

REPertoire CONVERGENCE
IN TWO MANGROVE ANTS, *ZACRYPTOCERUS VARIANS*
AND *CAMPONOTUS (COLOBOPSIS)* SP.

B.J. COLE

Department of Biology, Princeton University, Princeton, New Jersey, 08540 U.S.A.

Reçu le 21 juin 1979.

Accepté le 21 septembre 1979.

SUMMARY

The convergence of *Zacryptocerus varians* and *Camponotus (Colobopsis)* sp. is manifest in three ways: i) Structural convergence (shield-headed major workers, large eggs), ii) Qualitative behavioral convergence (high rate of oral trophallaxis, traffic in infrabuccal pellets, iii) Repertoire convergence (number of behavioral categories in common, behavioral distance).

Methods of analyzing repertoire convergence using techniques borrowed from numerical taxonomy may be especially useful in obtaining quantitative measurements of the relative effects of phylogeny and ecology in social insect behavior.

In contrast to the behavioral convergence of the minor workers, the major workers do not show this convergence. The major workers of *Colobopsis* are not as behaviorally specialized as the major workers of *Z. varians* and in accordance with current ergonomic theory are relatively more numerous.

An effort is made to account for the areas of convergence and divergence in features of their sociobiology.

RESUME

Convergence du répertoire chez deux fourmis de Mangrove *Zacryptocerus Varians* et *Camponotus (Colobopsis)* Sp.

La convergence évolutive de *Zacryptocerus varians* et de *Camponotus (Colobopsis)* sp. est manifeste dans trois domaines: 1 - une convergence de structures (ouvrières major dont la tête est structurée pour la défense; grands œufs); 2 - une convergence de structure comportementale (taux élevé de trophallaxies orales; échanges de boulettes infra-buccales); 3 - une convergence de répertoire comportemental (nombre d'items comportementaux en commun; distance comportementale).

Les méthodes d'analyse de convergence du répertoire comportemental, qui utilisent des techniques dérivées de la taxonomie numérique, peuvent être particulièrement utiles

pour obtenir des mesures quantitatives des effets relatifs de la phylogenèse et de l'écologie dans le comportement social des insectes.

Par contraste avec la convergence comportementale des ouvrières minor, les ouvrières major ne présentent pas cette convergence. Les ouvrières major de *Colobopsis* n'ont pas un comportement aussi spécialisé que les ouvrières major de *Z. varians* et sont relativement plus nombreuses, conformément à la théorie ergonomique habituelle.

Nous nous sommes efforcés de rendre compte des convergences et divergences dans les aspects de la sociobiologie des deux espèces.

The evolutionary phenomenon of convergence is one in which similar characteristics evolve under similar selective pressures in unrelated groups of organisms. Examples of convergence provide some of the most convincing examples of the efficacy of the ecological role in shaping form or function. Convergence to a particular behavior (e.g. social carrying in ants) or set of behavior (e.g. adaptations to arboreal environments in ants) or social structure (e.g. eusociality in bees, wasps, ants and termites) is well documented. One might also consider behavioral convergence as expressed by similarity in the total behavioral repertoire of two species. The major stumbling block is that for most species of animals, the task of obtaining a complete behavioral catalogue is formidable.

By contrast, the task of obtaining a complete ethogram of behavioral catalogue for a species of social insect is a relatively easy matter. Less than 50 hours of observation and cataloging between two and four thousand behavioral acts are sufficient to obtain a probability of .9995 that the next behavior will fall into a category already seen (WILSON and FAGEN, 1974).

As data on the complete behavioral catalogues of ants accumulate, it becomes possible to explore questions such as the degree of similarity within a set of related species, or within a set of ecologically similar, yet phylogenetically distinct species. In this paper I shall describe behavioral convergence in two species of ants, *Zacryptocerus varians* and *Camponotus (Colobopsis)* sp. This convergence is manifested in three general ways: i) They show convergence in non-behavioral aspects of their biology (e.g. egg size and shield-headed soldiers) which are relevant to their sociobiology. ii) They share a number of behavioral traits which are very unusual among ants in general. iii) They show convergence in their entire behavioral repertoire.

The species for which social ethograms were constructed are the myrmicines *Crematogaster ashmeadi*, *Xenomyrmex floridanus*, and *Zacryptocerus varians*, the pseudomyrmecine *Pseudomyrmex elongatus*, and the formicine *Camponotus (Colobopsis)* sp. I will usually refer to this latter species as *Colobopsis*. This species shows affinities to *C. impressus*, but is possibly a distinct species (WILSON, 1964). The comparison of the degree of convergence between *Z. varians* and *Colobopsis* is always made in the light of the similarity between these two species and their similarity with the three other species.

All of the species nest in hollow twigs on the red mangrove (*Rhizophora mangle*). Details of the ecological and behavioral relationships of the species will be presented elsewhere. Some ants differ in the size or position of their nest on the mangrove tree, however all must contend with the special problems of arboreal life, twig nesting, and living in an environment of limited fresh water (red mangrove grows in shallow salt or brackish water).

Species of the subgenus *Colobopsis* and the myrmicine tribe Cephalotini have two of the most bizarre caste systems of any ant. Each has a discrete minor worker caste and major worker caste. The head of the majors in both species is greatly modified for nest defense. In *Z. varians* the frontal carinae are enormously prolonged backward over the eyes, forming a flange which can be used to plug the nest or to bulldoze intruders out of the nest. In *Colobopsis* the front of the head is abruptly truncated and circular when viewed from the front. The truncation involves the clypeus, frontal lobes and mandibles of the major workers. The modification is not as dramatic as that of the major worker of *Z. varians* and a single ant is not as effective in plugging the twig nest. Several ants acting in concert can form a barrier to intruders.

MATERIALS AND METHODS

Colonies of the five species were collected from red mangroves in the lower Florida Keys. These ants are easily housed in glass tubes. The tubes had an inside diameter of 5 millimeters and were plugged at one end with cotton. They were housed in a plastic container containing a water source. The ants were fed drops of honey and pieces of insects. *Z. varians*, a nocturnal ant, was kept in constant 24 hour light in conformity with the method of WILSON (1976).

The entire plastic container containing the nest could be placed on the stage of a dissecting microscope. Observations were made at magnifications of from 7X to 30X. Most observations were made at 10X. All behavioral acts which were seen were counted. Behavioral acts were counted until an estimated sample coverage of .9995 or better was obtained (FAGEN and GOLDMAN, 1977). This was reached in *Z. varians* after 22.5 hours of observation and recording 3303 behavioral acts. For *Colobopsis* this sample coverage was reached after 19 hours of observation and a total sample of 1911 behavioral acts was recorded.

RESULTS

The social ethograms for the minor and major workers and the queens are presented in Table I. Thirty-one discrete behavioral categories in the minor worker and two categories in the major worker were observed in *Z. varians*. Twenty-eight behavioral categories in the minor worker and fifteen categories in the major worker were observed in *Colobopsis*. The estimated size of the behavioral repertoire for the minor workers, by the Fagen-Goldman method (FAGEN and GOLDMAN, 1977) is 40 for *Z. varians* and 36 for *Colobopsis*. The estimate for *Z. varians* compares quite favorably with the value of 42 given by WILSON (1976).

Table I. — Behavioral categories together with the fractional occurrence in the repertoire of the minor workers, the major workers and the queens of *Z. varians* and *Colobopsis* are shown.

Tableau I. — Catégories de comportements et probabilité d'apparition dans le répertoire des ouvrières minor, des ouvrières major et des reines de *Z. varians* et *Colobopsis*.

Behavioral Act	<i>Zacryptocerus</i>			<i>Colobopsis</i>		
	Minor	Major	Queen	Minor	Major	Queen
Total Act	3303	25	10	1911	457	15
Self-grooming	.3250	.56	.10	.3804	.317	.53
Antennal tipping	.0234	0	0	.0016	0	0
Lick wall of nest	.0100	0	0	.0120	0	0
Drag.: minor worker	0	0	0	0	.002	0
major worker	0	0	0	.0010	0	0
queen	0	0	0	.0021	.002	0
Allogroom: minor worker	.0550	0	0	.0345	.011	0
major worker	.0027	0	0	.0094	0	0
queen	.0039	0	0	.0078	.015	0
Lay normal egg	0	0	0	0	0	.07
Lay trophic egg	.0009	0	0	0	0	0
Carry insect remains	0	0	0	.0031	0	0
Carry infrabuccal pellets	.0030	0	0	.0042	0	0
Carry solid remains	.0006	0	0	.0010	0	0
<i>Brood care</i>						
Carry egg(s)	.0125	0	0	.0115	.004	0
Lick egg(s)	.0067	0	0	.0178	0	0
Carry larva(e)	.0477	0	0	.0340	.020	0
Lick larva(e)	.1388	0	0	.0900	.061	.07
Assist larval ecdysis	.0009	0	0	0	0	0
Meconium removal	0	0	0	.0005	.002	0
Carry pupa(e)	.0030	0	0	.0010	0	0
Lick pupa(e)	.0118	0	0	.0105	.007	.07
Feed egg to larva	.0018	0	0	0	0	0
Feed infrabuccal pellet to larva	.0070	0	0			
<i>Abdominal trophallaxis</i>				.0078	0	0
receive or solicit from minor	.0410	0	0	0	0	0
receive or solicit from major	.0043	0	0	0	0	0
receive or solicit from queen	.0018	0	0			
<i>Regurgitate</i>				0	0	0
with larva	.0653	0	0	.0597	.009	0
with minor worker	.2072	.44	.90	.1669	.471	.27
with major worker	.0033	0	0	.1125	.066	0
with queen	.0024	0	0	.0021	0	0
Feed on insect remains	.0012	0	0	.0141	.011	0
Feed on larva	.0009	0	0	.0010	0	0
Feed on egg	.0003	0	0	0	0	0
Feed on infrabuccal pellet	.0106	0	0	.0068	0	0
Share infrabuccal pellet	.0015	0	0	.0010	0	0
Feed on solid remains	.0009	0	0	.0010	0	0

Most of the behavioral categories listed are self-explanatory, however those which are not, or which are unique to one or the other of *Z. varians* or *Colobopsis* will be discussed below.

Antennal tipping

In this behavior the body is held rigid and the antennae held with the tips pointing towards one another and often touching. The legs are usually extended and the body quivers. The head is sometimes raised while the mandibles open. This behavior has been observed in the myrmicines *Cephalotes atratus*, *Pogonomyrmex badius*, *Leptothorax curvospinosus*, *Macromischa floridanus*, *Crematogaster ashmeadi*, *Xenomyrmex floridanus*, *Zacryptocerus varians* and most recently *Atta sexdens* (WILSON, pers. comm.). In addition I have seen a behavior in *Pseudomyrmex* which in all ways seems identical to antennal tipping except for the fact that the tips of the antennae are not brought together. In *Colobopsis* I have also seen what looks like typical antennal tipping. Thus antennal tipping or behavior very much like it, is widely distributed in at least two ant subfamilies.

Abdominal Trophallaxis

This behavior is apparently completely analogous to oral trophallaxis, except that the soliciting ant directs antennation and holds her mouthparts to the tip of the gaster of the donor ant. The donor frequently licks the tip of the gaster and appears to be obtaining some secretion from the donor. The origin of the secretion, whether from the ovaries, hindgut, poison gland or Dufour's gland is unknown. For a more comprehensive discussion of this behavior see WILSON (1976).

Oral Trophallaxis

One characteristic of the convergence between *Colobopsis* and *Z. varians* is the high rate of oral trophallaxis between workers. The regurgitation rate for other species of ant for which data are available range between 0 percent and 7.8 percent of the total behavioral acts. In *Z. varians* 21.3 percent (this study) or 22.8 percent (WILSON, 1976) and in *Colobopsis* 27.9 percent of the total behavioral acts involve regurgitation with adults. The frequency of oral trophallaxis far exceeds that of other ants and is a consequence of the dependence of these species on scavenging and liquid food.

Traffic in Infrabuccal Pellets

In most ants infrabuccal pellets are removed from the nest almost immediately. In *Z. varians* and *Colobopsis* the disposal of infrabuccal pellets is not a simple matter. The infrabuccal pellet is a compacted ball of solid material which is not passed to the crop, but collected in the

infrabuccal pouch and regurgitated from time to time. On over thirty occasions in *Z. varians* and *Colobopsis* I have observed a worker which has just regurgitated an infrabuccal pellet to feed at least part of it to a larva. In addition, they feed on their own infrabuccal pellets, licking them vigorously while, rotating them. This is a behavior which I have not seen in *Pseudomyrmex elongatus* although the frequency with which they handle infrabuccal pellets is much greater. In addition, I have seen several instances in both *Z. varians* and *Colobopsis* in which one worker gave up an infrabuccal pellet to another worker who appeared to be soliciting for it. Infrabuccal pellets are also transported from one site to another within the nest. This complex set of behavior dealing with infrabuccal pellets is another qualitative aspect of the convergence of these species and may be associated with water conservation.

Egg Size

The eggs laid by both *Z. varians* and *Colobopsis* are exceptionally large. For *Z. varians* the egg is 1.1-1.2 mm long, or at least one-fourth of the length of the gaster of the queen (WILSON, 1976). For *Colobopsis* the egg is about 1.3 mm long, approximately one-third the length of the gaster of the queen. In *X. floridanus* and *C. ashmeadi* the egg sizes are one-seventh to one-tenth the length of the gaster of the queen. As WILSON (1976) suggests, large eggs may be an adaptation to the dry arboreal nest environment. Large eggs which have a favorable surface to volume ratio may lose moisture at a lower rate.

CONVERGENCE IN THE BEHAVIORAL REPERTOIRE

Two methods of measuring similarity of the social behavior of the five species will be discussed. Both of these methods are useful for some purposes and each has its own peculiar set of biases.

Number of Behavioral Categories in Common

Figure 1 shows a dendrogram based on the number of behavioral categories which one species has in common with the other. This is a meaningful quantity only because the behavioral catalogue of all the species are very nearly complete and approach completeness to the same degree.

should be:

The distance shown in the dendrogram is $d = \sqrt{1 - S_{sm}}$ where S_{sm} is the simple matching coefficient (SNEATH and SOKAL, 1973). The simple matching coefficient is defined as $S_{SM} = \frac{m}{n}$, where m is the number of

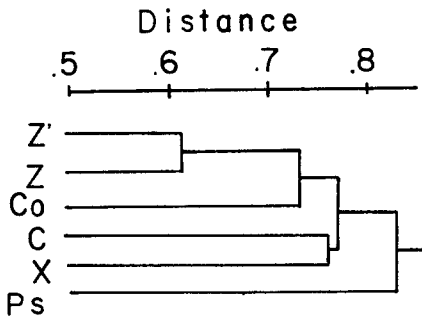


Fig. 1. — A dendrogram constructed from the Simple Matching Coefficients of the number of behavioral acts in common between species. Distance is $\sqrt{1 - S_{sm}}$. Clustering algorithm used is the complete linkage algorithm. For details see the text. Z' = *Z. varians* (WILSON, 1976), Z = *Z. varians* (this study). Co = *Colobopsis*, C = *Crematogaster ashmeadi*, X = *Xenomyrmex floridanus*, Ps = *Pseudomyrmex elongatus*.

Fig. 1. — Dendrogramme construit à partir des coefficients de comparaison du nombre d'items de comportements que les espèces ont en commun. La distance est $\sqrt{1 - S_{sm}}$. L'algorithme en bouquet qui a été utilisé est l'algorithme de lien complet. Pour davantage de détails : voir le texte. Z' = *Z. varians*, d'après WILSON, 1976. Z = *Z. varians* dans notre travail. Co = *Colobopsis*; C = *Crematogaster ashmeadi*; X = *Xenomyrmex floridanus*; Ps = *Pseudomyrmex elongatus*.

behavioral categories which two species share and n is the total number of behavioral categories observed in all species (n = 40).

The dendrogram is produced by the complete linkage algorithm. In this algorithm a candidate species is admitted into an existing cluster if it is closer to the most distant member of the existing cluster than it is to any other unclustered species, or the most distant member of another cluster (DE GHETT, 1978). Because the constraints on entering a cluster are severe, this method generally produces well defined clusters.

The two ethograms of *Z. varians* by WILSON (Z') and this study (Z) show a high degree of similarity. *Colobopsis* clusters with Z and Z'. *Crematogaster* and *Xenomyrmex* form a second cluster and *Pseudomyrmex* forms a cluster of its own.

Because this dendrogram is based on the number of behavioral categories of one species which are shared by another species, all behavioral categories are equally weighted. There are two problems with this method of comparison. First, because there are more rare types of behavior than common ones, the rare categories are weighted more heavily in the final figure. Second, because this measure deals only with the presence or absence of a particular behavioral category in the repertoire of two species, the frequencies of the category in the two species may be widely disparate and mask significant differences.

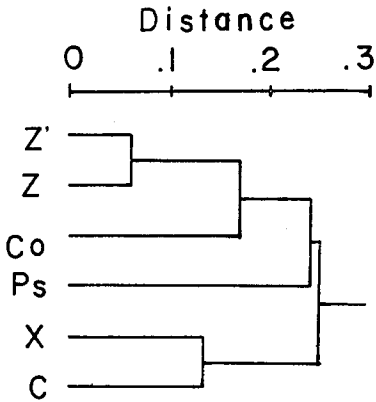


Fig. 2. — A dendrogram constructed from the behavioral distance between species, using the complete linkage algorithm. For details see text. Abbreviations as in Figure 1.

Fig. 2. — Dendrogramme construit à partir de la distance comportementale entre espèces au moyen de l'algorithme de lien complet. Voir le texte pour plus de détails. Les abréviations sont les mêmes que dans la Fig. 1.

Behavioral Distance

Figure 2 shows another dendrogram based on a similarity matrix calculated for all species pairs. The position of each species in a forty-dimensional behavioral space was described by the frequency of each behavioral category in the repertoire. The geometric distance:

$$D_{1,2} = \sqrt{(a_1 - a_2)^2 + (b_1 - b_2)^2 + \dots + (n_1 - n_2)^2}$$

was calculated between each pair of species where a, b, etc. are the frequencies of behavioral categories in the repertoire of each species. As above the dendrogram is based on the complete linkage algorithm.

The results of this analysis are agreement with the results of the previous method of analysis. The two replicates of *Z. varians* are the most similar. Forming a cluster with *Z. varians* is *Colobopsis*. *Pseudomyrmex* forms its own cluster and *Crematogaster* and *Xenomyrmex* form a cluster. This method of looking at the degree of similarity in the social behavior of two species has the disadvantage of placing more emphasis on the more common behavioral categories. A behavioral category which is quite common and present in all species, such as self-grooming may contribute substantially to the total distance between species by virtue of a small relative fluctuation; large relative fluctuations in rare categories contribute little to the distance between species.

DISCUSSION

Whether the test of similarity emphasizes rare behavioral categories (number of behavioral categories in common) or the common behavioral categories (behavioral distance), the pattern of a high degree of similarity between *Z. varians* and *Colobopsis* is the same. Because of the phylogenetic remoteness of the two genera (the phyletic lines to which they belong diverged in the Cretaceous), one can reasonably say that there is convergence in the complete behavioral repertoires of these species.

In a broad and admittedly oversimplified sense, the number of behavioral categories that two species share is more dependent upon phylogeny while the behavioral distance is more related to ecology. Once a behavioral category is present in the repertoire of a species, depending upon its social or ecological needs, the species may vary the amount of energy or time that it devotes to the category and thus the frequency with which it is performed. *Colobopsis* and *Z. varians* have very similar ecological adaptations which no doubt contribute to the reduction in the behavioral distance between the two species.

The degree of similarity between the two replicates of *Z. varians* inspires confidence in the techniques for constructing complete social behavior ethograms. Different colonies were used, at different times, under different culture conditions, in different places and observations were made by different people who came up with essentially the same results.

While the convergence in behavior between the minor worker caste of *Colobopsis* and *Z. varians* is remarkable, the major worker castes do not show this sort of convergence. Morphologically, the major worker caste of *Colobopsis* is not as specialized as *Z. varians*. Major workers of *Colobopsis* are about 1.38 times the length of the minor workers. Major workers of *Z. varians* are about 1.60 times the length of the minors. The mandible of the *Colobopsis* major is not as reduced as in the *Z. varians* major worker. The modification of the head into a plugging device is not as profound in *Colobopsis* as it is in *Z. varians*.

The majors of *Colobopsis* are not as specialized behaviorally as the majors of *Z. varians*. *Z. varians* major workers are lethargic and in the 22.5 hours of observation, I recorded 25 behavioral acts which fell into two categories, self-grooming and regurgitation with the minor worker. Fifteen behavioral categories were recorded from the major workers of *Colobopsis*. When approximately the same number of behavioral acts had been recorded from the minor workers of *Colobopsis* (after about 4 hours of observation) they fell into twenty-five categories. This indicates that the major worker caste is indeed more specialized than the minor worker caste and that the reduction in the size of the behavioral catalogue is not the result of simply observing fewer behavioral acts. The majors of *Colobopsis* participated to some extent in brood care and other activities, but a striking preponderance of their activity involved oral trophallaxis. At times the gaster of major workers of *Colobopsis*, in addition to their role in colony defense, function as a trophic caste or a colony storage organ (WILSON, 1974). One might classify the majors as semi-repletes by analogy with the repletes of *Myrmecocystus*, the honey ants.

WILSON (1968) and OSTER and WILSON (1978) suggest that as a caste becomes more specialized the efficiency of the caste to perform a particular

task increases and the proportion of that caste within the colony will decrease. Because of the extreme specialization of *Z. varians* majors for colony defense and the co-specialization of *Colobopsis* majors on colony defense and as semi-repletes, one would expect a lower ratio of majors to minors in *Z. varians* than in *Colobopsis*. Majors are found at a frequency of about 1 to 10 in *Z. varians* and found in a ratio of about 1 to 3 *Colobopsis*.

The most unusual features of the sociobiology of *Colobopsis* and *Z. varians* are shown in figure 3, with an attempt to account for the cause of both the convergence and divergence in their sociobiology.

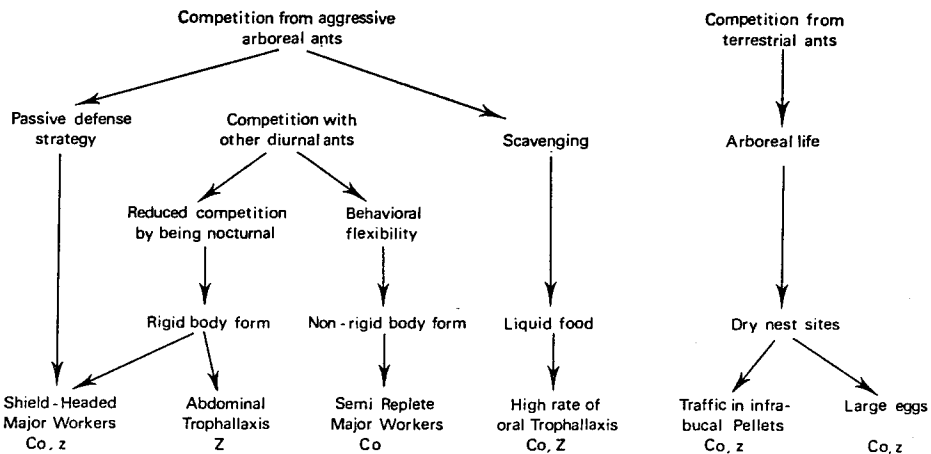


Fig. 3. — The major areas of convergence and divergence in the sociobiology of *Z. varians* and *Colobopsis* with postulated selective causes. Co refers to *Colobopsis* and Z refers to *Z. varians*.

Fig. 3. — Les principaux points de convergence et de divergence dans la sociobiologie de *Z. varians* et *Colobopsis*, avec les causes de sélection possibles. Co = *colobopsis*; Z = *Z. varians*.

The nest sites of these species are quite dry and it is likely that the large size of the eggs and the consumption and traffic in infrabuccal pellets are adaptations for water conservation.

Both species rely heavily on liquid food. Neither species feeds solid food to the larvae other than infrabuccal pellets or trophic eggs. This reliance on liquid food in *Z. varians* is certainly associated with the fact that it is a scavenger. The reduced mandibles are associated with scavenging and the passive defense strategy.

In red mangrove, *Colobopsis* is never the dominant ant species. *Crematogaster ashmeadi* or *Camponotus floridanus* are almost always found in

association with *Colobopsis*. These are very aggressive ants which are more predaceous in their habits. *Colobopsis* is forced by these species into a heavier reliance on scavenging and as a consequence on liquid food. The high rate of oral trophallaxis and the development of a semi-replete major worker caste are probably adaptations to this form of food-gathering.

The passive colony defense strategy exhibited by these species in response to the presence of other, aggressive species, has no doubt led to the development of the plug-headed or shield-headed major worker. This development is more profound in *Z. varians* and probably associated with the fact that the major workers of *Colobopsis* cannot afford to sacrifice their behavioral flexibility by total specialization on colony defense. *Z. varians* does not have the great pressures for behavioral flexibility because it is the only nocturnal mangrove ant in the Florida Keys. WILSON (1976) suggests that the development of the rigid body form is associated with the development of abdominal trophallaxis. The rigid, armored body prevents self-grooming of the abdominal tip, a self-grooming movement seen in virtually all other ants (WILSON, 1962).

ACKNOWLEDGEMENTS. — I gratefully acknowledge the help of a number of people on various drafts of this manuscript. Michael DOUGLAS and Henry HORN were of special help. I would also like to thank Douglas GREEN, Diane WIERNASZ, John SCHNEIDER, Anthony JANETOS, David TONKYN and Edward O. WILSON for helpful comments, suggestion and discussion.

Literature Cited

- DE GHEIT V. J., 1978. — Hierarchical cluster analysis. In: *Quantitative Ethology*, Patrick Colgan, Ed. Wiley-Interscience Publication, John Wiley and Sons, pp. 115-145, New York.
- FAGEN R.M., GOLDMAN R.N., 1977. — Behavioral catalogue analysis methods. *Anim. Behav.*, 25, 261-274.
- OSTER G.F., WILSON E.O., 1978. — Caste and Ecology in the Social Insects. *Princeton University Press*, Princeton NJ, 352.
- SNEATH P.H.A., SOKAL R.R., 1973. — Numerical Taxonomy, the Principles and Practice of Numerical Classification. *W.H. Freeman and Company*, Publ., San Francisco. (ch. 4.)
- WHEELER W.M., BAILEY I.W., 1920. — The feeding habits of pseudomyrmecine and other ants. *Trans. Am. Philos. Soc.*, 22, 235-279.
- WILSON E.O., 1962. — Behavior of *Dacetone armigerum* (Latreille); with a classification of self-grooming movements in ants. *Bull. Mus. Comp. Zool., Harv. Univ.*, 127, 403-422.
- WILSON E.O., 1964. — Ants of the Florida Keys. *Breviora.*, no. 210, 1-14.
- WILSON E.O., 1968. — The ergonomics of caste in the social insects. *Am. Natur.*, 102, 41-66.
- WILSON E.O., 1971. — The Insect Societies. The Belknap Press of *Harvard University Press*, Publ., Cambridge, Mass. pp. 279-281.
- WILSON E.O., 1974. — The soldier of the ant *Camponotus (Colobopsis) fraxinicola* as a trophic caste. *Psyche*, 81, 182-188.
- WILSON E.O., 1976. — A social ethogram of the neotropical arboreal ant, *Zacryptocerus varians* (Fr. Smith). *Anim. Behav.*, 24, 354-363.
- WILSON E.O., FAGEN R.M., 1974. — On the estimation of total behavioral repertoires in ants. *J. N.Y. Entomol. Soc.*, 82, 106-112.