

3.3 THE EVOLUTION OF HOST-PLANT AFFILIATION, BODY SIZE AND SEXUAL DIMORPHISM IN HUMMINGBIRD FLOWER MITES (ASCIDAE: *RHINOSEIUS* AND *TROPICOSEIUS*)

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A sound phylogenetic hypothesis is not only a Rosetta stone for understanding the evolutionary origin of ecological and behavioral features of organisms, but sometimes also allows us to test ideas about the developmental or functional significance of these features. The work we outline here relies on phylogeny reconstruction to illuminate ecological origins and patterns, and looks to ecology to help make sense of phylogenetic patterns.

The mites treated in this paper comprise the sister genera *Rhinoseius* and *Tropicoseius* (Baker and Yunker 1964 as defined by Naskrecki and Colwell, in press) of the mesostigmatic family Ascidae. Together with an ecologically and behaviorally convergent lineage within the confamilial genus *Proctolaelaps* Berlese, these genera are known by the common name "hummingbird flower mites" (Colwell 1973 and later references; Dobkin 1984, 1987, 1990). All known species of hummingbird flower mites share an obligate affiliation with the flowers of hummingbird-pollinated plants and are transported between inflorescences in the nasal cavities of hummingbirds. Both sexes of most species disperse in this way. Courtship, mating, and oviposition occur on the host plant. Hummingbird flower mites are capable of consuming significant quantities of nectar and pollen. Quantitative field experiments with *Proctolaelaps kirmsei* suggest that this mite has a significant negative effect on its host plant, *Hamelia patens* Jacq. (Rubiaceae), through nectar and pollen consumption, and probably an equally significant impact on hummingbirds, through competition with the birds for nectar (Colwell 1995, Paciorek *et al.* 1995).

The affiliation of hummingbird flower mites with their host plants is quite specific and characteristically exclusive, although some cases of consistent host-sharing are known (Colwell 1979, 1986a, 1986b). The mites have been shown to prefer the nectar of their own typical host species to the nectar of hosts of other hummingbird flower mite species in the same assemblage (Heyneman *et al.* 1991). In contrast, the mites are quite opportunistic with

regard to hummingbird carriers. The mites that any given individual hummingbird carries generally represent whatever mixture of flowers the bird is currently visiting (Colwell 1973, 1979, 1986a). Thus, although important biogeographically, data on the hummingbird hosts of hummingbird flower mites turns out to be of little evolutionary interest.

Within a local community in the tropical lowlands, many hummingbird flower mite species are monophagous on plants that flower all year. Others exploit plants with limited flowering seasons, whether in the tropical lowlands or at higher elevations or higher latitudes, by shifting between host plants seasonally (Colwell and Naeem 1994). At least one species, *Tropicoseius chiriquensis*, is a long-distance seasonal migrant as a passenger on migrating hummingbirds (Colwell and Naeem 1979). Some species of hummingbird flower mites that are monophagous locally inhabit related plant species or even unrelated ones in other localities. For example, in the well-studied Trinidad assemblage (Colwell 1986a, Dobkin 1984, 1987, 1990, OConnor *et al.* 1991 in press), *T. heliconiae* is known exclusively from *Heliconia psittacorum* (among native plants; it is also found in Trinidad in cultivated bromeliads), although three other species of *Heliconia* grow in the same or adjacent habitats. On a broader geographical scale, however, there are records of *T. heliconiae* from nine other species of *Heliconia* elsewhere, as well as from several other plant genera (Naskrecki and Colwell, in press).

Hummingbirds (family Trochilidae), a strictly New World family of more than 300 species, breed from Alaska (Rufous Hummingbird, *Selaphorus rufus* [Gmelin]) to Tierra del Fuego (Green-backed Firecrown, *Sephanoides sephaniodes* [Lesson]) (Skutch 1973). At tropical latitudes, wet lowland rainforest typically supports 10-25 sympatric hummingbird species (Feinsinger and Colwell 1978, Colwell and Coddington 1994). Hummingbird species tend to replace one another along elevational gradients (from sea level to more than 5,000 m elevation in the Andes [Feinsinger *et al.* 1979]), with only three to

five species typically in tropical highland assemblages. Endemic hummingbird species inhabit the Juan Fernandez archipelago (Colwell 1989) and the Greater and Lesser Antilles (Tyrrell and Tyrrell 1990).

Hummingbird flower mites are found throughout most of the geographical range of hummingbirds (and the plants they pollinate). Range limits for these mites, as presently known, are posted by *Tropicoseius* species from sites in Arizona and Northern California; central Chile; southern Brazil; the Ecuadorean altiplano; Dominica, W. I; and Jamaica. Variation in the species richness of sympatric assemblages of hummingbird flower mites parallels that of their host plants and hummingbird carriers (Colwell 1979). In lowland rainforest of Trinidad, W. I., for example, 17 species of hummingbird flower mites coexist (seven species of *Tropicoseius* and 9 of *Proctolaelaps*) (O'Connor *et al.* 1991, in press; Naskrecki and Colwell, in press), whereas only two species (*Tropicoseius colwelli* and *Rhinoseius richardsoni*) are found at 3,000 m in Costa Rica (Colwell 1973). The host plant affiliations of the mites in these two assemblages have been constant for more than two decades (O'Connor *et al.* 1991, in press; Naskrecki and Colwell, in press).

Table 1 lists plant families and genera whose hummingbird-pollinated species typically host hummingbird flower mites. Most of the families listed, as well as some of the genera (such as *Lobelia*, *Psychotria*, and *Costus*) include species pollinated by other vectors. Table 2 lists plant families and genera for which the hummingbird-pollinated species examined support no hummingbird flower mites. Clearly, these are plant lineages that have escaped colonization by mites, in spite of daily exposure to them. The mechanism of resistance is unknown, although there is weak evidence that the nectar of some "miteless" hummingbird-pollinated plants may repel mites (Heyneman *et al.* 1991).

In this paper, we examine patterns of biogeography and host plant affiliation of hummingbird mites in the light of a phylogenetic hypothesis for the mites. We also take a preliminary look at phylogenetic patterns of mite morphological features that are affected by host affiliation, focusing on body size and on sexual size dimorphism.

MATERIALS AND METHODS

Between 1964 and 1994, the number of described species in the genera *Rhinoseius* and *Tropicoseius* rose from 11 (as originally described by Baker and Yunker [1964]) to 42. In the upcoming work by Naskrecki and Colwell (in press) six species fall into synonymy and 12 species are described as new, resulting in a total of 48 species (11 in *Rhinoseius* and 37 in *Tropicoseius*). Although some tentative groupings of species have been published (Fain *et al.* 1977, Fain 1992), ours is the first study to attempt a

Table 1. Some common host plant genera of hummingbird flower mites.

Family	Genus
Bromeliaceae	<i>Aechmia</i> , <i>Gravisia</i> , <i>Pitcairnia</i> , <i>Puya</i> , <i>Guzmania</i>
Heliconiaceae	<i>Heliconia</i>
Marantaceae	<i>Calathea</i>
Zingiberaceae	<i>Renealmia</i>
Costaceae	<i>Costus</i>
Amaryllidaceae	<i>Bomarea</i>
Apocynaceae	<i>Mandevilla</i>
Cucurbitaceae	<i>Psiguria</i> , <i>Gurania</i>
Gesneriaceae	<i>Besleria</i> , <i>Columnnea</i> , <i>Alloplectus</i>
Leguminosae	<i>Erythrina</i>
Companulaceae	<i>Centropogon</i> , <i>Lobelia</i> , <i>Burmeistera</i> , <i>Siphocampylus</i>
Rubiaceae	<i>Psychotria</i> , <i>Hamelia</i> , <i>Isertia</i> , <i>Palicourea</i>
Scrophulariaceae	<i>Castilleja</i>
Ericaceae	<i>Cavendishia</i> , <i>Macleania</i> and 16 others
Gesneriaceae	<i>Alloplectus</i> , <i>Columnnea</i>
Lythraceae	<i>Cuphea</i>
Marcgraviaceae	<i>Marcgravia</i>

Table 2. Some common plant genera and families in which hummingbird-pollinated species lack hummingbird flower mites.

Family	Genus
Acanthaceae	<i>Aphelandra</i> (3 exceptions), <i>Justicia</i> , <i>Odontonema</i> , <i>Pachystachys</i>
Asteraceae	<i>Dahlia</i>
Lamiaceae	<i>Salvia</i>
Onagraceae	<i>Fuchsia</i> (1 exception)
Polemoniaceae	<i>Loeselia</i>
Ranunculaceae	<i>Aquilegia</i>
Scrophulariaceae	<i>Mimulus</i> , <i>Penstemon</i> , <i>Lamourouxia</i> , <i>Russelia</i>
Solanaceae	<i>Cestrum</i>
Loranthaceae	<i>Gaiadendron</i>
Malvaceae	<i>Malvaviscus</i> , <i>Hibiscus</i>
Fouquieriaceae	<i>Fouquieria</i>
Passifloriaceae	<i>Passiflora</i>
Convolvulaceae	<i>Ipomoea</i>
Verbenaceae	<i>Stachytarpheta</i>

reconstruction of the phylogeny of hummingbird flower mites through formal cladistic analysis.

Work is completed on the genera *Rhinoseius* and *Tropicoseius* (Naskrecki and Colwell, in press), the focus of this paper. A companion study of the hummingbird/flower affiliated *Proctolaelaps* is underway.

The study included all described species previously included in the genus *Rhinoseius* (*sensu* Lindquist and Evans 1965), plus the 12 new species described (Naskrecki and Colwell, manuscript). In addition to examining types or paratypes for virtually all described species, we examined many thousands of specimens collected by Colwell and his collaborators over the past 25 years from scores of hosts plants and birds in a dozen countries.

Especially important sources of new material were fluid collections of floral material, made for botanical systematic studies, from three important plant groups: John Kress's material for the monocot genus *Heliconia* (Heliconiaceae), James Luteyn's collections of floral material for the families Ericaceae and Campanulaceae, and Bruce Stein's collections of *Centropogon* (Campanulaceae). Phylogenetic work already completed on the host plants by these authorities presents a valuable opportunity for comparison of mite phylogenetic hypotheses with those of their host plants, especially for *Heliconia*. Kress' *Heliconia* collections yielded thousands of mite specimens from several dozen species of *Heliconia* from collecting localities throughout the range of this extremely diverse (about 200 species) and widespread genus. Luteyn's material yielded mite specimens from some 40 species of ericads in 18 genera.

To generate a hypothesis of the phylogenetic relationship of mite species, we performed a cladistic analysis based on numerical parsimony. The analysis was done using PAUP 3.1.1 for Macintosh (Swofford 1993). We used MacClade 3.02 (Maddison and Maddison 1992) to study character distribution.

RESULTS

Phylogeny

The cladistic analysis included 41 out of the 48 species of *Rhinoseius* and *Tropicoseius* (= *Rhinoseius sensu* Lindquist and Evans 1965) recognized in this study. Seven previously described species were excluded from the analysis because either only one sex is known, or specimens were not available for examination at the time of the analysis.

In the cladistic analysis of the 41 ingroup species, 49 morphological characters were used. The data matrix included both male and female characters. Details appear in Naskrecki and Colwell (in press). No characters relating to host plant affiliation, geographical or altitudinal distribution, or any ecological characteristics of the species were included in the data matrix.

Characters were polarized by outgroup comparison with four species representing three genera of Melicharini, the tribe that also includes the ingroup taxa. These included two species of *Proctolaelaps*; *Melichares agilis*

Hering; and *Xanthippe clavisetosa* Naskrecki and Colwell (1995), a new species and genus that may be the sister group of the monophyletic lineage comprising *Rhinoseius* and *Tropicoseius*.

Analysis (for details see Naskrecki and Colwell [in press]) yielded a phylogenetic hypothesis of a basal split of the ingroup into two clades. The topology of the tree and distribution of apomorphies clearly support the monophyly, and consequently the reinstatement of the genus *Tropicoseius* Baker and Yunker, 1964, which was synonymized by Lindquist and Evans (1965) with *Rhinoseius* Baker and Yunker, 1964.

Within the genus *Tropicoseius*, we recognize three monophyletic species groups: the *chiriquensis* (13 species), *braziliensis* (five species), and *wetmorei* (19 species) groups. Two species groups are proposed within *Rhinoseius*: the *rafinskii* (six species) and *richardsoni* (five species) groups. Diagnoses of both genera and the groups within them appear in Naskrecki and Colwell (in press).

A weak point of the resulting tree was an unresolved relationship among certain species of the *wetmorei* group. On the other hand, the monophyly of this group is well supported. With the objective of resolving relationships among species of the *wetmorei* group, we performed a second analysis, in which we used 14 new characters, none of which had been used in the broader analysis. The new characters are useful in distinguishing species within this group (relative length and arrangement of setae, minor but consistent variations in the shape of the ventral shield, characters of the female spermatheca), but are highly homoplastic at the generic or tribal level. We polarized these 14 new characters using as outgroups two species of the *braziliensis* group, the sister clade of the *wetmorei* group.

There is a clear parallel to this two-stage strategy in the standard practice in molecular systematics of using more conservative regions of the genome for the study of relationships among higher taxa, and more variable regions for species- and population-level studies.

Host-plant affiliations

When the host plant affiliations of *Rhinoseius* and *Tropicoseius* species are mapped onto the phylogeny reconstructed from purely morphological characters, as outlined above, it becomes clear that this group of mites is quite conservative with regard to host plant affiliation, at least at the level of host plant genera and families. The brief overview presented here is based on a more thorough analysis by Naskrecki and Colwell (in press).

With only one exception, every species in the genus *Rhinoseius*, for which host plant records exist has been collected from plants of the family Ericaceae, a species of the *richardsoni* group almost exclusively. In contrast, only a single errant specimen of any species of the genus *Tropicoseius* is known from this plant family. Clearly, the

most parsimonious hypothesis of origin for the genus *Rhinoseius* is that the ancestor of the group occupied an ericaceous host.

In the sister genus *Tropicoseius*, the *chiriquensis* group is apparently the most basal lineage. Among those species in the *chiriquensis* group for which adequate host plant records exist, all are affiliated with plants of the family Campanulaceae, several species almost exclusively so. Thus, the most parsimonious hypothesis of origin for the *chiriquensis* group is an ancestral affiliation with campanulaceous hosts.

Rhinoseius species are apparently restricted to tropical latitudes, whereas *Tropicoseius* species reach both the latitudinal and altitudinal limits for hummingbird flower mites. In the New World tropics, hummingbird-pollinated species of the family Ericaceae are largely restricted to cool and high montane regions (Luteyn 1989). Thus, if *Rhinoseius* originated in an ericaceous host, that host was almost certainly a tropical montane species. Likewise, the hummingbird-pollinated Campanulaceae (with the exception the north temperate species, *Lobelia cardinalis*, which lacks hummingbird flower mites) are almost exclusively tropical and montane in distribution. Moreover, ericaceous and campanulaceous hosts often grow side by side in the same habitats in tropical montane regions and are visited by the same hummingbirds (see, for example, Colwell 1973). Taking these facts and inferences into account, we propose a montane tropical origin for the *Rhinoseius-Tropicoseius* clade as a whole.

The next most basal lineage within *Tropicoseius*, after the *chiriquensis* group, is the *braziliensis* group. All species of this group are found in hosts of the family Bromeliaceae, at least two of the species exclusively so, based on known records. At least two species in this group occupy the flowers of *Puya* spp. (Bromeliaceae), a genus that co-occurs throughout the Andean highlands in the same habitats as mite hosts in the family Campanulaceae as well as Ericaceae, suggesting a possible tropical highland origin of the *braziliensis* group with subsequent spread into lowland bromeliads.

Within *Tropicoseius*, the group that includes the most derived species, the *wetmorei* group is primarily affiliated with plants of the genus *Heliconia* (Heliconiaceae). This speciose plant genus (200-250 species) is restricted to the tropical lowlands and lower montane elevations. New World *Heliconia* species are exclusively hummingbird-pollinated (Berry and Kress 1991). Within the *wetmorei* group, the most basal species show a pronounced affiliation with the genus *Costus* (Costaceae) as well as with *Heliconia*, suggesting affiliation with *Costus* may have occurred first. Plants of these two genera grow side by side in early successional habitats, and are often pollinated by the same hummingbirds. The eight species in the *wetmorei* group known exclusively from *Heliconia* form a clade of their own.

Speciation in *Rhinoseius* and *Tropicoseius* clearly manifests a high degree of conservatism with regard to host affiliation, at the plant generic and familial level. Nonetheless, Naskrecki and Colwell (in press) document numerous cases of polyphagy at this level, with mites occupying not only a typical host for their species group but also unrelated plants, often those characteristically occupied by sister clades of mites. Presumably, such cases of polyphagy set the evolutionary stage for definitive host shifts such as those that must have taken place between the major clades within *Rhinoseius* and *Tropicoseius*.

Body size dimorphism

Host-plant floral morphology and phenology impose many constraints on the mites that inhabit the flowers (Colwell and Naeem 1994). Among other things, host affiliation determines an optimum body size, with a number of important ecological consequences. Hummingbird flower mites must be small enough to carry on their daily lives among the stamens, anthers, and style of their host flower, which are typically closely spaced within a tubular corolla. Because both sexes disperse on hummingbirds in most species of this group (Colwell and Naeem 1994), individuals of both sexes must be able to move quickly from within the flower to the bill of a visiting hummingbird, during its one- to three-second visit to the typical flower. Among males, the complex and rapid movements of courtship and mating and aggressive male-male interactions that take place within the flower (Colwell 1985) may set an upper bound on body size. Females are probably less constrained by the need for mobility within the flower, as they are typically much less active than males.

Moreover, it appears that the optimum body size varies roughly in proportion to flower size, presumably through the correlation of flower size with "room to move" among the floral organs within the corolla. Thus, both male and female hummingbird flower mite species affiliated with larger flowers tend to have larger bodies (Colwell 1986a).

Body size affects population structure. Hummingbird flower mite populations are subdivided into constellations of transitory "breeding groups," each group consisting of the mites inhabiting a single inflorescence. The level of resources available to a group is set by the nectar and pollen production of the inflorescence, minus losses to legitimate flower visitors and other nectar and pollen thieves. Large mites have smaller breeding group sizes than smaller mites, for the same level of available resources. In turn, the size of breeding groups in hummingbird flower mites is closely correlated with sex ratio, both of breeding groups and of dispersers on hummingbirds (Colwell 1981, 1982; Wilson and Colwell 1981; Colwell and Naeem 1994), and probably with among-group genetic variation.

Sexual dimorphism in body size among hummingbird flower mites is common but varies greatly among species, both in magnitude and direction. As Fig. 1 shows, among large-bodied species (as measured by the intersexual mean), males tend to be larger than females (as measured by the intersexual difference), whereas, among small-bodied species, males tend to be smaller than females. In mid-sized species, the sexes are about equal in size. To describe this pattern another way, female body size varies less than male size, among species. Since sexual size dimorphism shifts steadily with increasing body size, this pattern can also be described as allometric (Gross 1984). However one chooses to describe it, the pattern raises two separate questions: Is it statistically significant? If so, what, if anything, does it mean?

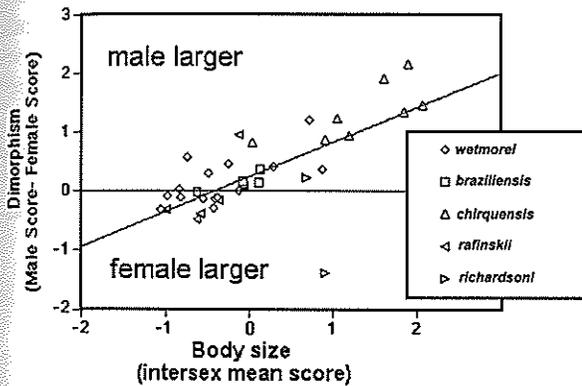


Fig. 1. Sexual size dimorphism (intersexual difference) as a function of body size (intersexual mean) in hummingbird flower mites of the genera *Rhinoseius* and *Tropicoseius*. The symbols listed in the legend represent species groups, not single species. To characterize body size, we measured the length and width of the dorsal shield, at homologous points, in 6 males and 6 females of the 38 species for which we had sufficient material. To combine length and width into a single measure of relative size, we performed a simple principal components analysis on the two variables mean length and mean width, for the 38 species pooled. Scores on the first principal component, which accounts for more than 95% of the variance, were then taken as an overall measure of body size for each gender of each species.

The principal statistical issue is made plain by noting in Fig. 1 that points for species from each clade (monophyletic species group) tend to cluster on the graph. In evolutionary terms, the most parsimonious explanation for this pattern is that body size and sexual size dimorphism are relatively conservative, species within each clade retaining more-or-less the ancestral condition for that clade. In statistical terms, this means that the points within clades are not independent, so that the degrees of freedom for regression are inflated. To account

for this phenomenon, we computed independent phylogenetic contrasts (Harvey and Pagel 1991, Garland *et al.* 1992) for male and female size scores. Plotting the female contrasts against male contrasts, the slope of the major axis would be unity, were there no relation between dimorphism and size. In fact, the slope is significantly less than unity, confirming that the pattern shown in Fig. 1 holds even after removing the effect of phylogenetic sample-size inflation.

What does this pattern mean? Sexual dimorphism in hummingbird flower mites shows all the classical earmarks of sexual selection. In addition to body size (and the usual gender differences directly involved in insemination), male and female hummingbird flower mites differ in other characteristics. Males typically bear longer dorsal setae than females, which can be modified in other ways as well. In *Rhinoseius* males, certain setae in the middle of the dorsum are strikingly modified into stout spines. In *Tropicoseius* males, especially those of the *chiriquensis* group, the second leg of the male is greatly enlarged, with setae enlarged to form opposing, raptorial spines or pegs. The dorsal spines of *Rhinoseius* and the raptorial second legs of *Tropicoseius* males are probably important in male-male combat within the species having these traits, and are known to be used in interspecific combat (Colwell 1973).

Sexual dimorphism is complicated in some species by male polymorphism: non-genital sexual dimorphism is absent in some males (homeomorphic males) and well-developed in other males (heteromorphic males) of the same species, usually with many intermediates (Hunter 1972, Fain 1992, Naskrecki and Colwell, in press). Although behavioral evidence is so far lacking, male polymorphism may function in the same way it does in other animal social systems, in which homeomorphic males either "sneak" matings without stimulating male-male aggressive defense of females by the heteromorphic males (*e. g.* Gross 1984), or homeomorphic males actually mimic females, distracting competing males from mating with females (Mason and Crews 1985).

Fairbairn and Preziosi (1994) reviewed the literature on allometry for sexual size dimorphism and proposed a unifying theory for both hypoallometry (females larger than males, but less so in larger species) and hyperallometry (males larger than females, and increasingly so in larger species). Their hypothesis is that sexual selection for larger males, based on male-male interactions, is a cause of both hypoallometry and hyperallometry for sexual size dimorphism in clades that arise from small ancestral species in which females are larger than males. In other words, even in species in which all females are larger than all males, individual males that are larger than other conspecific males tend to have more mates. Further, Fairbairn and Preziosi suggest that the underlying, interspecific correlation between male and female size (common to virtually all studies of

dimorphism) is likely to be based largely on shared patterns of natural selection on body size. They found support for these ideas in their work with water striders (Gerridae), in which females are larger than males.

To our knowledge, hummingbird flower mites are the first known case, at least among arthropods, in which the entire spectrum from female-biased sexual size dimorphism (with hypoallometry) to male-biased sexual size dimorphism (with hyperallometry) is known for the species in a single, relatively small, monophyletic group (Fig. 1). Moreover, this appears to be the first opportunity to study these patterns in a group for which the phylogeny has been rigorously reconstructed. While a full analysis of sexual dimorphism in these mites will appear elsewhere, preliminary considerations suggest that the Fairbairn-Preziosi hypothesis may be pertinent.

As argued earlier, flower size may set the optimum body size for both sexes under natural selection. Theoretically (Lande 1980), females will reach optimal size at evolutionary equilibrium in spite of sexual selection on males, whereas male size will be a compromise set by the processes of natural and sexual selection. In male elephant seals or primates, natural selection presumably puts the brakes on the tendency for males to become larger and larger under sexual selection. In contrast, among hummingbird flower mites, two opposing aspects of sexual selection may set male size. Larger males may win fights with smaller males once engaged, but smaller males may be better able to maneuver within the flower, not only during male-male combat, but in finding females and successfully courting them. In the cramped quarters of smaller flowers optimal male size may be smaller than optimal female size, whereas, in the more open intrafloral environment of larger flowers, optimal male size may exceed the size natural selection sets for females. It is also possible that sexual selection for larger males is generally stronger in species farther to the right in Fig. 1, independent of flower size and morphology.

SUMMARY

Hummingbird flower mites feed and reproduce within the inflorescences of hummingbird-pollinated plants. Both sexes travel between plants on hummingbirds. Host plant specificity and fidelity is very high. By means of a cladistic analysis based on morphological characters, we reconstructed the phylogeny of a monophyletic group consisting of 41 species belonging to the genera *Rhinoseius* Baker and Yunker 1964 (sensu stricto) and *Tropicoseius* Baker and Yunker 1964 (Ascidae), including 12 new species, plus four outgroup species. *A posteriori* mapping of host plant affiliations on the cladogram reveals a striking pattern of origin and radiation for these mites, with one clade (*Rhinoseius* sensu stricto) in dicotyledonous groups of the tropical highlands, and a gradual evolutionary shift within the sister clade (*Tropicoseius*) to lowland habitats and monocotyledonous hosts. Phylogenetic shifts in body size and sexual size dimorphism within these genera produce an allometric pattern spanning the range from small species with females larger than males to large species with males larger than females. We suggest that physical constraints in the intra-floral micro habitat and sexual selection on male size produce this pattern.

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