Evolutionary Lability and Phylogenetic Utility of Behavior in a Group of Ant-Guest Staphylinidae Beetles

JAMES A. DANOFF-BURG[1]

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ABSTRACT Despite being commonly used as systematic characters earlier this century, relatively few systematists currently use behavioral information for phylogenetic reconstruction. A natural experiment provided by the inferred phylogenetic relationships and host associations of a tribe of ant guest beetles allows for a novel test of the phylogenetic utility of behavior. Historical and current evolutionary forces have acted in opposition during recent behavioral evolution, making it possible to determine the relative evolutionary lability of two general classes of behavioral characters. I dissected the behavioral phenotype into two components and tested for the relative presence of these two opposing forces on each behavioral component. Behavior was broken up into the continuously differing behavioral component (durations of functionally similar beetle behaviors) and the discretely differing behavioral component (species-typical behaviors). Conducting a series of statistic and cladistic tests on each component separately, I concluded that current evolutionary forces primarily determined the continuous behavioral component, because it was most similar among heterogeneric, nestmate beetle species. In contrast, I concluded that ancient evolutionary forces determined the discrete component because it was most similar among congeneric, non-nestmate species. These results support two hypotheses. First, the durations for which behaviors are performed evolve quicker than do species-typical behavioral traits. Second, species-typical behavioral characters are often as nonhomoplastic for phylogenetic reconstruction as are morphological characters.

KEY WORDS ant-guest beetles, behavioral evolution, ancient evolutionary forces, coevolution, myrmecophily, cladistics

WHETHER AND HOW to combine disparate types of phylogenetic characters remain as some of the most contested issues in evolutionary biology. Some argue that disparate character matrices should be combined only if they do not conflict with each other based on a variety of measures (de Queiroz et al. 1995, Huelsenbeck et al. 1996), whereas others suggest they should always be combined a priori (Kluge 1989, Kluge and Wolfe 1993, Nixon and Carpenter 1996, Brower et al. 1997). Despite these disagreements, nearly all systematists agree that as much data as possible should be included in phylogenetic analyses (but see Bull et al. 1993).

Much of the debate has centered on the relationship between morphological and molecular characters (see review in de Queiroz et al. 1995). Characters derived from behavior, previously a focus of systematics (e.g., Lorenz 1941, Tinbergen 1959), have been largely excluded from the debate. Behavioral characters are easily measured, plentiful, and are a novel source of information for many taxa (McLennan et al. 1988, de Queiroz and Wimberger 1993, Miller and Wenzel 1995, see also chapters in Martins 1996).

Unfortunately, most systematists do not commonly use behavioral characters (but see e.g., McLennan et al. 1988, Prum 1990, Wenzel 1992, 1993, Wimberger and de Queiroz 1996, and Martins 1996). A recent scan of three volumes of the journal *Systematic Biology* (volume 46, no. 1–volume 48, no. 3) produced 69 zoological articles that used character data of any kind for reconstructing phylogenies. Of these, behavioral or other life history information was mentioned only five times and only one included them as systematic characters. Proctor (1996) surveyed 291 zoological studies from six systematics journals published during a survey period that ended in 1993. She found that only 6% of the articles incorporated any behavioral data, a trivial difference from the 1% that I obtained above (see also Sanderson et al. 1993).

In an effort to find out why behavior is so rarely used in phylogenetics, Proctor (1996) surveyed 52 systematists, including botanists and mycologists as well as zoologists, and reported that 54% of them said that they use behavioral characters in systematics to some degree. That this figure is so far above those obtained from reviews of the published material may suggest that these biologists were not a representative sampling of the systematic community. Nonetheless, these

[1] Snow Entomological Museum, University of Kansas, Lawrence, KS 66045. Current address: Center for Environmental Research and Conservation, Columbia University, 1200 Amsterdam Avenue, MC 5557, New York, NY 10027 (e-mail: jdb@cerc.columbia.edu).

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respondents said that the most common reason that they do not use behavioral characters was either that they are not available or that they would be too costly or time consuming to collect. Although true for many species, behavioral characters are not universally difficult to collect. For many large and apparent species, such as vertebrates, or for some behavioral remnant characters, such as spider webs (Coddington 1986, Coddington and Levi 1991, Griswold et al. 1998) or wasp nests (Wenzel 1992, 1993, Miller and Wenzel 1995), behavioral characters are often as easy to collect as morphology or DNA sequence data.

The dearth of behavioral information in systematics may also reflect the perception (de Queiroz and Wimberger 1993) that behavior is too rapidly evolving and thus less useful for phylogenetic reconstruction than other phenotypic components (Hodos 1976, Aronson 1981). Through time, characters that are rapidly evolving may be the first to adapt to novel evolutionary regimes (Ryan 1996). Labile characters could then conform to new evolutionary forces quicker than do more conservative traits (Jander 1976, Greene and Burghardt 1978, Martins et al. 1998), such as grooming (Wenzel 1992, Miller and Wenzel 1995). As a consequence, labile characters would tend to be strongly convergent when a novel evolutionary regime affects even distantly related taxa (Tallamy and Wood 1986, LaChaise and McEvey 1990) under this hypothesis.

The myrmecophilous (ant guest) beetle tribe Sceptobiini (Coleoptera. Staphylinidae: Aleocharinae) provides a unique natural experiment to test for the evolutionary lability and phylogenetic utility of behavioral and morphological traits. The five species in this tribe are all obligate, highly integrated ant guests, extensively grooming the host ants and being groomed in return, such that some species spend >80% of the time in the nest interacting with host ants (Danoff-Burg 1996). The beetles have never been collected away from their host ants and seem to derive all their food during host ant-grooming bouts (Danoff-Burg 1996).

A cladistic analysis based on 38 morphological characters places the five species of the demonstrably monophyletic tribe in two genera, *Dinardilla* and *Sceptobius* (Fig. 1; Danoff-Burg 1994). The beetles live in nests of one of three Dolichoderine ant species (Table 1) in the genus *Liometopum* (Danoff-Burg 1996). The beetles are naturally distributed such that pairs of heterogeneric sceptobiines are nestmates in each of two ant hosts (Table 1). A fifth sceptobiine (*S. lativentris* Fenyes) lives in *L. occidentale* Emery nests without a nestmate *Dinardilla* species (Table 1). The three ant host species have geographically distinct distributions, although all three live in juniper-oak, mid-elevation xeric habitats of the southwestern United States and Mexico (Creighton 1950, Gregg 1963). Nests of their ant hosts comprise the only suitable habitat for the sceptobiines, outside of which the beetles quickly die (Danoff-Burg 1996). Every collection record of the beetles has been in or very near ant nests or foraging trails (Danoff-Burg 1994).

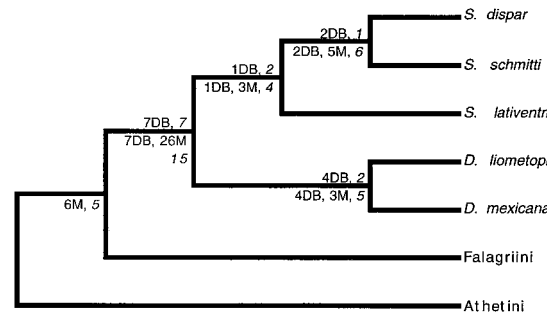


Fig. 1. Single most parsimonious cladogram of the Sceptobiini. When only the 11 discrete behavioral characters from all five Sceptobiini were analyzed (excluding the Athetini outgroup), the tree was 14 steps long (CI = 1.0, RC = 1.0). When the 11 discrete behavioral characters were combined with 38 morphological characters from an earlier analysis (Danoff-Burg 1994), the tree is 67 steps long (CI = 0.81, RC = 0.63). Number of unambiguous synapomorphies that are either discrete behavioral (followed by a "DB") or morphological characters (followed by an "M"), as well as the decay index values (italicized) for each analysis are included on the tree. Values above the branches refer to the analysis using only the discrete behavioral characters, those below the branches are for the combined analysis.

A consequence of the natural host associations and phylogenetic relationships among the beetles is that heterogeneric nestmate beetles currently coexist in identical ecological conditions that are posed by their shared host ant species, promoting convergence among nestmate beetles. Therefore, current ecological evolutionary forces may be over-riding traits that were derived long ago within the sceptobiine generic ancestors. If so, then heterogeneric, nestmate beetle species could become more similar to each other in labile and thus rapidly evolving characters, such as behavior, than congeneric but non-nestmate beetle species.

Two competing hypotheses were evaluated concerning the speed of behavioral evolution relative to morphological evolution. First, if behavioral characters are more labile than morphology, they should have conformed more strongly to the more recently evolved evolutionary forces posed by the current host associations. In the process, the more recently evolved current host associations would have over-ridden behavioral similarities among beetle species that origi-

Table 1. Ant host associations of the Sceptobiini

Ant host (Consistent with "Current Evolutionary Forces")	Beetle genus (Consistent with "Ancient Evolutionary Forces")	
Liometopum[a]	*Sceptobius*	*Dinardilla*
L. apiculatum Mayr	*S. dispar* Sharp	*D. mexicana* Mann
L. luctuosum Wheeler	*S. schmitti* Wasmann	*D. liometopi* Wasmann
L. occidentale Emery	*S. lativentris* Fenyes	—

—, *L. accidentale* lacks an associated *Dinardilla* species.

[a] Following the taxonomic arrangement of Wheeler and Wheeler (1986).

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nated in response to ancient evolutionary forces. Therefore, heterogeneric, nestmate beetle species should be more similar in behavior than congeneric non-nestmates. Alternatively, if behavioral characters are as conservative as morphological characters, they should have retained the effects of the ancient evolutionary forces, as has occurred with morphological characters. In this case, congeneric species would be most similar in behavior.

I tested these hypotheses by dissecting the behavioral phenotype into two components: what I will refer to as the continuous behavioral component (the duration for which homologous behaviors were performed) and the discrete behavioral component (the manner in which stereotyped, species-typical behaviors are performed). These components represent two separate sources of phylogenetic data and thus two separate possible instances of convergence. Continuous behaviors have long been thought to be more evolutionarily labile than discrete behaviors, a hypothesis that dates back to the early ethologists (Tinbergen 1959, Johnsgard 1967), but has not been sufficiently tested within a single lineage. As a result, these two aspects of behavior may have responded differently to the same evolutionary forces, with each reflecting a different force due to their evolutionary lability and relative inferred time of origin.

Materials and Methods

Each component of the behavior may have originated primarily due to the forces associated with either the current ant host association (hereafter referred to as "Current forces" or "effects") or due to ancient ecological, physiological, or other evolutionary forces that may no longer be present but were influential at the time of the formation of the ancestor to the two beetle genera (hereafter referred to as "Ancient forces" or "effects"). If nestmate, heterogeneric species were most similar to each other, I concluded that the Current forces have determined the behavior of the Sceptobiini. If congeneric, non-nestmate species (as determined by an earlier morphologically based analysis; Danoff-Burg 1994) were most similar behaviorally, I concluded that the beetles have retained the effect of Ancient forces.

The discrete and continuous behavioral components were evaluated separately. Four outcomes are therefore possible. First, both components could retain only the effects of Ancient forces. As a result, both components could be used in phylogenetic analyses, because they would have then passed the test of congruence with other data sets (Danoff-Burg 1994), the best test of character utility (Wenzel 1992). Second, both components could have conformed only to the Current forces, in which case neither should be used in phylogenetic analyses. Third, only one of the components could have conformed to Current forces, whereas the other has retained the effect of Ancient forces. In which case, I conclude that only that component retaining the Ancient effects should be used in phylogenetic analyses and that the component conforming to the Current forces is more rapidly evolving. Last, it is also possible that the story may not be this clear. The behavioral components could each reflect both or neither Ancient or Current forces such that both or neither of the above forces may significantly differ, in terms of similarities among species. If so, I conclude that some combination of both forces have been at work on that behavioral component.

I did not explicitly measure rates of change or evolution (sensu Gingerich 1993, Gittleman et al. 1996). Rather, I merely evaluated the time that these two behavioral components originated relative to each other and to morphology. The causative explanation for the maintenance of the Ancient and phylogenetically consistent patterns (i.e., stabilizing selection [Hansen 1997], phylogenetic niche conservation [Lord et al. 1995], neutral selection [Ryan 1996], or chance similarity among related species [as suggested by Hennig's "Auxiliary Principle;" Hennig 1965]) was inconsequential for these tests. If nestmate heterogeneric beetles were most similar, Current forces consistent with the ant host associations were said to have over-ridden the effects of Ancient forces. I excluded the fifth sceptobiine, *S. lativentris*, from most tests, because it does not have a heterogeneric nestmate *Dinardilla* species (Table 1). Consequently, the effects of Current evolutionary forces on behavioral evolution within *S. lativentris* could not be detected.

Several recent studies have demonstrated the importance of incorporating phylogeny in comparative analyses (review in Martins and Hansen 1996). Failure to recognize nested levels of relatedness when they are present may produce elevated type I statistical errors (Martins et al. 1998). However, nested levels of intrageneric relatedness are inapplicable here, because *S. lativentris* was excluded, thereby removing the possibility of nestedness. As such, nested ANOVAs or more modern comparative techniques that control for varying levels of phylogenetic relatedness (review in Martins and Hansen 1996) were not required.

I made four assumptions for these tests. First, I assumed that the well-supported and robust tree based on morphological characters (Danoff-Burg 1994) is correct and that congeneric beetles are each other's closest relatives. Second, I assumed that those congeneric beetles living with different ant host species currently experience distinct ecological pressures. The many behavioral, ecological, climatic, vegetation, soil, and habitat differences of the three ant species (Wheeler 1905; Gregg 1963; Van Pelt 1971; de Conconi et al. 1982, 1983, 1987a, 1987b, 1987c; Perez et al. 1984; Ramos-Elorduy et al. 1992) and the disjunct distributions of the host ant species (Creighton 1950, Gregg 1963, Wheeler and Wheeler 1986) support this assumption. Third, I assumed that the ant hosts or forces consistent with them are the primary Current evolutionary agent affecting the behavior of the beetles, because the ants create most of the ecological forces with which they regularly interact. The assumption is supported in that only once has a sceptobiine beetle (*S. lativentris*) been collected out of ant nests, and that individual was collected near foraging host ants

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Table 2. Descriptive ethogram for quantitative behavioral variables

Variable or character	Behavior begins when:
1. Beetle self-grooming variable (seven summed characters)[a]	
Beetle grooming own foreleg	Foreleg run through mthpts
Beetle grooming own midleg	Foreleg rubs midleg
Beetle grooming own hindleg	Foreleg rubs hindleg or hindleg run through mthpts
Beetle grooming own antennae	Antennae run through mthpts or forelegs rub antennae
Beetle grooming own head	Foreleg rubs head
Beetle grooming own thorax	Legs rub thorax
Beetle grooming own abdomen	Legs rub abdomen
2. Beetle grooming ants variable (seven summed characters)[b]	
Beetle on ant foreleg	Legs or mthpts rub ant foreleg
Beetle on ant midleg	Legs or mthpts rub ant midleg
Beetle on ant hindleg	Legs or mthpts rub ant hind leg
Beetle on ant antennae	Legs or mthpts rub ant antennae
Beetle on ant head	Legs or mthpts rub ant head
Beetle on ant thorax	Legs or mthpts rub ant thorax
Beetle on ant abdomen	Legs or mthpts rub ant abdomen
3. Beetle partially mounted[c] on ants variable (four summed characters)[b]	
Back partial mount	Beetle mounts ant from posterior
Front partial mount	Beetle mounts ant from anterior
Left partial mount	Beetle mounts ant from left side
Right partial mount	Beetle mounts ant from right side
4. Beetle fully mounted[c] on ants variable (five summed characters)[b]	
Back complete mount	Beetle mounts ant from posterior
Front complete mount	Beetle mounts ant from anterior
Left complete mount	Beetle mounts ant from left side
Right complete mount	Beetle mounts ant from right side
Unknown direction	Beetle mounts ant from unknown area
5. Beetle away from all ants[d] (one character)[b]	
Beetle away from all ants	Beetle located away from all ants
6. Beetle near one to five ants[d] (one character)[b]	
Beetle near one to five ants	Beetle near a cluster of one to five ants
7. Beetle near six or more ants[d] (one character)[b]	
Beetle near six or more ants	Beetle near a cluster of six or more ants

[a] Each behavioral character stopped when the beetle paused activity for longer than 10 s.
[b] Each behavioral character stopped due to either ant or beetle action.
[c] Partially mounted beetles still had at least one leg on the substrate; fully mounted beetles had all six legs on the mounted ant.
[d] A beetle was near ants when they were within one body length of the ants.

(Danoff-Burg 1996). The beetles also quickly die when ants are removed under laboratory conditions, even if the beetles are provided with food and water *ad libitum* (Danoff-Burg 1996). Last, I assumed that nestmate beetle species currently experience similar evolutionary forces, because the ants respond similarly to contact by either of their nestmate beetle species (Danoff-Burg 1996).

Data Collection. Both continuous and discrete behavioral data were collected from the four included beetle species using laboratory introduction experiments. A beetle and a sampling of 50 worker ants from the same nest were collected. The ants were then introduced into an experimental arena and allowed to acclimate for a minimum of 3 h (range = 3–12 h, average = 4 h). Experimental arenas were petri dishes (1.5 cm high by 12 cm in diameter), the bottom of which was covered with a 5-mm layer of moistened plaster of paris. The ants were provided with fruit jelly, breadcrumbs, and cheese ad libitum in the arenas. After the initial ant acclimation period, an individual beetle was added to the experimental arena for observation and data collection. Beetles were introduced only into experimental arenas with ants from the same colony of origin.

After a 2-min postintroduction acclimation period, I recorded the duration (in seconds) of all 26 observable beetle behaviors (Table 2) for a 10-min experimental period. Raw data were simultaneously logged into an event recorder and audio taped during experimentation. Data were later annotated, entered into a spreadsheet, and checked using the audio recordings. Beetles were removed from the dish after the 10-min period and placed in alcohol. Voucher specimens were deposited in the Snow Entomological Museum, University of Kansas, Lawrence, KS. I conducted 31–50 introduction replicates (mean = 45) for each beetle species (Table 2). Comprehensive ethograms for each species and discussion of the functional value of these behavioral patterns are given elsewhere (Danoff-Burg 1996).

Sceptobius dispar Sharp and *D. mexicana* Mann beetles were collected from nests located in the Chisos Basin, Big Bend National Park, Brewster County, TX, and from nests located 8 km E of Pine Springs near Guadalupe Mountains National Park, Culberson County, TX. Continuous behavioral data from these two sites were pooled for the final analysis of these two species after testing for and rejecting between-site effects. Continuous behavioral data for *S. schmitti* Wasmann and *D. liometopi* Wasmann were collected from *L. luctuosum* nests located 25 km W Socorro, Socorro County, NM, at the Water Canyon State Campground. Data for *S. lativentris* were included for

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Table 3. Discrete phylogenetic behavioral characters

Character	Plesiotypic (0)	Apotypic (1)	Apotypic (2)
1. Full mount on an ant (all legs off ground)	Did not mount ants	Groomed but did not completely mount ants	Fully mounted the ants while grooming them
2. Antennal grab and groom[a]	Absent	Present	
3. Grooming ant venter or dorsum	Did not groom ants	Groomed only on the dorsum of the ants	Occasionally groomed the venter of an ant
4. Simultaneously grooming multiple ants	Did not groom ants	Exclusively groomed individual ants	Simultaneously groomed multiple ants when possible
5. Beetles tapping on ant mouthparts	Absent	Present	
6. Alarmed ventral abdominal flicking	Absent	Present	
7. Dorsal abdominal curl[b]	Absent	Present	
8. Response to being stepped on by passing ants	Fled when contacted	Pressed themselves to the substrate	
9. Beetles forcibly restraining ants	Absent	Present	
10. Beetle movement across ant pile	Avoided ant pile	Only ran over the dorsa of the ants	Also pushed through the ant pile
11. Hind leg grooming	Bent metatarsi laterally to mouthparts[c]	Metatarsi not bent laterally	

A behavior does not occur within a species when it was not observed during any of the experimental replicates for that species or during ad hoc observations.

[a] Events occurred when a beetle that was already grooming an ant grasped the antennae of the ant with its mandibles and forcibly restrained the ant while it continued to groom the body of the ant.

[b] Events occurred when a beetle was attacked and forcibly restrained by an ant (afterwards the ants usually relented and released the restrained beetle).

[c] Events occurred when beetle pulled the leg forward perpendicular to the body and thus bent the body along the longitudinal axis into a C shape, curving away from the side of the groomed hind leg.

the two of the analyses of discrete behavioral components using beetles found with *L. occidentale* ants that were collected 4 km S of Alta Sierra, Sequoia National Forest, Kern County, CA. Discrete behavioral characters (Table 3) were collected during additional long-term introduction sessions over 14 d using ad libitum sampling. I collected the data from all species during May–August of 1993 and 1994 but pooled all data from each species after determining that year was not significant as a main effect.

Continuous Data Analyses. Raw data on behavioral duration were consolidated by summing the duration of each of the 26 beetle behaviors within each replicate to provide the total length of time that a behavior occurred within a replicate. The data from multiple behaviors were then summed within a behavioral category to construct seven condensed behavioral variables that were used for statistical analyses (Table 2).

Time-budget data generally sum to one over all behavioral classes (i.e., the unit-sum constraint; Aebischer et al. 1993). As a result, time-budget data are frequently nonindependent (Martin and Bateson 1993), in that when one behavior lasts longer, others must occupy less of the total time. To minimize this problem, I collected these data such that multiple behaviors could occur simultaneously. The probability of non-independence is therefore lessened and the problem of the unit-sum constraint is reduced. Nonetheless, a limited unit-sum constraint may still remain, because a beetle cannot simultaneously perform all behaviors. I therefore converted the continuous variables using the log-ratio transformation method of Aebischer et al. (1993) before statistical analysis.

Six of the condensed behavioral variables were log-ratio transformed using the beetle self-grooming variable as the denominator in the following equation.

$$\text{Ln}\,(O/S),$$

where O is the original data point and S is the corresponding beetle self-grooming data point for that replicate. Beetle self-grooming was chosen as the denominator of the transformation because it was the only variable with nonzero data in all replicates. All other variables had 18% or more replicates with zero values.

Natural-log transformation of the O/S product improves the normality of the samples (Aebischer et al. 1993). The net effect of the log-ratio transformation is that the distribution of the transformed value is centered with relation to the mean value of the trait (Aebischer et al. 1993). Aebischer et al. (1993) suggested that the results of analyses using this transformation are independent of the choice of the variable used for the denominator S.

The data from the continuous component of beetle behavior were evaluated using three analyses. Two sets of analysis of variance (ANOVA) analyses were conducted using two separate transformations of the continuous data. First, the natural-log transformed data for each variable were individually analyzed. Second, the log-ratio transformed variables were each individually analyzed. The log-ratio transformed data were used to ascertain the impact of the unit-sum constraint.

In these two sets of statistical analyses, each variable (Table 2) was individually analyzed using two-way ANOVA tests with Ancient and Current as the independent variables. Operationally, each beetle genus formed a unique category for the Ancient variable (*Sceptobius* species were assigned a value of 1 and *Dinardilla* species, a value of 2), and each ant host formed a unique category for the Current variable (beetles living with *L. apiculatum* were assigned a

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Table 4. Summary statistics (mean ± 1 SE) of the raw data for each continuous variable per replicate in seconds

Species	*n*	Self grooming	Grooming ants	Partially mounted on ants	Fully mounted on ants	Away from ants	Near 1–5 ants	Near 6 or more ants
Dinardilla liometopi	48	1,025 ± 637	400 ± 649	115 ± 173	100 ± 162	208 ± 224	136 ± 190	247 ± 285
Dinardilla mexicana	50	451 ± 370	876 ± 870	230 ± 215	214 ± 217	10 ± 44	138 ± 242	429 ± 263
Sceptobius dispar	31	538 ± 426	808 ± 584	330 ± 215	155 ± 171	42 ± 93	198 ± 252	365 ± 278
Sceptobius schmitti	50	1,372 ± 652	2,080 ± 1218	319 ± 239	15 ± 48	61 ± 131	202 ± 251	325 ± 266

Some values average more than the 600-s experimental period because multiple actions (Table 2) were summed to create these variables.

value of 1, and those with *L. luctuosum*, a value of 2). If Ancient has not been over-ridden by Current during behavioral evolution, then congeneric species will not differ but heterogeneric nestmate species will, and only Ancient will be a significant main effect. In contrast, if Current has over-ridden Ancient, then heterogeneric nestmate beetle species will not differ but congeneric species will, and only Current will be a significant main effect. Last, if both Ancient and Current have shaped the current phenotype, then both will be significant and both nestmates and congeners will be similar to each other for this behavioral component.

The third analysis of the continuous component was done using parsimony methods. Data from the mean values (Table 4) of the continuous variables of sceptobiine behavior were converted into characters (Table 5) based on arbitrary character state divisions of similar sized value classes (Wimberger and de Queiroz 1996). Phylogenetic analyses were performed using PAUP version 3.1.1 (Swofford 1991). All characters were equally weighted and treated as unrooted; multistate characters were coded as unordered and analyzed using the exhaustive search option to ensure that all minimal length trees were acquired. Decay index values (Bremer 1994) were calculated to estimate degree of support for the nodes for both discrete and continuous characters. These values were calculated using MacClade version 3.0 (Maddison and Maddison 1992) by multiple search iterations using the above parameters. MacClade was also used for character analysis and optimization. If Ancient forces have not been over-ridden by Current forces, then the most parsimonious tree will group congeneric species. The resultant tree will be the same as that derived using only morphological characters (Danoff-Burg 1994). In contrast, if Current has over-ridden Ancient to any degree, a tree different from the morphologically derived tree will result. At the most extreme, heterogeneric, nestmate species will be most closely related in this latter case.

Table 5. Behavioral character matrices

Taxon	Continuous characters 1234567	Discrete characters 11 12345678901
D. liometopi	2112311	20211111111
D. mexicana	1224114	20211111111
S. dispar	1233223	11121010120
S. schmitti	2331222	11121010120
S. lativentris		21221010120
Falagriini		00000000000

Discrete Data. The discrete behavioral component from all five sceptobiines was analyzed by reconstructing the tribal phylogeny using only behavioral characters and then comparing the result to the earlier, morphologically based analysis (Danoff-Burg 1994). Initial hypotheses of behavioral homology for 11 species-typical traits were determined using the criterion of special similarity (Wenzel 1992). Ten of the 11 behavioral characters used here involve interactions with their normal host ant species (Table 3) and should be the first to respond to forces imposed by and coincident with the Current host ant associations. As such, the test for the presence of Current forces is a rigorous one.

Myrmecocephalus arizonicus Casey of the sister tribe Falagriini was included as the outgroup taxon for the systematic analysis of discrete behavioral characters. Seevers (1978) first suggested uniting the Falagriini and the Sceptobiini into the supertribe Falagriinea; this conclusion has been supported by later studies (Hoebeke 1985, Danoff-Burg 1994, Ashe and Ahn 1995). *Myrmecocephalus arizonicus* is a free-living predator and specimens used for the study were found near Socorro, NM, in identical habitats to those of *L. luctuosum.* This species was selected because it is similar in size to the sceptobiines and lives near *L. luctuosum* in the leaf litter and likely interacts with this ant. Outgroup specimens were tested in the presence of ants to gather discrete character information in the same experimental arenas used for the sceptobiines. Individual *M. arizonicus* beetles were introduced into the observation arena with 50 *L. luctuosum* ants. Ten replicates were conducted using 10 unique individuals. After a 2-min acclimation period, the behavior of each beetle was observed for 10 min. Because of the extreme pugnacity of the ants toward the beetles, the *M. arizonicus* self-grooming character was observed in the absence of ants.

Three phylogenetic analyses were conducted with the same search parameters and evaluation tools used for the phylogenetic characters derived from the continuous data. First, I analyzed the discrete behavioral data, including only the four species used in the analyses of the continuous component. Second, I included all five sceptobiines and the falagriine outgroup and used only discrete behavioral data. Last, I included all five sceptobiines and both outgroup taxa and then used both the discrete behavioral (Table 5) and mor-

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Table 6. ANOVA test results of the continuous variables

Variable (time spent)	Ancient forces		Current forces		Ancient X Current	
	F-ratio	*P*	F-ratio	*P*	F-ratio	*P*
	Natural-log transformed data					
Self-grooming	2.67	NS (0.10)	21.94	***	0.27	NS (0.61)
Grooming ants	8.05	**	0.24	NS (0.63)	9.37	**
Partially mounted	8.64	**	1.29	NS (0.26)	0.79	NS (0.38)
Fully mounted	1.03	NS (0.31)	0.39	NS (0.53)	0.44	NS (0.83)
Away from ants	0.08	NS (0.78)	6.75	*	4.78	*
Near 1–5 ants	0.80	NS (0.37)	7.37	**	0.22	NS (0.64)
Near 6 or more ants	0.75	NS (0.39)	2.13	NS (0.15)	0.04	NS (0.84)
	Log-ratio transformed using self-grooming as the denominator data					
Grooming ants	10.01	**	18.44	***	1.73	NS
Partially mounted	2.34	NS (0.13)	16.08	***	1.12	NS (0.29)
Fully mounted	2.45	NS (0.12)	2.29	NS (0.13)	6.43	*
Away from ants	0.40	NS (0.53)	5.38	*	0.07	NS (0.79)
Near 1–5 ants	0.13	NS (0.72)	25.98	***	0.00	NS (0.99)
Near 6 or more ants	2.41	NS (0.12)	23.32	***	2.65	NS (0.11)

Variables were individually analyzed using two-way ANOVAs with both current evolutionary forces due to ant host associations (Current) and ancient evolutionary forces (Ancient) as the independent variables for both forms of the data, with df = 3, 175.

*, $P < 0.5$; **, $P < 0.01$; ***, $P < 0.001$; NS, not significant.

phological (Danoff-Burg 1994) character matrices in a combined evidence analysis. The results of these three analyses were compared with the phylogeny based on morphological characters (Danoff-Burg 1994) for topological congruence.

As with the character data derived from the continuous data, if Ancient forces have not been over-ridden by Current forces during behavioral evolution, then the most parsimonious tree to result from the discrete data will be the same tree as that derived from morphological characters (Danoff-Burg 1994). In contrast, if Current forces have over-ridden Ancient forces to any degree, a tree different from the morphologically derived tree will result.

Results

Continuous Behavior

ANOVA Year and Location. The between-year comparisons of the untransformed seven variables for all four beetle species were not significant (*S. dispar:* $F = 2.07$; df = 6, 24; $P = 0.10$; *S. schmitti:* $F = 1.43$; df = 6, 43; $P = 0.23$; *D. liometopi:* $F = 0.21$; df = 6, 41; $P = 0.97$; *D. mexicana:* $F = 2.07$; df = 6, 43; $P = 0.08$). I concluded that there was no significant annual variation among the individuals sampled for these species and combined data collected in different years for subsequent analyses. Similarly, the behavior of *S. dispar* ($F = 1.76$; df = 6, 24; $P = 0.15$) and *D. mexicana* ($F = 2.07$; df = 6, 43; $P = 0.08$) did not significantly differ between the two collection sites. I concluded that there was no significant between-site variation within these two species and combined data collected at different locations for these two species for subsequent analyses.

ANOVA Individually Analyzed Variables. The analyses of the continuous data when alternatively natural-log transformed or log-ratio transformed provided somewhat divergent results from each other. Few natural-log transformed variables were significant for either factor (Table 6). Two of the three variables that involved the most interactions with ants (beetle grooming ants and beetle partially mounted) were significant for Ancient forces, whereas the three variables that involved the fewest ant interactions (beetle self-grooming, beetle away from all ants, and beetle near one to five ants) were significant for Current forces. Two variables (beetle grooming ants and beetle away from ants) were significant for the interaction term. Examination of the raw data averages (Table 4) revealed that the beetles living with *L. apiculatum* did not differ from each other in terms of the grooming ants variable, but that the two with *L. luctuosum* did. The other significant interaction term was likely due to the large amount of time that *D. liometopi* spent away from ants relative to the other species (Table 4).

Five of the six log-ratio transformed variables were significant for Current forces when individually analyzed using two-way ANOVA tests. The only variable for which Current forces were not significant was time spent fully mounted on ants (Table 6). In contrast, only one of the six variables was significant for Ancient forces (time spent grooming ants). One of the variables (beetle fully mounted on ants) was significant for the interaction term (Table 6). Closer examination of the raw data averages for time fully mounted revealed that beetle species within *L. apiculatum* nests did not differ greatly from each other but those living with *L. luctuosum* did.

Phylogenetic Analyses. The analyses using only the seven phylogenetic characters derived from the continuous data produced two equally most parsimonious trees (length = 15, CI = 0.93, RC = 0.47). The first tree grouped nestmate heterogeneric species together, whereas the second tree grouped non-nestmate congeneric species together. The first tree conflicted with Fig. 1, whereas the second was completely congruent with Fig. 1. Neither tree was well supported in that the

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branch lengths were equal to one and the decay value was zero. When these continuous characters were treated as ordered from lowest to highest values, only the first tree grouping nestmate, heterogeneric species together was obtained (length = 16, CI = 0.88, RC = 0.53), with two additional synapomorphies supporting the tree relative to when the characters were treated as unordered.

Discrete Characters

Outgroup. The outgroup falagriine *M. arizonicus* beetles were promptly attacked and restrained by numerous ants in each of the 10 replicate introductions. One to four ants simultaneously restrained and attacked the beetles in these replicates. Once restrained, the beetles were not released for the duration of the 10-min observation period. In four of 10 replicates, the beetles were at least partially dismembered within the observation period and all were at least partially dismembered within 30 min. No *M. arizonicus* beetles ever initiated contact or attempted to mount the ants.

Phylogenetic Analyses. When only the four sceptobiines with heterogeneric nestmate beetles were analyzed using data from the unordered discrete characters, a single unrooted tree resulted (length = 8, CI = 1.00, RC = 1.00) that grouped non-nestmate, congeneric beetles. The tree was well supported by eight unambiguous synapomorphies and a decay index at the one node of eight steps. The tree was congruent with Fig. 1. No difference in any index values or topology was obtained if the characters were treated as ordered.

When all five sceptobiines and the outgroup falagriine beetle were included in an analyses using all discrete behavioral characters, a single most parsimonious tree was produced (Fig. 1, length = 12, CI = 1.00, RC = 1.00). This tree had the identical topology of that of the phylogeny derived from morphological characters (Fig. 1; Danoff-Burg 1994). All of the nodes in the shortest tree were well supported and each node had multiple supporting behavioral synapomorphies (Fig. 1). Because the outgroup *M. arizonicus* may not be informative for character polarity, I also conducted the same analysis but excluded this outgroup species. The same tree and index values resulted (Fig. 1, length = 8, CI = 1.00, RC = 1.00).

When the 11 discrete behavioral characters were combined with the 38 morphological characters (from Danoff-Burg 1994) and analyzed, the identical tree was produced as when either matrix was independently analyzed (Fig. 1, length = 67, CI = 0.81, RC = 0.63). Based on the decay index values, the strongest supported node on the tree is that uniting the five sceptobiines together into a tribe (Fig. 1). All relationships within the tribe were strongly supported, with decay index values of at least 4 (range = 4–6) at each subgeneric clade. The addition of the morphological data to the discrete behavioral data only doubled the decay index value at each node, on average (Fig. 1) despite there being almost four times as many morphological characters as discrete behavioral characters.

Discussion

Relative Evolution of Behavioral Components. The two behavioral components of the myrmecophilous Sceptobiini beetles represent two distinct phylogenetic data sets and therefore two separate possible instances of evolutionary convergence. Based on my analyses, it appears that the continuous behavioral component is more evolutionary convergent and has evolved much more recently than the discrete component. Therefore, each component may reflect forces that were active on the Sceptobiini at different times in the evolutionary past.

When statistically analyzed, most of the continuous behavioral components of the Sceptobiini have conformed to the influences of the Current evolutionary forces, whereas very few have conformed to the Ancient evolutionary forces. When the continuous data were phylogenetically analyzed, the resultant two trees were alternatively consistent with each of the two evolutionary forces. At a minimum then, the present form of the continuous behavioral component seems to have been formed largely by the current ant host associations, with only a selection of behaviors still retaining the influence of ancient evolutionary forces.

The two different forms of the continuous data sets yielded slightly different outcomes when statistically analyzed. However, the natural-log data are fundamentally flawed in that each variable is not independent of the others (Martin and Bateson 1993); they are therefore subjected to the unit-sum constraint (Aebischer et al. 1993) and are less reliable than the log-ratio transformed data. Conclusions drawn from them should be made carefully. In contrast, the log-ratio transformed data are likely to be minimally affected by the unit-sum constraint, if at all. However, the log-ratio transformed data may not be themselves perfect. These data may be affected by the choice of the denominator for the transformations, despite assertions to the contrary (Aebischer et al. 1993). Beetle self-grooming not only had a significant *F*-ratio for Current forces, it was the largest among all seven natural-log transformed variables (Table 6). However, this objection is an undemonstrated possibility, whereas the natural-log transformed data are intrinsically not independent of each other. Therefore, the log-ratio transformed data will be the focus of the remaining discussion of the continuous analyses.

Five of the six (all but beetles being fully mounted) log-ratio transformed variables were significant for the Current evolutionary forces. Because nearly the entire continuous behavioral component was most similar among nestmate species, it seems that the ant hosts may have over-ridden the influence of Ancient evolutionary forces that would have otherwise have produced shared similarities among congeneric species.

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Therefore the continuous variable may have evolved recently relative to morphology (Danoff-Burg 1994).

In contrast, only the Ancient evolutionary forces seem to have determined the discrete behavioral component, such that congeners are more similar to each other in discrete characters. The remnants of Ancient evolutionary forces have been retained among the discrete characters, despite the large convergent pressure of the host ants on heterogeneric, nestmate beetles. The discrete behaviors are therefore likely to be slowly evolving relative to continuous behaviors, likely at a rate that is comparable to that of morphology.

These data therefore support the early hypothesis that most continuous behaviors are more rapidly evolving than are discrete characters (Tinbergen 1959, Johnsgard 1967). Because of the evolutionary conservation among discrete behaviors, data derived from this behavioral component seem to be as useful as morphological characters (Danoff-Burg 1994) for reconstructing the phylogeny of the Sceptobiini. In contrast, continuous information may not be ideal characters for use for reconstructing phylogeny but may be most appropriate for recognizing incipient species (Blair 1953, de Queiroz and Wimberger 1993) and for diagnosing ant host effects.

Current Evolutionary Forces. The continuous behavioral component seems to be most similar among heterogeneric, nestmate beetle species. However, determining the primary Current evolutionary mechanism underlying this trend, if any, was beyond the scope of these analyses. Further research should focus on the specific selective forces posed by the current host ant species or whether the similarities among nestmates merely came about because of nonadaptive and nondirectional homoplasy (as suggested by Hennig's auxiliary principle, Hennig 1965).

Some subset of the ecological situation posed by the host ant species is the most obvious choice for the selective force molding continuous beetle behavior. Chief among these possibilities are the interactions with the host ants themselves, as it is with them that the beetles interact the most, deriving shelter, food, and protection from the association. The extreme symbiotic reliance by the beetles on the host ants could force nestmate beetles to adapt similarly to the environmental conditions presented by the host ants (Kistner 1979, Danoff-Burg 1996).

However, it is also possible that the similarities among the heterogeneric nestmate species were caused by other factors (e.g., abiotic factors, trophobiont species such as aphids or mealybugs that are tended by the ants, or nest materials) that are coincident with the host ants. The adaptive value of traits should be invoked only if a selective force can be demonstrated to be acting directly on the trait (Ryan 1996). Future studies along these lines should explore the causative mechanisms creating these patterns.

The continuous component of the beetle behavior could be merely transitory phenotypic responses to the environment that are not genetically fixed or heritable (Eisenberg et al. 1972). For example, sceptobiines may facultatively alter the continuous behavioral component in response to their current host species. Therefore, when introduced into nests of a given species of *Liometopum* ant, a beetle of any sceptobiine species will always act in a manner determined by that host species, irrespective of their normal ant host species. Anecdotally, the beetles seem to be incapable of dramatically altering their behavior in response to novel environmental conditions of this order. When placed into the artificial environments (film canisters with water and food) in which they were held in preparation for these experiments, the beetles seem to have performed continuous self-grooming behaviors as they did during the experiments (J.A.D-B., unpublished data).

However, a hypothesis of behavioral phenotypic plasticity may be difficult to test. During the three times that have I introduced *S. schmitti* beetles into nonhost *Liometopum apiculatum* ants, they were attacked and dismembered (J.A.D-B., unpublished data). If the observed similarities among nestmate beetles in these continuous behaviors were demonstrated to be phenotypically plastic, the above conclusions would not be supported.

Ancient Evolutionary Forces. In contrast to the continuous behavioral component, the discrete component of behavior originated in response to Ancient evolutionary forces only. When the discrete behavioral characters were analyzed separately, a single most parsimonious tree resulted that was identical to that obtained when only morphological characters were used (Danoff-Burg 1994), with no character conflict. Therefore, all of the measured species-typical behaviors of the sceptobiines are most similar among congeneric, non-nestmate beetle species.

Current evolutionary forces accounted for most of the continuous behavioral component, but the presence of Ancient evolutionary forces was still detected during both analyses of the continuous component. Surprisingly, the only continuous variable that was also significant for Ancient forces in the statistical analyses was grooming ants, a variable that involved substantial and direct interactions with the host ants (partially mounting the host ants was also significant in the natural-log transformed analysis). Behaviors involving direct interactions between beetles and ants may be among the most important reflections of how the beetles have responded to the evolutionary forces presented by the host ants (Kistner 1979). For this reason, it would be expected that grooming ants would be the first of the continuous component to conform to the Current evolutionary forces and thus swamp out the remnant effects of Ancient forces. This was not observed in the sceptobiines. Because it has retained the mark of the Ancient forces, this variable may be of utmost ecological importance, possibly in partitioning the resources (Feder et al. 1995) that may be present on the bodies of the ants between the nestmate sceptobiine species, such as nest pheromones and food.

In the phylogenetic tests of the continuous variables the remnant effects of Ancient forces were also detected in the two resultant conflicting trees. However,

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if the continuous phylogenetic characters were treated as ordered, only the tree that allied heterogeneric nestmate species resulted, indicating the influence of Current evolutionary forces. Although less desirable from the standpoint of pure parsimony, this character ordering is in accordance with the currently favored scenario for the evolutionary progression of myrmecophiles. Several researchers (Seevers 1965, Kistner 1979) have hypothesized that more intimate interactions with the host ants become increasingly common as myrmecophiles evolve to become more host specific and obligate guests. Therefore, although Ancient evolutionary forces can be seen to have determined a portion of the current continuous behavioral component, it is a smaller portion than that determined by the Current evolutionary forces.

In sum, the entire discrete component and the grooming ants continuous variable are most similar among congeneric, non-nestmate beetle species, thereby reflecting Ancient evolutionary forces. However, neither congruence with phylogeny nor statistical agreement with the resultant taxonomy can be causal explanations for trait origin (Westoby et al. 1995). They are instead descriptions of trait pattern evolution that has arisen in the past, possibly because of adaptation to evolutionary forces that no longer exist, and have continued to the present (Westoby et al. 1995).

The retention of the effects of Ancient evolutionary forces in some of the behavioral phenotype has occurred despite strong Current forces posed by the host ants promoting convergence. It is most likely that these species-typical behaviors originated in the generic ancestors to the current species and have been retained—most likely because of stabilizing selection (Hansen 1997), phylogenetic niche conservation (Lord et al. 1995), neutral selection (Ryan 1996), chance similarity among related species (Hennig 1965), or some type of historical constraints (Greene and Burghardt 1978, Harvey and Purvis 1991, Arnold 1994). Future research could explore these hypotheses to explore the mechanisms responsible for the maintenance of these traits derived long ago.

Sceptobiine Behavioral Evolution. A testable evolutionary scenario can be built to explain these results. The most parsimonious scenario that explains behavioral evolution within the Sceptobiini is that the behavioral aspects that continue to show the effects of Ancient forces first originated within the ancestors of each of the two beetle genera. The extant host associations and the well-supported phylogeny support this idea.

Character displacement (Grant 1994) or random drift (Templeton 1989) could have caused two sympatric nestmate lineages to form from the ancestor to the Sceptobiini within the nest of the *Liometopum* ancestor, resulting in the production of the two ancestral generic taxa. If true, then there must have been strong selection for divergence (Felsenstein 1981, Rice 1987) to partition the resources available to the beetles within these nests. The discrete behavioral component and the grooming ants continuous variable, all of which still retain the effects of the Ancient evolutionary forces, likely originated at this time (Fig. 2, event number 1).

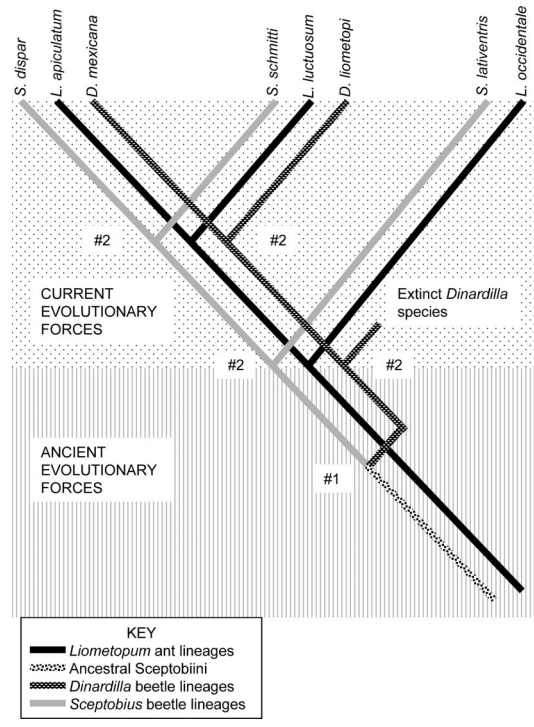


Fig. 2. Coevolutionary scenario for the Sceptobiini. Speciation event number 1 is the speciation of the ancestral Sceptobiini into the two extant genera within nests of the ancestral *Liometopum* host ant. Number two speciation events are those occurring within the beetle genera in response to ant host speciation.

Later, the extant beetle species were produced during two cospeciation events as the *Liometopum* ancestor speciated allopatrically (Fig. 2, event number 2). The ancestral *Dinardilla* species living with *L. occidentale* either subsequently went extinct or was not transferred to nests of this incipient species. After these two cospeciation events occurred, the Current evolutionary forces and thus most of the continuous component likely originated. This step of the scenario would require these three *Liometopum* ant species to be closest relatives, a systematic analysis that has yet to be accomplished (Shattuck 1995).

Phylogenetic Implications. The differential evolutionary speed of these two behavioral components in the Sceptobiini may have broader implications for character choice when reconstructing phylogeny. It is likely that much of the conflict over the use of behavioral characters in systematics has occurred because some systematists have inadequately differentiated between discrete and continuous behavioral components when derogating the use of behavioral characters (e.g., Hodos 1976, Aronson 1981).

Although some components of behavior may be more homoplasious than some components of morphology (Slater 1986), this does not mean that all of

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behavior is too quickly evolving to be used in phylogenetic reconstruction. The sceptobiine data support the view that most continuous behaviors may evolve too quickly and would then be too homoplastic to be used to reliably reconstruct phylogeny. Even the continuous component of those behaviors that have been suggested to be among the most phylogenetically conserved behaviors, such as self-grooming (Wenzel 1992, Miller and Wenzel 1995), may have evolved too quickly to be phylogenetically useful (Table 6). However, discrete characters of nearly all classes are at least as phylogenetically informative as other data, even those that require interactions with the host ants.

It therefore may be beneficial to clearly differentiate between discrete and continuous characters a priori when choosing appropriate systematic characters (Gittleman et al. 1996) for inclusion. Selection of the appropriate discrete behavioral characters for systematics can only be done with reference to other data sets, as congruence is the best test of character utility (Wenzel 1992). Therefore, at least within the Sceptobiini, when correctly chosen behavioral characters may be at least as evolutionarily conservative and informative as other useful characters.

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