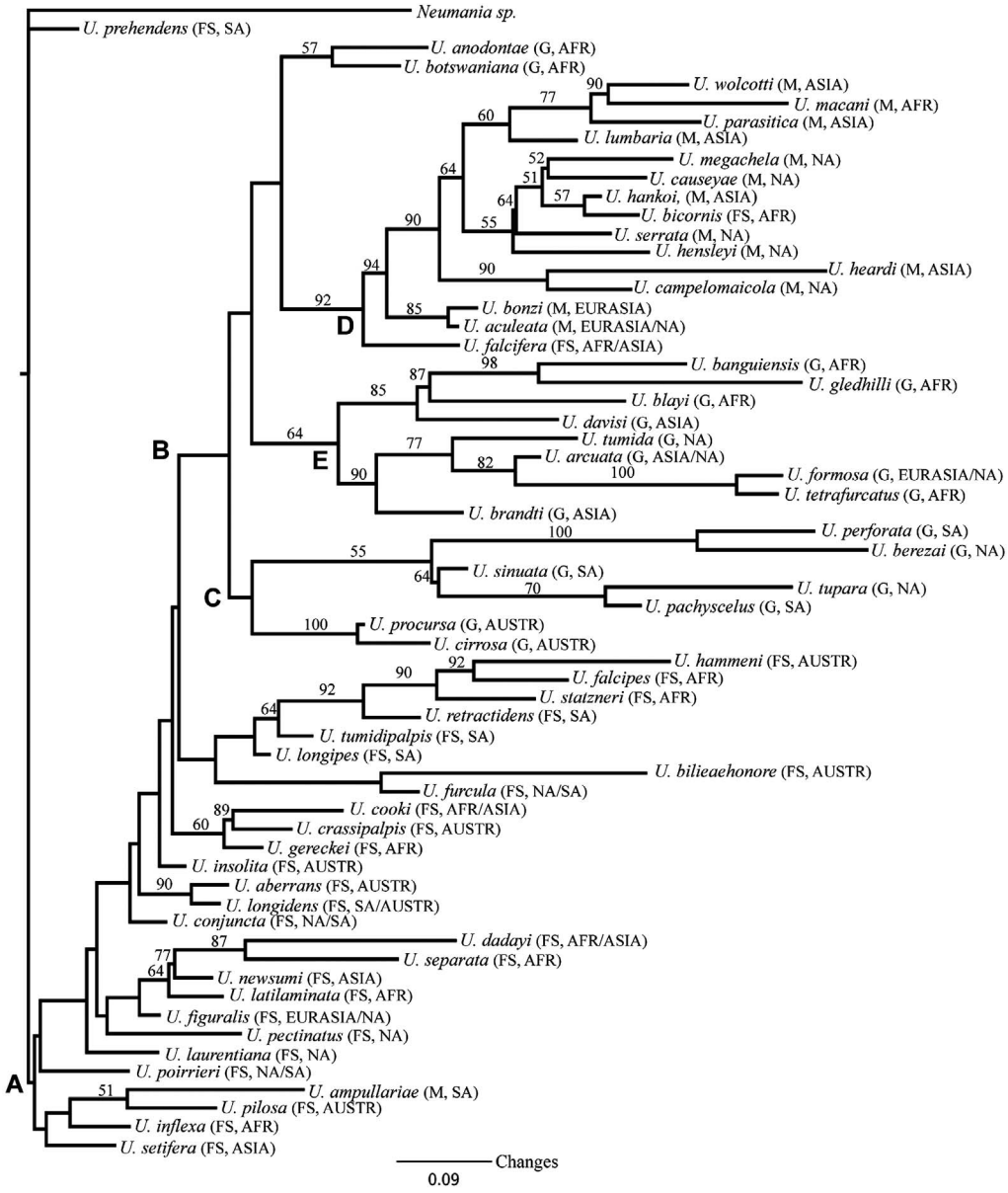

Figure 2.—Bayesian tree based on 158 morphological characters for representative species from 53 subgenera of *Unionicola* mites. Numbers above branches represent posterior probability values. Letters indicate notable clades: A=free-swimming mites; B=Mollusk mites; C=Australian, South American, and North American gill mites; D=mantle mites; E=African, Eurasian, and North American gill mites. Abbreviations in parentheses: FS=free-swimming mites; G=gill mites; M=mantle mites; NA=North America; SA=South America; AFR=Africa; AUSTR=Australia.

swimming mites, there appears to be no distinct relationship between the taxa that comprise these clades and their geographic distributions. The tree also shows several lineages of free-swimming mites forming a basal grade with molluscan mites. Mollusk mites appear to represent a monophyletic grouping (see node labeled B) and are divided into two major clades, with Australian gill mite subgenera along with gill mites from South America and

North America forming one clade (see node labeled C) and *Unionicola* mantle mites (see node labeled D) and gill mites from Africa, Eurasia, and North America forming the other (see node labeled E). Two species of gill mites (*U. anodontae* and *U. botswaniana*) from the subgenus *Iridinicola* appear to be sister taxa to the mantle mites. This latter group of mites appears to represent a more derived lineage within the genus.

The tree that resulted from the Bayesian phylogenetic analysis of the morphological data for *Unionicola* mollusk mites (e.g., representative species from 30 subgenera) is presented in Fig. 3. Based on the typology of this tree, the Australian gill mites are a separate clade (see node labeled A) from a large monophyletic grouping that includes the world's remaining gill mites along with all of the mantle mites (see node labeled B). Within this larger clade, there is a branch that includes gill mites from North and South America (see node labeled C). Another well-supported monophyletic grouping within the larger mollusk mite branch is one that is formed by African and Laurasian gill mites along with the mantle mites (see node labeled D). This mollusk mite tree, like the tree generated for *Unionicola* subgenera, supports a sister group relationship between mantle mites (see node labeled E) and African and Laurasian gill mites (see node labeled F). The mollusk mite tree has been reproduced with the subgeneric designations of the species used to generate the tree being shown in parentheses (Edwards & Vidrine 2013). With few exceptions, species that have been taxonomically assigned to the same subgenus form distinct clades.

There are some consistencies in the general patterns depicted by both the *Unionicola* and mollusk mite trees. For example, the typologies of these trees suggest that the mollusk mites represent a monophyletic clade. In addition, they suggest that the mantle mites are a sister taxon to the African and Eurasian gill mites. A close affinity between mantle mites and gill mites was also indicated by Edwards et al. (2010) in their paper assessing evolutionary relationships among molluscan-mite subgenera of North America. Furthermore, the phylogenetic hypothesis for the *Unionicola* mollusk mites, especially the gill mites, appears to dovetail our present understanding of the diversification of these mites. The Australian mites are thought to represent the least derived group of gill mites and these mites are the first clade to branch in the proposed tree for mollusk mite taxa. In the mollusk mite tree the South American and North American gill mites form a distinct clade from a monophyletic grouping that includes African gill mites and mantle mites. These groupings are consistent with the hypothesis that mites on the South American and African continents represent early radiations of *Unionicola* from an ancestral stock occurring in Australia that occurred in Pangaea prior to its break-up. Mites from the subgenus *Unionicolides* occur in both the South American and North American continents and their occurrence in North America appears to represent a secondary radiation that coincides with the diverse radiation of their host mussels on this continent. Mites from the subgenus *Prasadatax* from India appear to have characteristics that are shared by African gill mites and many of the mite subgenera from Eurasia. These African and Eurasian mites occur largely as a distinct clade in the mollusk mite tree. Not surprisingly, three subgenera (*Dimockatax, Unionicola,* and *Wolcottatax*) that occur both in Eurasia and North America form a monophyletic grouping. Vidrine (1986) has previously argued that mites from these North American subgenera represent descendant lineages from the Eurasian continent.

It is important to note that the morphological trees generated for the *Unionicola* subgenera and the mollusk mites should be viewed as working hypotheses. We are now in a position to collect sequence data for a broad array of taxa from specific regions of these trees to test the validity of the proposed relationships. To this end, an initial first step might be to sample and examine relationships among the globally distributed, highly speciose, monophyletic clade of mollusk mites. Future studies could expand on these research findings through a comprehensive assessment of the evolutionary history among the closely related *Unionicola* free-swimming mites.

RESOLVING *UNIONICOLA* PHYLOGENY USING GENOME-LEVEL CHARACTERS

In an approach that is complementary to morphological and sequence-based molecular phylogeny, my lab has begun to sequence the mitochondrial genomes of *Unionicola* mites in an effort to assess the potential contributions of genome-level rearrangements and other unique events toward phylogenetic reconstruction

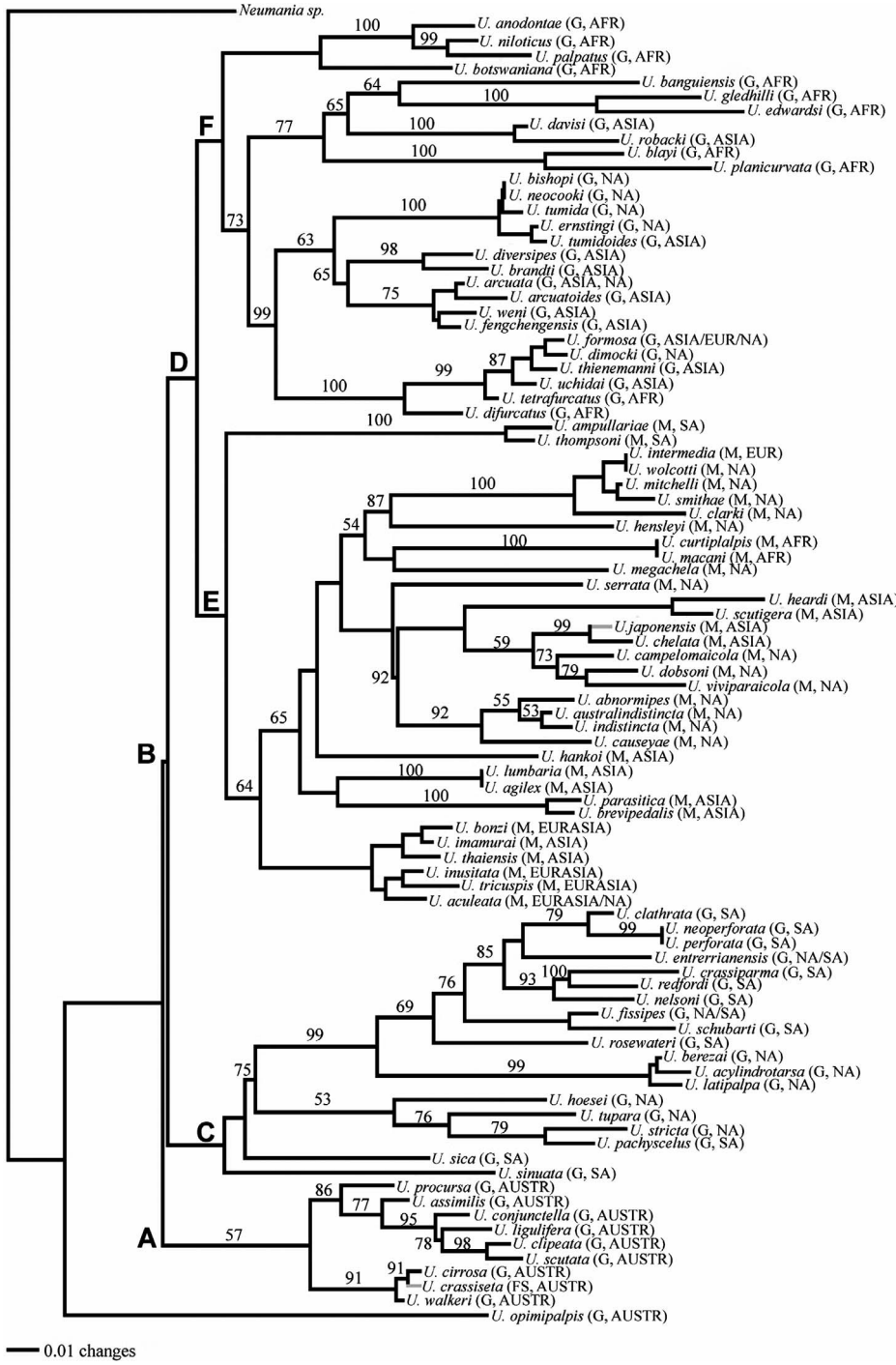

Figure 3.—Bayesian tree based on 139 morphological characters for representative species from 30 subgenera of *Unionicola* mollusk mites. Numbers above branches represent posterior probability values. Letters indicate notable clades: A=Australian gill mites; B=gill mites, excluding those from Australia and mantle mites; C=gill mites from North and South America; D=African and Laurasian gill mites along with the mantle mites; E=mantle mites; F=African and Laurasian gill mites. Abbreviations in parentheses: G=gill mites; M=mantle mites; FS=free-swimming mites; AFR=Africa; AUSTR=Australia; EUR= Europe; NA=North America; SA=South America.

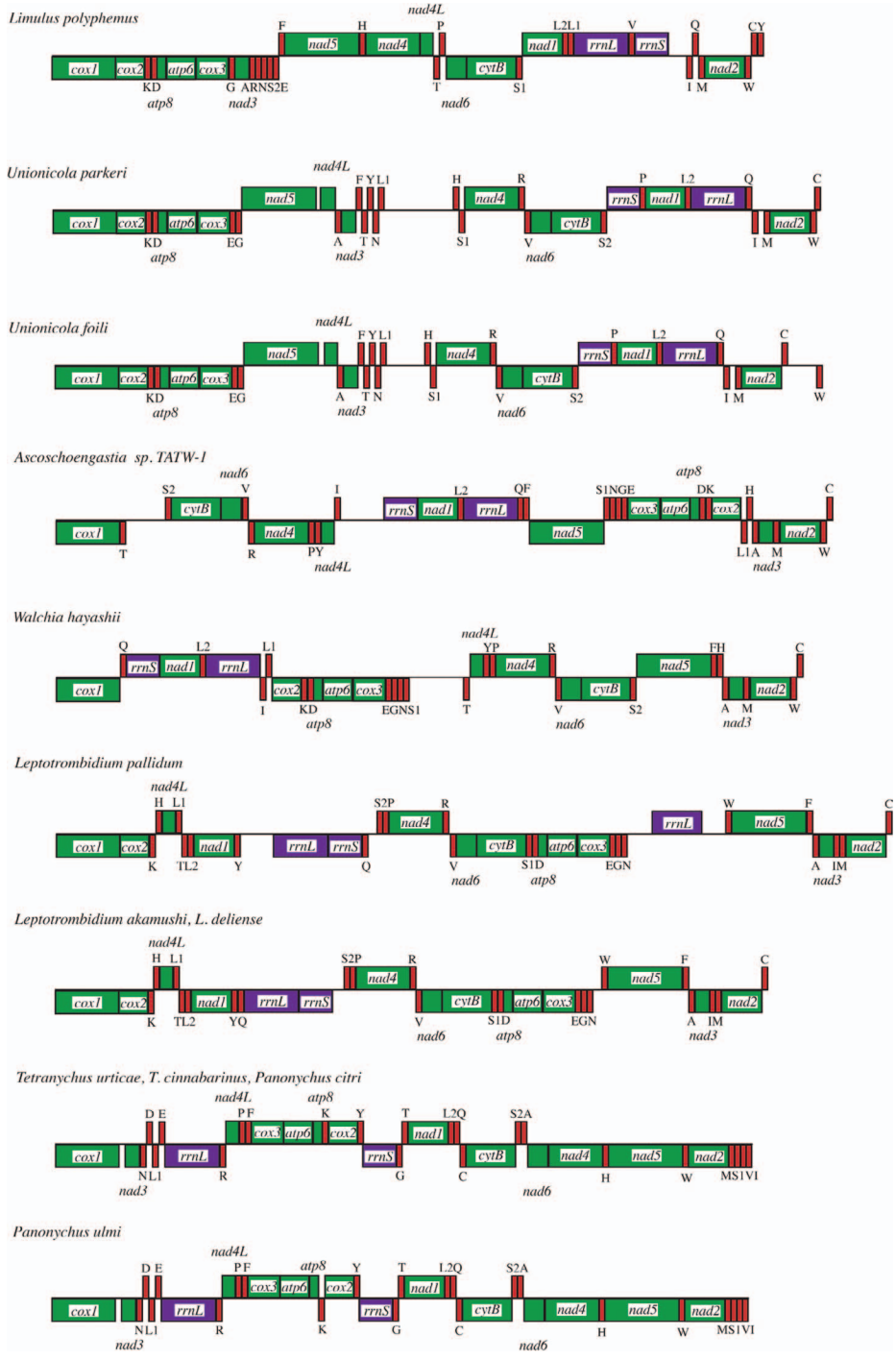

Figure 4.—Comparison of the mitochondrial genome structures of Trombidiformes mites and the horseshoe crab *Limulus polyphemus*. Green: protein-coding genes, red: tRNA genes, purple: rRNA genes. Circular genome sequences were linearized at the 5' end of the cox1 gene. Genes transcribed in the same direction as cox1 (left to right) are shown below the line, and genes transcribed in the opposite direction are shown above the line. For protein-coding and rRNA genes, the gene names are shown either in the rectangle or above or below the line. For tRNA genes, gene names are abbreviated with the single-letter abbreviation for the amino acid specified. (Modified from Edwards et al. 2011.)

among *Unionicola* mites. As a first step to this approach, the complete mitochondrial genomes of two species of *Unionicola* gill mites, *Unionicola foili* (subgenus *Unionicola*; Ernsting et al. 2009) and *U. parkeri* (subgenus *Unionicolides*; Edwards et al. 2011), have been sequenced. The annotation of these mitochondrial genomes indicated unique gene orders, highly rearranged in comparison to other Trombidiformes mites (Fig. 4). Moreover, a comparison of the mitochondrial genome sequence between *U. foili* and *U. parkeri* revealed genome-level synapomorphies, including tRNA rearrangements, a significantly longer long noncoding region between tRNAs for *U. parkeri,* and differences in reading frames between species mitochondrial genes (Edwards et al. 2011). Overall, the differences in genome structure between relatively closely-related *Unionicola* underscore the potential for molecular synapomorphies to be phylogenetically informative within the genus.

FUTURE DIRECTIONS

Resolving the evolutionary history of *Unionicola* mollusk mites will provide us with countless avenues for future research. For example, a robust phylogeny of *Unionicola* mollusk mites could be examined in the context of the phylogenetic history of their host mussels. A comparison of the evolutionary relationships between mollusk mites and their host mussels would present an ideal opportunity to address not only the degree to which their phylogenies are congruent, but to understand the mechanisms responsible for mediating those patterns, including the effects of dispersal capacity by mites (Downes 1989), competitive exclusion (Davids et al. 1988), and behavioral specificity (Edwards & Dimock 1995). Also, once general patterns of host utilization by symbiotic species have been elucidated, and the relationship of these mites to free-swimming species has been reconstructed, we can begin to address the ecological and evolutionary processes responsible for patterns of host association, at both the regional scale (emphasizing the importance of contemporary ecological factors) and over broad geographical areas (emphasizing the importance of historical biogeography).

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