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PHYLOGENY OF DERMANYSSOIDEA (ACARI: PARASITIFORMES) SUGGESTS MULTIPLE ORIGINS OF PARASITISM

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ABSTRACT — The Dermanyssoidea is an extremely diverse lineage of mites that are found as free-living predators as well as facultative and obligate parasites of mammals, birds, lepidosaurs, and various arthropod groups. The primitive condition in the group is assumed to be that of free-living predators, and parasitism is thought to have evolved numerous times throughout Dermanyssoidea. In non-phylogenetic treatments, the subfamily Hypoaspidinae (Laelapidae) has been hypothesized as the most primitive group within Dermanyssoidea, and the subfamily Laelapinae has been was suggested as the source of most parasitic lineages. This study uses the 28S region (domains 1-3) of the nuclear rDNA array to address phylogenetic relationships within Dermanyssoidea and the evolution of parasitism. Results suggest parasitism of vertebrates and arthropods has evolved a minimum of eight independent times, and the majority of these events have occurred outside of the Laelapinae.

KEYWORDS — Dermanyssoidea; Laelapinae; parasitism; phylogeny

INTRODUCTION

Parasitism has evolved many times throughout the history of life. Parasites are widely studied because of their effects on humans, domesticated animals, and food crops, but research often focuses on how to prevent or eradicate the parasite. Parasitic dermanyssoid mites are no exception and have been studied for centuries. *Dermanyssus gallinae* (De Geer, 1778), a common blooding feeding parasite of chickens, was described and studied in the eighteenth century. The mite now known as *Varroa destructor* Anderson and Trueman, 2000, has been a major pest of honeybees worldwide, causing intense economic impacts (Sammataro *et al.* 2000; Zhang 2000). *Ornithonyssus sylviarum* (Canestrini and Fanzago, 1877) transmits Western Equine Encephalitis among birds. and *O. bacoti* (Hirst, 1913) has been shown to act as both reservoir and vector of Korean hemorrhagic fever of humans in Asia (Mullen and OConnor 2002). However, the number of dermanyssoid mites known to be of actual human importance is miniscule compared to the diversity of parasitic lineages in the superfamily utilizing a wide range of hosts.

The ecological amplitude of dermanyssoid mites is phenomenal, and life-histories across the superfamily include free-living, soil dwelling predators, arthropod predators in vertebrate and invertebrate nests or colonies, facultative and obligatory vertebrate ectoparasites, and respiratory and auditory

endoparasites of birds, mammals, and lepidosaurs. Among approximately 70 recognized families of mesostigmatid mites only 17 contain confirmed parasites of vertebrates. With the recent exclusion of the families Spinturnicidae and Spelaeorhynchidae from Dermanyssoidea (Dowling and OConnor *in press*), 13 traditionally recognized families remain in the superfamily, making Dermanyssoidea the most ecologically diverse group of mesostigmatid mites.

Taxonomic history and the evolution of parasitism

Dermanyssoidea has a long and quite convoluted taxonomic history. Many classification schemes, often contradictory, have been proposed by different researchers, typically based more upon ecology and host associations than any character evidence (Berlese 1892, 1913; Vitzthum 1943; Zumpt and Patterson 1951; Baker and Wharton 1952; Evans, 1955, 1957; Evans and Till 1966; Karg 1965, 1971; Radovsky 1967; Krantz 1978; Casanueva 1993; Strong 1995; Lindquist *et al.* 2009; Dowling and OConnor *in press*). During these revisions, the superfamily has included from one (Evans and Till 1966) to 16 families (Lindquist *et al.* 2009) depending on the taxonomic scheme followed. Much of the confusion is because dermanyssoids exhibit such wide ecological amplitude and display high levels of morphological variability, it has been difficult to develop a robust phylogenetic hypothesis based solely upon morphological characteristics. Most classifications have utilized traditional taxonomic methods, grouping by overall similarity and elevating morphologically divergent taxa to higher taxonomic rank.

For the purposes of this study, we use names from the most recent classification scheme of Lindquist *et al.* (2009) with modifications based on Johnston (1982) and Dowling and OConnor (*in press*) as a guide to discussing families, phylogenetic relationships, and the evolution of parasitism. The modification outlined in Dowling and OConnor (*in press*) is the removal of two families of bat-associated mites, Spinturnicidae and Spelaeorhynchidae, which based on molecular evidence and a broad representation of parasitiform families, strongly grouped with the superfamily Eviphidoidea rather than with Dermanyssoidea. Modifications of Johnston (1982) include treatment of Haemogamasidae and Hirstionyssidae as families rather than laelapid subfamilies. This leaves 16 families for analysis and discussion: Dasyponyssidae, Dermanyssidae, Entonyssidae, Haemogamasidae, Halarachnidae, Hirstionyssidae, Hystrichonyssidae, Iphiopsididae, Ixodorhynchidae, Laelapidae, Larvamimidae, Macronyssidae, Manitherionyssidae, Omentolaelapidae, Rhinonyssidae, and Varroidae.

Prior authors have suggested the parasitic lineages of Dermanyssoidea appear to be derived from free-living hypoaspidine ancestors, the Hypoaspidinae Vitzthum being a catch-all group including free-living and arthropod associated species (Vitzthum 1942; Evans 1955, 1957; Radovsky 1969, 1985). Fourteen of the 16 dermanyssoid lineages recognized in this study comprise species that are exclusively parasitic. These families of parasites include Varroidae found with bees; Rhinonyssidae found in bird respiratory systems; Macronyssidae found primarily as nidicolous ectoparasites of mammals, but some genera include ectoparasites of birds and ecto- and endoparasites of lepidosaurs; Dermanyssidae primarily ectoparasites on birds, with several species on mammals; Ixodorhynchidae, Omentolaelapidae, and Entonyssidae all exclusively on snakes, with the latter found endoparasitically in the lungs; and Dasyponyssidae, Hystrichonyssidae, Manitherionyssidae, and Halarachnidae, all parasitic on mammals, with the latter being endoparasitic. Of the remaining two families, Laelapidae includes the full gamut of life-histories and associations including free-living predators, nidicoles in the nests and colonies of vertebrates and insects, facultative and obligate ectoparasites of vertebrates and arthropods, and rare auditory endoparasites of marsupial mammals. Casanueva (1993) elevated Iphiopsidinae *sensu* Evans (1955) to family level to house associates of millipedes, centipedes, arachnids, and terrestrial crustaceans. Unfortunately, none of these taxa were available for molecular analysis and the monophyly and phylogenetic position of the family cannot be tested.

Waage (1979) discussed two types of evolutionary routes to parasitism. In Type A routes, associations with hosts preceded adaptations for parasitic feeding. Type F routes involved adaptations to feeding on a host that preceded the actual association, such as the stylet mouthparts of nectar-sucking mosquitoes that were easily adaptable to blood-feeding (Radovsky 1985). The evolution of parasitism in dermanyssoid mites may be a combination of the two routes. Radovsky (1985) has shown that mesostigmatid mites in general are very well pre-adapted to parasitism. The chelicerae are adapted, even in the most primitive, free-living, predatory forms, for feeding on secretions, scales, scabs, and even for tearing into the skin of young vertebrates to reach a blood meal. The chelicerae of many free-living dermanyssoids are much more generalized than those of many other predatory mesostigmatids, which may have provided the necessary advantage to invade the nidicolous niche. In fact, the morphological change from the general dermanyssoid cheliceral type in some parasites is so subtle that without the context of a host, it would be difficult to tell the mite was an obligate parasite (Evans 1955; Radovsky 1985). Even though this generalized cheliceral form is suitable for parasitism, more specialized, slender, edentate chelae modified for piercing skin are widely found throughout Dermanyssoidea.

A second key feature that helped lead to the radiation of parasitic lineages within Dermanyssoidea and not in most other mesostigmatid groups may be the utilization of an exceptional number of niches by primitive "*Hypoaspis*"morphotypes (Radovsky 1985). Members of the *Hypoaspis*-complex are found in soil, litter, decaying substrates, the nests of social insects, burrows and galleries of beetles, and in the nests and on the bodies of mammals and birds. Most *Hypoaspis* species studied are predators (Karg 1961; Nelzina *et al.* 1967) and have not been shown to have any predilection to feeding on a host, but the association as a predator in vertebrate nests has been hypothesized to be the origin of vertebrate parasitism in dermanyssoid mites (Radovsky 1969), i.e. the type A route of Waage. While most Mesostigmata have characteristics suitable for parasitism, it may be that hypoaspidines were the first predators to colonize and utilize vertebrate nests, and they competitively limited other predatory mesostigmatids. Other mesostigmatid groups, such as Parasitidae and Ologamasidae, contain species that are obligate nest predators, but laelapids are typically the most abundant and commonly encountered.

This study presents the first large-scale phylogenetic analysis of Dermanyssoidea and attempts to examine the evolution of parasitic lineages within the superfamily. Molecular sequence data are used to avoid the complications of convergent evolution due to multiple origins of parasitism that have plagued morphological studies.

METHODS

Molecular protocol

DNA was extracted from ethanol-preserved or freshly collected mites using a Qiagen DNeasy® Tissue Kit and protocols therein with slight modifications. Typically, one or two mites were used for each extraction, depending on the size and freshness of the specimens. A clean minutin pin was used to pierce each body to allow the release of dissolved tissues while retaining an intact cuticle for vouchering. The other change to the Qiagen protocol involves the length of the incubation period. For mite extraction, the length of the incubation period has been extended to 12-24 hours, which allows for maximal recovery of DNA. All other steps in the Qiagen protocol were left unaltered. Standard double-stranded 50μL PCR amplifications were performed using the Perkin Elmer Gene Amp PCR system 2400.

Domains 1-3 from the 28S nuclear ribosomal DNA gene region were selected for potential phylogenetic information in this study. To increase primer specificity a new pair of overlapping primers was designed for 28S domains 1-3 (43F 5′-GCT GCG AGT GAA CTG GAA TCA AGC CT-3′; 929R 5′-AGG TCA CCA TCT TTC GGG TC-3′) based on sequences originally obtained using 28S primers from Park and Ó Foighil (2000). The reaction conditions for these PCR amplifications were

as follows: initial denaturation at 94° for 2min; followed by 35 cycles of denature at 94° for 25s, anneal at 53° for 20s, and extension at 72° for 1min; with a final extension at 72° for 7mins after completion of all cycles. Each 50μL reaction contained a mixture of 31μL dH_2O, 5μL PCR buffer, 3.5μL $MgSO_4$, 3.5μL 10mM dNTP, 2μL of each 10mM primer, 0.125μL Invitrogen Platinum *Taq* Polymerase, and 3μL DNA.

The target region was separated from contaminant PCR products by gel electrophoresis using 1.5% agarose gel, excised with sterilized scalpel blades, and cleaned of agarose using the Qiagen QIAquick® Gel Extraction Kit and protocols therein. Sequences were edited and compiled using Sequence Navigator (Parker 1997). Base-calling ambiguities between strands were resolved by following the called base on the cleanest strand or by using the appropriate IUB ambiguity code if both strands exhibited the same ambiguity.

Sequence Alignment

Sequences were aligned in MAFFT (Katoh *et al.* 2002) using the L-INS-i strategy (Katoh *et al.* 2005), which is a slow but accurate method of alignment. Alignments were done on the MAFFT server at http://align.bmr.kyushu-u.ac.jp/mafft/online/server/. The resulting alignment was visualized using BioEdit (Hall 1999). The full alignment length was used in all analyses without removal of any data or structural regions such as loops.

Phylogenetic Analyses

Aligned sequences were subjected to phylogenetic analyses using parsimony and Bayesian methods. An attempt was made to include as many representative dermanyssoid families as possible. The final dataset includes 8 of 15 dermanyssoid families (primarily lacking the small, very rare, and host-specific families) and four eviphidoid species as outgroups as determined by a previous study (Dowling and OConnor *in press*). A complete list of taxa used in the study can be found in Table 1.

Parsimony analysis was implemented using PAUP* 4.0b10 (Swofford 2002) with parsimony informative characters treated as unordered and unweighted. The entire dataset was subjected to 10,000 random addition replicates and tree bisection-reconnection (TBR) branch swapping. Support for nodes was calculated using 10,000 bootstrap pseudoreplicates using heuristic searches employed within each replicate including 100 random addition replicates and TBR branch swapping.

Bayesian analysis was performed using MRBAYES ver. 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). Because the starting conditions for Bayesian analyses can affect the probability of becoming trapped on local optima (Huelsenbeck *et al.* 2002), two independent runs of four heated Markov chains were performed. The appropriate substitution model was determined for the dataset by MrModeltest (Nylander 2004).

Relative fit on a neighbor-joining tree calculated from Jukes-Cantor corrected distances (Jukes and Cantor, 1969) was tested for 56 different models of nucleotide substitution using Akaike Information Criterion (AIC; Akaike 1973, 1974). Parameters for site-specific rate heterogeneity (Γ-distributed rate parameter; Yang 1994) and for the proportion of invariant sites (I) were also assessed to determine whether inclusion improved the fit of the model to the data. The model determined to be the best fit was the one for which additional parameters no longer significantly improved the log-likelihood score.

The GTR+Γ+I model of nucleotide substitution was specified and the analysis was allowed to proceed for 10 million generations. Uniform interval priors were assumed for all base parameters except base composition, which assumed a Dirichlet prior. Likelihood scores of each chain were printed every 100 generations to monitor the runs and determine when stationarity had occurred. Burnin, or the removal of the early generations during which likelihood scores fluctuate as stationarity is approached, was determined after the runs were completed. The remaining generations were used to produce a majority rule consensus tree of the results.

TABLE 1: List of taxa (ingroup and outgroup) included in the phylogenetic analyses based upon domains 1-3 of 28S nuclear rDNA sequence data. Collection numbers refer to either museum or field numbers. All data is stored in the University of Michigan Museum of Zoology Acari database. († denotes Outgroup).

Species	Classification	Voucher Number	Genbank 28S
Dermanyssus gallinae	Dermanyssoidea: Dermanyssidae	AD502	FJ911771
Dermanyssus quintus	Dermanyssoidea: Dermanyssidae	AD518	FJ911769
Dermanyssus hirsutus	Dermanyssoidea: Dermanyssidae	AD587	pending
Haemogamasus reidi	Dermanyssoidea: Haemogamasidae	AD003	pending
Haemogamasus sp.	Dermanyssoidea: Haemogamasidae	AD373	FJ911772
Brevisterna morlans	Dermanyssoidea: Haemogamasidae	AD589	FJ911773
Raillieta caprae	Dermanyssoidea: Halarachnidae	AD593	FJ911774
Echinonyssus sp.	Dermanyssoidea: Hirstionyssidae	AD205	FJ911775
Androlaelaps casalis	Dermanyssoidea: Laelapidae	AD001	pending
Pseudoparasitus sp.	Dermanyssoidea: Laelapidae	AD005	pending
Tricholaelaps comatus	Dermanyssoidea: Laelapidae	AD010	pending
Echinolaelaps sculpturatus	Dermanyssoidea: Laelapidae	AD011	pending
Echinolaelaps insignis	Dermanyssoidea: Laelapidae	AD017	pending
Steptolaelaps liomydis	Dermanyssoidea: Laelapidae	AD039	pending
Laelaps mazzai	Dermanyssoidea: Laelapidae	AD041	pending
Gigantolaelaps mattogrossensis	Dermanyssoidea: Laelapidae	AD042	FJ911777
Laelaps manguinihosi	Dermanyssoidea: Laelapidae	AD045	pending
Androlaelaps sp.7	Dermanyssoidea: Laelapidae	AD050	pending
Laelaps multispinosus	Dermanyssoidea: Laelapidae	AD051	FJ911778
Echinolaelaps mercedeae	Dermanyssoidea: Laelapidae	AD073	pending
Gigantolaelaps sp.	Dermanyssoidea: Laelapidae	AD086	pending
Laelaps stupkai	Dermanyssoidea: Laelapidae	AD089	pending
Androlaelaps schaeferi	Dermanyssoidea: Laelapidae	AD090	FJ911779
Dinogamasus sp.1	Dermanyssoidea: Laelapidae	AD103	FJ911780
Androlaelaps sp.3	Dermanyssoidea: Laelapidae	AD154	pending
Andreacarus sp.	Dermanyssoidea: Laelapidae	AD156	pending
Gaeolaelaps aculeifer	Dermanyssoidea: Laelapidae	AD173	FJ911787
Echinolaelaps sp.2	Dermanyssoidea: Laelapidae	AD183	pending
Echinolaelaps sp.3	Dermanyssoidea: Laelapidae	AD184	pending
Holostaspis isotricha	Dermanyssoidea: Laelapidae	AD195	FJ911786
Androlaelaps sp.8	Dermanyssoidea: Laelapidae	AD196	pending
Euandrolaelaps sp.	Dermanyssoidea: Laelapidae	AD197	FJ911781
Laelaps sp.2	Dermanyssoidea: Laelapidae	AD200	pending
Laelaps dispar	Dermanyssoidea: Laelapidae	AD203	pending
Stratiolaelaps lamington	Dermanyssoidea: Laelapidae	AD216	pending
Gaeolaelaps sp.	Dermanyssoidea: Laelapidae	AD218	pending
Cosmolaelaps sp.	Dermanyssoidea: Laelapidae	AD219	pending
Coleolaelaps sp.	Dermanyssoidea: Laelapidae	AD252	pending
Laelaps sp.3	Dermanyssoidea: Laelapidae	AD267	pending
Andreacarus petersi	Dermanyssoidea: Laelapidae	AD268	FJ911782
Dinogamasus sp.2	Dermanyssoidea: Laelapidae	AD269	pending
Echinolaelaps sp.1	Dermanyssoidea: Laelapidae	AD274	pending
Echinolaelaps sp.4	Dermanyssoidea: Laelapidae	AD276	pending

TABLE 1: Continued.

Species	Classification	Voucher Number	Genbank 28S
Laelaps spinigera	Dermanyssoidea: Laelapidae	AD287	GU440613
Hypoaspis sp.1 s.s.	Dermanyssoidea: Laelapidae	AD306	GU440616
Andreacarus gymnuromys	Dermanyssoidea: Laelapidae	AD332	GU440617
Andreacarus eliurus	Dermanyssoidea: Laelapidae	AD333	GU440618
Laelaspis sp.	Dermanyssoidea: Laelapidae	AD378	FJ911783
Androlaelaps madagascariensis	Dermanyssoidea: Laelapidae	AD404	FJ911784
Laelaps vansomereni	Dermanyssoidea: Laelapidae	AD418	GU440619
Liponysella sp.	Dermanyssoidea: Laelapidae	AD419	GU440620
Androlaelaps sp.6	Dermanyssoidea: Laelapidae	AD420	GU440621
Androlaelaps sp.5	Dermanyssoidea: Laelapidae	AD421	GU440622
Laelaps zumpti	Dermanyssoidea: Laelapidae	AD423	GU440623
Androlaelaps sp.1	Dermanyssoidea: Laelapidae	AD427	GU440624
Androlaelaps sp.2	Dermanyssoidea: Laelapidae	AD428	GU440625
Laelaps kochi	Dermanyssoidea: Laelapidae	AD429	GU440626
Androlaelaps sp.4	Dermanyssoidea: Laelapidae	AD430	GU440627
Blaberolaelaps sp.	Dermanyssoidea: Laelapidae	AD479	FJ911785
Laelaps sp.1	Dermanyssoidea: Laelapidae	AD480	GU440628
Andreacarus zumpti	Dermanyssoidea: Laelapidae	AD516	GU440629
Hymenolaelaps sp.	Dermanyssoidea: Laelapidae	AD565	GU440631
Mysolaelaps sp.	Dermanyssoidea: Laelapidae	AD572	GU440632
Neolaelaps spinosus	Dermanyssoidea: Laelapidae	AD604	GU440634
Laelaps pavlovskyi	Dermanyssoidea: Laelapidae	AD617	GU440635
Laelaps clethrionomydis	Dermanyssoidea: Laelapidae	AD618	GU440636
Laelaps hilaris	Dermanyssoidea: Laelapidae	AD620	GU440637
Laelaps muris	Dermanyssoidea: Laelapidae	AD621	GU440638
Steatonyssus occidentalis	Dermanyssoidea: Macronyssidae	AD080	GU440594
Ophionyssus natricis	Dermanyssoidea: Macronyssidae	AD113	FJ911788
Ornithonyssus bursa	Dermanyssoidea: Macronyssidae	AD152	FJ911789
Pellonyssus reedi	Dermanyssoidea: Macronyssidae	AD283	GU440612
Parichoronyssus sp.	Dermanyssoidea: Macronyssidae	AD289	GU440614
Radfordiella oudemansi	Dermanyssoidea: Macronyssidae	AD295	GU440615
Steatonyssus furmani	Dermanyssoidea: Macronyssidae	AD297	FJ911776
Ichoronyssus miniopteri	Dermanyssoidea: Macronyssidae	AD330	FJ911791
Ornithonyssus wernecki	Dermanyssoidea: Macronyssidae	AD552	GU440630
Rhineocius grandis	Dermanyssoidea: Rhinonyssidae	AD007	GU440585
Sternostoma porteri	Dermanyssoidea: Rhinonyssidae	AD591	FJ911792
Ptilonyssus toxostomae	Dermanyssoidea: Rhinonyssidae	AD592	FJ911793
Varroa destructor	Dermanyssoidea: Varroidae	AD071	FJ911801
Alliphis sp.	Eviphidoidea: Eviphididae	AD142	FJ911753
Eviphis sp.	Eviphidoidea: Eviphididae	AD169	FJ911754
Macrocheles sp.2	Eviphidoidea: Macrochelidae	AD132	FJ911758
Macrocheles sp.1	Eviphidoidea: Macrochelidae	AD143	FJ911756

RESULTS

Sequence characteristics

Sequence alignment of 28S rDNA was fairly straightforward with very few gaps in the total alignment, which included 856 characters. Base composition of all taxa was examined because base compositional heterogeneity is known to affect phylogenetic inference (Galtier and Gouy 1998; Galtier *et al.* 1999; Lockhart *et al.* 1994). No individual taxa were found to significantly diverge in average base composition from other taxa, therefore indicating that problems associated with base composition heterogeneity are negligible.

Phylogenetic analysis

The data matrix consisted of 856 aligned nucleotide characters from domains 1-3 of the 28S rDNA gene region for 81 ingroup taxa representing eight families and 39 dermanyssoid genera. Four outgroup taxa were used from the superfamily Eviphidoidea, including species of *Eviphis* and *Alliphis* (Eviphididae) and two species of *Macrocheles* (Macrochelidae). Parsimony analysis of the data matrix included 360 parsimony informative characters and resulted in 105 most parsimonious trees (L = 2448). Modeltest 3.6 (Posada and Crandall 1998) using AIC identified the GTR+Γ+I model with no molecular clock as the best fit for the dataset. The Parsimony and Bayesian analyses produced trees topologically similar trees. Branches on the consensus tree with Bayesian posterior probabilities and parsimony bootstraps both greater than 85% are depicted as thicker lines on the tree (Figure 1). Remaining branches have both statistical measures between 70-84% or in some cases one value greater than 85%, but the other lower. All branches below 70% were collapsed on the tree.

Overall, tree topologies from both analyses are comparable and fairly well resolved, identifying ten major clades that will be discussed (labeled A-J in Figures 1 and 2). Clade A represents the first branch of the ingroup and consists of parasitic mites from three families including *Echinonyssus* (Hirstionyssidae), *Brevisterna* (Haemogamasidae), *Haemogamasus* (Haemogamasidae), and *Dermanyssus* (Dermanyssidae). Clade B contains a group of predatory (*Gaeolaelaps*, *Pseudoparasitus*), nidicolous (*Euandrolaelaps*, *Hymenolaelaps*, *Steptolaelaps*), arthropod-associated (*Dinogamasus*) and vertebrate parasites including *Neolaelaps* from bats and clade C containing a paraphyletic Macronyssidae with Rhinonyssidae derived from within Macronyssidae. Clade D consists of the honeybee parasite *Varroa* (Varroidae), arthropod associates (*Coleolaelaps*, *Hypoaspis (s. str.)*, *Holostaspis*, *Laelaspis*, *Cosmolaelaps*), and the remaining dermanyssoids. Clade E includes the genus *Andreacarus*, a group of parasitic laelapines restricted to the African giant pouched rat (*Cricetomys gambianus* Waterhouse) on mainland Africa and on nesomyine rodents, tenrecs, and carnivores throughout Madagascar, and *Liponysella* restricted to Malagasy lemurs. Clade F represents the subfamily Laelapinae minus those taxa traditionally placed here but falling in more basal clades. Clade G consists entirely of Old World laelapine mammal associates in the genera *Laelaps, Echinolaelaps*, and *Tricholaelaps*. Within Clade G is Clade H, representing a group of *Laelaps* species all associated with arvicoline rodents. Clade I consists entirely of Old World species of *Androlaelaps*, all of them found in association with small mammals, and Clade J contains all New World species from several genera of mammal associated laelapids (including *Androlaelaps*) and the endoparasitic *Raillietia caprae* (Halarachnidae).

DISCUSSION

Evolution of parasitism

Radovsky's (1969) vision of parasite evolution in Dermanyssoidea (Figure 2) included a core consisting of the primitive, free-living Hypoaspidinae, with two major lineages arising from within, the Haemogamasinae and Laelapinae. Haemogamasinae was thought to include a range of predatory-to-obligate-haematophagous mites, but was considered to have undergone a limited adaptive radiation (Radovsky 1985). The remaining parasitic dermanyssoid families were hypothesized to derive from within Laelapinae, a group defined by Tipton (1960) to include 16 genera of small mam-

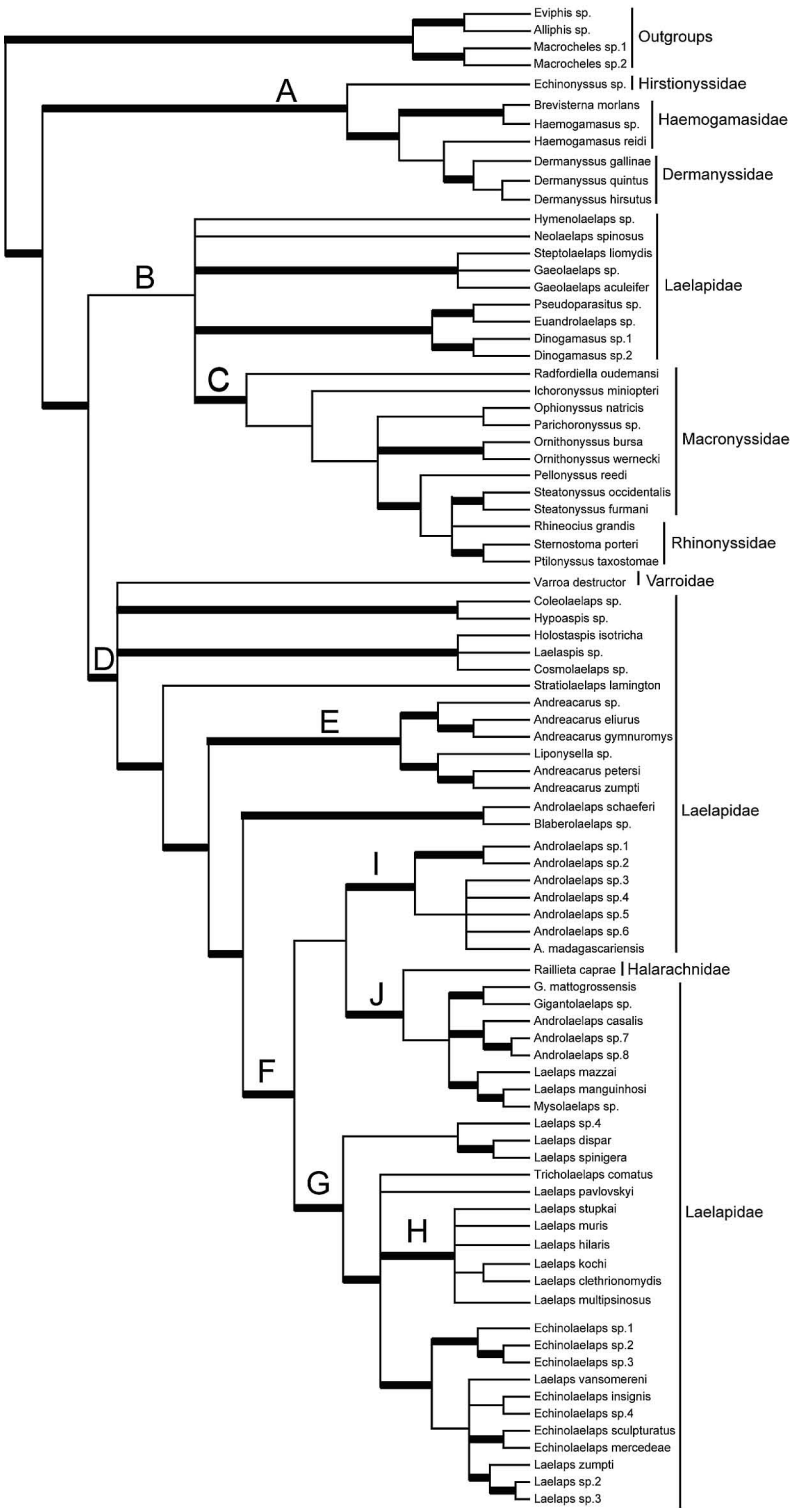

FIGURE 1: Phylogenetic hypothesis of dermanyssoids relationships. Thickened black lines represent branches supported by posterior probabilities and bootstrap values greater than 85%. Remaining branches have both statistical measures between 70-84% or in some cases one value greater than 85%, but the other lower. All branches below 70% were collapsed on the tree. Labels A-J are referred to in the text.

mal associates. Radovsky (1969) indicated *Androlaelaps* should also be placed within Laelapinae, and Laelapinae (including *Androlaelaps*) could be distinguished from Hypoaspidinae by specialization of the male chelicerae in laelapine mites. Results of the current phylogenetic analyses suggest placement of *Androlaelaps* within Laelapinae to be appropriate. The results also indicate a number of scenarios different from Radovsky's hypothesis of dermanyssoid evolution. The following discussion on the evolution of parasitism based upon our results will refer to Figure 2, where vertebrate parasitic lineages are denoted by dashed branch lines. Additionally, obligate associates of arthropods are denoted by stars next to the names.

The deepest split in the phylogenetic hypothesis proposed here does occur between haemogamasids (Figure 2; Clade A) and the remaining dermanyssoids as predicted by Radovsky (1969). However, clade A also includes Hirstionyssidae, represented by *Echinonyssus*, and Dermanyssidae, represented by three species of *Dermanyssus*. This phylogenetic arrangement indicates Haemogamasidae and Hirstionyssidae as lineages independent from other Laelapidae and much like that proposed by Johnston (1982) although it is unclear whether they should be considered separate families.

Grouping of these three families has not been suggested before due to obvious morphological differences. Haemogamasids are typically large and hypertrichous both dorsally and ventrally, which often obscures setal position and count. They have a range of cheliceral forms, from the ancestral hypoaspidine type, to long, slender, edentate chelicerae used for piercing vertebrate skin. Hirstionyssids have been differentiated from other laelapines by the presence of large cuticular hooks and spines present on their coxae, typically the largest on coxae II, and by edentate chelicerae specialized for piercing mammal skin. Similar cuticular hooks and spines are present in the unrelated genera *Pseudancoranyssus* (Laelapinae) (large hook from base of coxae I) and *Andreacarus* and *Neoparalaelaps* (Laelapinae) (spines on various coxae) and may not necessarily be a good character for differentiating major groups. Other than hooks and spines, hirstionyssids and dermanyssids are superficially similar based on external morphology. Both tend to exhibit reductions in sclerotization and setal count and size, which is common among parasitic groups (Evans 1963). Both groups also have modified chelicerae for parasitism, though dermanyssid chelicerae represent the extreme end of the spectrum and are diagnostic for the family. Dermanyssid chelicerae are extremely elongated at the second cheliceral segment, with highly reduced and edentate digits, causing the chelicera to resemble a stylet. Hirstionyssids on the other hand, possess slender, edentate cheliceral digits that strongly resemble the chelicerae of the *Haemogamasus liponyssoides* group. The chelicerae of the dermanyssoid family Hystrichonyssidae, not included in this study, are strikingly similar to those of the Dermanyssidae, except that it is the first cheliceral segment that is enormously elongated. The size and shape of cheliceral segments and digits varies dramatically across the Dermanyssoidea, which indicates that the chelicerae are an evolutionarily flexible character that is prone to morphological convergence on parasitic function. Microscopic examination of dermanyssoid chelicerae may reveal differences in similar cheliceral morphologies that will allow statements of homology to be made, but currently those data are not available.

The phylogenetic hypothesis indicates that an early split occurred between the common ancestor of *Dermanyssus*, *Haemogamasus* and *Echinonyssus* and the ancestor of the remaining Dermanyssoidea. Because the sister taxa to Dermanyssoidea are exclusively predatory, the likely common ancestor of the two groups was a free-living predator. This makes sense in terms of *Haemogamasus* because of the predatory nature of *Haemogamasus pontiger* and some other haemogamasids such as *Eulaelaps*, and the nidicoles in the *H. reidi* group. However, no known hirstionyssids or dermanyssids exhibit this range of ecologies and all are thought to be exclusively parasitic. One explanation is that the first exploration of the parasitic niche evolved into what we now consider the family Hirstionyssidae and intermediate ecologies persisted among the haemogamasid-dermanyssid lineage. It will be

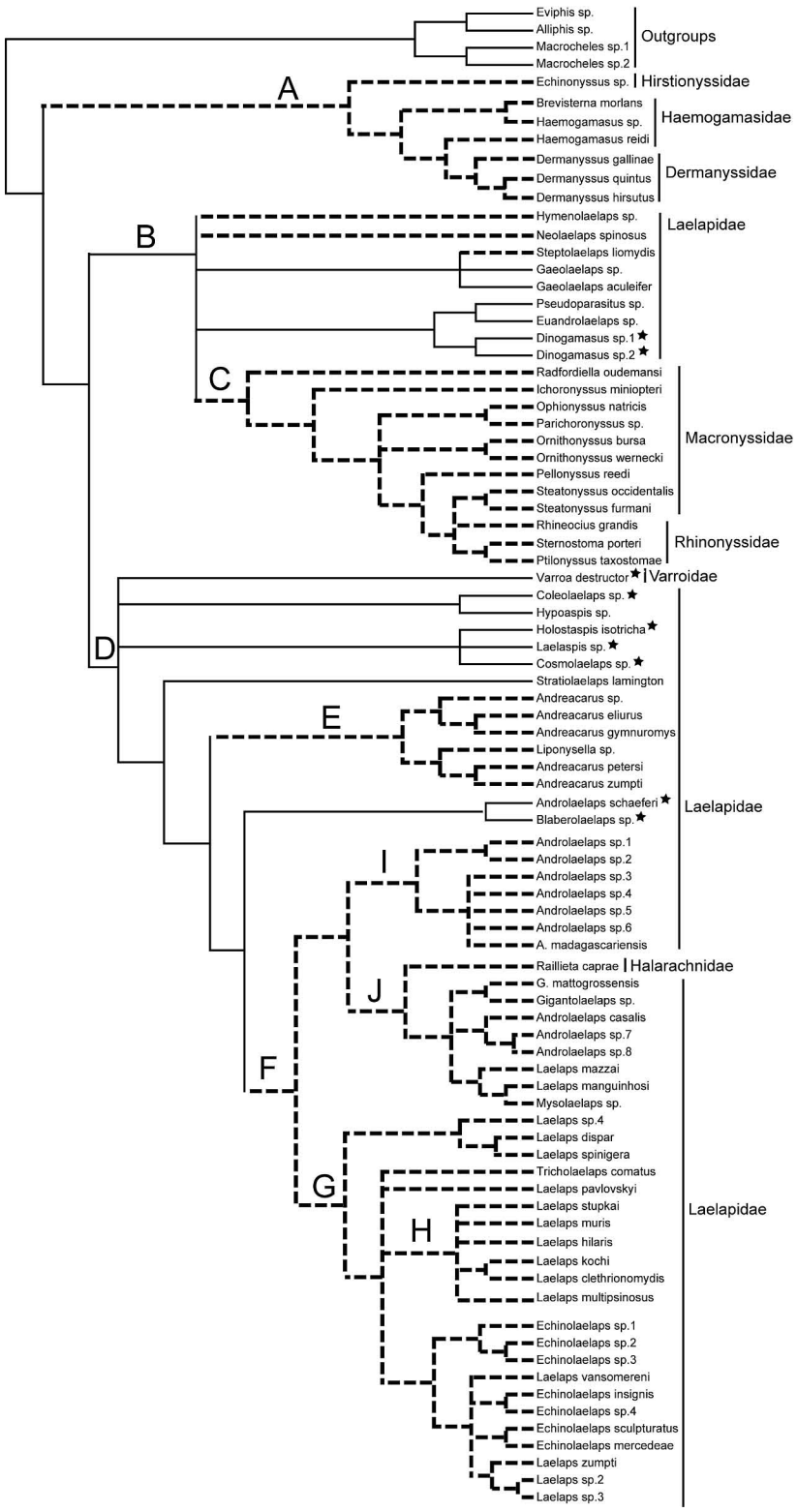

FIGURE 2: Phylogenetic hypothesis from Figure 1 with vertebrate parasitic lineages denoted by dashed branches and arthropod associates labeled with a star. Labels A-J are referred to in the text.

important in future studies of this clade to include members of the various *Haemogamasus* groups, and the other haemogamasid genera that show varying levels of host use, as well as a wider sampling of the Hirstionyssidae. Further inclusion of additional primitive predatory hypoaspidines may affect the composition and topology of the clade as well.

The placement of Dermanyssidae within a paraphyletic Haemogamasidae has never been considered before due to the morphological dissimilarity between the two groups. However, initial morphological examination has discovered that there are some cheliceral similarities between the two genera. Both exhibit chelicerae with interior concave margins, in Dermanyssidae functioning as a tube for the stylet-like structure. Additionally, in haemogamasids, when the chelicerae are more elongate and slender, the elongation occurs in the second cheliceral element. Additional taxa and character evidence including other gene regions and closer inspection of morphology will be required before any hypotheses on the evolution of Dermanyssidae can be tested.

The remainder of the phylogeny exhibits extreme polyphyly of the family Laelapidae. This is to be expected based upon Radovsky's hypothesis of parasite evolution, but the parasitic lineages do not appear to all arise from the subfamily Laelapinae. The remainder of the phylogeny consists of two large clades (B and D). Among the laelapids in Clade B, exclusive of the internal Clade C, three different parasitic genera are found, although their relationships to other members of the clade are for the most part unresolved.

The genus *Steptolaelaps* is found in association with heteromyid rodents in the New World. This genus appears as sister to species of *Gaeolaelaps*, which are assumed to be predatory, and thus represents an independent origin of parasitism from predatory Hypoaspidinae. *Steptolaelaps* has been considered part of the Laelapinae (Tipton 1960), though based upon morphology, it does not fit the typical laelapine description. Furman (1955) described *Steptolaelaps* as superficially similar to *Neolaelaps* due to heavy and spine-like anterior ventral setae on coxae II and III, and both ventral setae of coxae I spine-like. Both genera also have broader gnathosomal setae, similarly stout leg I, and epigynal shields with three pairs of setae. The chelicerae of *Steptolaelaps*, however, are very different from *Neolaelaps*, and combined with the fact that *Neolaelaps* species are restricted to Old World Megachiroptera, Furman (1955) was reluctant to hypothesize any further relation between the two genera. The results of this study clearly show separation from the main lineage of Laelapinae, where the majority of taxa belong to clade F, and that *Steptolaelaps* does not form a sister group to *Neolaelaps*.

The other two parasitic lineages, *Hymenolaelaps* and *Neolaelaps* are part of the unresolved base of Clade B and therefore no hypothesis about whether they represent independent origins of parasitism from Clade C can be made. Furman (1972) stated that *Hymenolaelaps*, found primarily on neotropical caenolestid marsupials (our data), is intermediate in characteristics between Laelapidae and Macronyssidae. He also stated *Hymenolaelaps* superficially resembles *Neolaelaps*, but regarded *Hymenolaelaps* as an example of independent evolution of elongate, non-grasping and weakly toothed chelicerae and placed the genus within Laelapinae. The results of the molecular analysis indicate it is more likely that *Hymenolaelaps* is more closely related to *Neolaelaps* than Laelapinae.

The other parasitic member of Clade B, *Neolaelaps*, does share one ecological characteristic in common with Macronyssidae (Clade C), parasitism of bats. *Neolaelaps* and *Notolaelaps* (not included in this study) represent the only laelapid genera found parasitic on bats, in this case both parasitizing Old World Megachiroptera. Macronyssids are primarily bat parasites, but are restricted to Microchiroptera. *Neolaelaps* and *Notolaelaps* have been hypothesized as the closest laelapid relatives to Macronyssidae (Radovsky 1967), but our results neither falsify nor corroborate this statement. Further data is necessary to resolve the relationships within Clade B.

The Macronyssidae and Rhinonyssidae lineage forms a monophyletic group (Clade C) and represents another transition to parasitism from within non-laelapine laelapids. Macronyssids are a successful group of parasites that evolved an as-

sociation with bats, as indicated by the bat restricted genera *Radfordiella* and *Ichoronyssus* at the base of the clade, and subsequently colonized other vertebrate groups including lepidosaurs, rodents, and birds. In the past, Macronyssidae has been divided into two subfamilies (Zemskaya 1966; Radovsky 1967, 1969), Macronyssinae (*Radfordiella*, *Ichoronyssus*, and *Parichoronyssus* in our dataset) and Ornithonyssinae (*Ophionyssus*, *Ornithonyssus*, *Pellonyssus*, and *Steatonyssus* in our dataset). Our preliminarily results indicate that macronyssid evolution may be more representative of a grade than a split into two distinct clades, but addition of more macronyssid diversity is necessary.

The evolution of rhinonyssid mites from within Macronyssidae has been hypothesized by previous authors (Domrow 1969, 1987; Radovsky 1994) and appears strongly supported in our phylogenetic hypothesis. Morphologically, many species of primitive rhinonyssids (e.g. genus *Tinaminyssus*) are very similar to species in the macronyssid genera *Pellonyssus* and *Steatonyssus*. Additionally, macronyssids and rhinonyssids share a unique developmental modification in which the deutonymph is completely inactive and quickly passed and the other stages are feeding stages.

Lastly, besides vertebrate parasites and predatory mites, Clade B also contains *Dinogamasus*, an obligate associated of xylocopine bees. The few observations on the biology of *Dinogamasus* suggest a cleaning mutualism, with the mites feeding on cuticular exudates and contaminants on the surface of the larval and pupal bee host (Skaife 1952). Interestingly, the sister clade to *Dinogamasus* comprises *Pseudoparasitus* and *Euandrolaelaps*, both commonly found living in nests of arthropods and some vertebrates, but not known to be parasitic. This clade may represent a transition from living facultatively within a nest to an obligate association with a host.

The base of Clade D consists of a number of arthropod associated lineages. Among these may be one of the most well-known mite species, *Varroa destructor*, a honeybee parasite that has decimated *Apis mellifera* populations worldwide. Also included at the base of this clade are *Coleolaelaps* and *Hypoaspis (s. str.)*, all typically found associated with beetles and *Holostaspis*, *Laelaspis*, and *Cosmolaelaps*, commonly associated with ants. Because this portion of the tree is unresolved, we cannot draw any conclusions about whether these all constitute one large clade of arthropods associates. We can say however, that all of these arthropod associates along with *Dinogamasus*, discussed earlier, and the two cockroach associates (*Androlaelaps schaeferi* and *Blaberolaelaps*) found further up in the tree show that laelapids have been ecologically active at exploiting arthropod associations throughout time. Since this study did not focus on extensively collecting arthropod associates, it clearly shows that further study of arthropod associations is necessary and that these may turn out to be much more diverse than the vertebrate associations. On a side note, *A. schaeferi* was originally described as *Gromphadorholaelaps schaeferi,* but the species was later transferred to *Androlaelaps* (Karg 1991). Due to the well supported separation from other *Androlaelaps* species it appears the synonymy is not supported.

Clade E represents another vertebrate parasitic clade arising from non-laelapine origins. This clade includes the genus *Andreacarus (s. str.)*, which includes 13 species of mites parasitic on various mammal groups. Three species of mainland African *Andreacarus* are restricted to *Cricetomys gambianus* Waterhouse (*A. petersi* and *A. zumpti* included here), whereas ten species are present on nesomyine rodents, tenrecs, and carnivores in Madagascar. Interestingly, the first species described, *A. petersi*, was actually described as a parasite of *Hemimerus talpoides* Walker, a dermapteran parasite of *Cricetomys* (Radford 1953). Subsequent collections of *A. petersi* from the fur of *Cricetomys* without the presence of *Hemimerus* suggested they were actually parasitic on rodents and phoretic on *Hemimerus* (Tauffliеb 1956). Whether the association with *Hemimerus* preceded the association with cricetomyines is unknown, but the fact that the results from the phylogeny show numerous arthropod associated lineages prior to Clade E is interesting.

The clade itself is split into two subclades, one including the mainland African species and *Liponysella*, a mite found on Madagascar lemurs, and the other clade including all Madagascar rodent asso-

ciates. These results would suggest two separate invasions of Madagascar by an ancestor of these mites, one possibly coming over with a nesomyine ancestor and radiating with the rodents and the other colonizing lemurs. Results are still preliminary, and some critical taxa are still missing before hypotheses involving the invasion of Madagascar by laelapid mites can be properly addressed.

The remainder of the phylogeny (Clade F) represents one large parasitic clade consisting of the subfamily Laelapinae and the endoparasitic Halarachnidae. Halarachnids had been previously hypothesized, like the other parasitic lineages, to be derived from the Laelapinae (Furman 1979; Radovsky 1985). Morphologically, most halarachnids are regressive, but members of the Raillietiinae, which Furman (1979) considered as primitive halarachnids, still exhibit a number of laelapid-like characters. The phylogeny supports this origin within Laelapinae, and it will now be important to further sample this diverse group of endoparasites to determine the evolutionary history of mammal endoparasitism.

The Laelapinae represents a very successful foray into the mammal parasitic niche and the results of this study display a few interesting patterns worth mentioning. Within Laelapine there is a well supported split between associates of Old and New World hosts. In one group (Clade G) three genera found on primarily Old World murine rodents strongly cluster together, *Laelaps (s. str.)*, *Echinolaelaps*, and *Tricholaelaps*. Of the three, only *Laelaps* (*s. lat*.) is also found in the New World, however, Neotropical *Laelaps* (Clade J) are far removed from these species indicating that the genus *Schistolaelaps* should be revived for those species. Additionally, the molecular data shows no reason for *Laelaps (s. str.)*, *Echinolaelaps*, and *Tricholaelaps* to remain as separate taxonomic units and should all be synonymized into one genus as has been the treatment by some authors. However, further examination including additional taxa, molecular data, and morphological characters is necessary to establish a strong classification for the group. Clade H forms an interesting group of *Laelaps* species consisting entirely of mites restricted to arvicoline rodents. So far no arvicoline *Laelaps* have fallen outside of this clade and no non-arvicoline mites have fallen within it. Depending on how the base of Clade G is resolved with further data, there may be interesting biogeographical patterns that emerge in this genus because arvicolines are one of the few groups of muroid rodents with a holarctic distribution.

On the other side of Clade F we find a split between Old World *Androlaelaps* collected from small mammals in Tanzania and Madagascar (Clade I) and Clade J consisting of species collected in the USA. These US collected species may all be part of the *A. casalis* complex, which is known to have a holarctic distribution. All three US *Androlaelaps* are similar in morphology and exhibit minor genetic differences even though they were collected from a squirrel nest (*A. casalis*), treehole litter (*Androlaelaps* sp.7), and a *Formica* ant nest (*Androlaelaps* sp. 8). As mentioned previously, *A. casalis* is a generalist feeder that reproduces best on a mixed diet of arthropod and vertebrate blood and the above results may indicate that it is a truly holarctic species. These results also identify the Old World as the origin of Laelapinae (minus *Steptolaelaps*) and that both *Laelaps* and *Androlaelaps* may require revisionary work in the future.

Overall, laelapine mites have experienced a huge radiation on small mammals, as witnessed by the great diversity of species. The only parasitic lineages within Laelapinae are parasitic laelapids and Halarachnidae with none of the other dermanyssoid families clustering here as prior authors had predicted. All members of Laelapinae as here considered are in some way associated with vertebrates, though some *Androlaelaps* can be found in decaying material away from the nest environment. As witnessed in *Androlaelaps*, varying levels of parasitism, or dependence on a blood meal, exists and the transition from opportunistically feeding from a host to actively seeking out a blood meal is easy to imagine. Whether the association with vertebrate nests began through an association with arthropods or resulted from an attraction to a concentrated food supply in the form of microarthropods inhabiting nests is debatable. The phylogeny indicates that the sister group to Laelapinae con-

sists of laelapids associated with arthropods in what may or may not be parasitic relationships. On the other hand, sampling is limited, and an effort to collect additional free-living and arthropod associated laelapids is necessary.

Multiple lineages arising from predatory laelapid ancestors suggest that pre-adapted features of cheliceral morphology and the ability to utilize a diversity of food sources were extremely important to the evolution of parasitism in Dermanyssoidea. The nest environment also played an important role in the evolution of parasitism, especially in Laelapinae, which has undergone an amazing radiation on rodent hosts. The basal clade in the tree, including haemogamasids, hirstionyssids, and dermanyssids, parallels Laelapinae in its evolutionary path towards parasitism. Both major groups include species that are predominantly predatory (*Haemogamasus* and *Androlaelaps*) followed by a transitional gradient towards obligate parasitism in related species. Haemogamasids were the first to go down this path, but compared to the laelapines, were not nearly as successful. If hirstionyssids and dermanyssids truly are related to Haemogamasidae, and not an artifact, the early offshoot from the basal dermanyssoid was considerably more successful than previous authors have considered.

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