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TAXONOMIC CONGRUENCE AND DISPARITY IN AN INSULAR ANT FAUNA: *RHYTIDOPONERA* IN NEW CALEDONIA

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Abstract.—Patterns of taxonomic congruence were examined in 17 species of *Rhytidoponera* endemic to New Caledonia, using disparate data sets based on allozymes and morphology. These ants belong to four informal "species groups," one of which is monotypic. Both phenetic (UPGMA clustering) and cladistic (minimum-length tree estimation) methods were employed. Adams-2 and strict consensus trees were constructed for all pairs of equivalent rival trees. Since the rival trees were fully resolved or nearly so, the degree of resolution of the consensus trees was used to assess the amount of taxonomic congruence and was measured with the consensus indices of Colless (1980; CI_C) and Rohlf (1982:138; CI_R). In addition, the confidence limits of the minimum-length tree based on the composite (allozymes + morphology) data set were estimated by 20 trial samplings of the data set, using a bootstrap method proposed by Felsenstein (1985).

The rival data sets both produced single phenograms. Several topologically distinct minimum-length trees (cladograms) were found for both data sets. Both phenetic and cladistic methods gave poorly resolved consensus trees ($CI_C = 0.27$, $CI_R = 0.24$ for the strict consensus phenogram; $CI_C = 0.20$ to 0.33, $CI_R = 0.07$ to 0.26, for strict consensus cladograms). In the strict consensus trees, the "species groups" were generally preserved, but species-level relationships were not. The Adams-2 consensus trees were similar but also contained some resolved clusters of species within the largest species group. Bootstrapped confidence limits of the minimum-length tree derived from the composite data set were very broad, indicating that only a few tree partitions (subsets) were statistically significant. These subsets generally corresponded to the "species groups." Based on limited conclusions about relationships among the New Caledonian *Rhytidoponera* (probable monophyly of the three major species groups and of the group as a whole relative to extant congeners in Australia and New Guinea) and on the observation of limited vagility due to the absence of winged queens, I argue that these species represent an archaic element in the ant fauna of New Caledonia, dating back to the early Tertiary. Poor resolution of relationships in the specialized and speciose *pulchella* group may reflect multiple, contemporaneous differentiation of taxa. [Taxonomic congruence; bootstrap; ant phylogeny; *Rhytidoponera*; New Caledonia.]

The concept of taxonomic congruence has come to denote the degree of agreement between different classifications of the same group of organisms (Mickevich, 1978, 1980). When the rival classifications are based on different data sets analyzed by the same taxonomic method, taxonomic congruence provides a measure of the extent to which that method returns similar results in the face of shifting character sets. The character sets may be randomly chosen subsets or nonrandom partitions of the data base. There has been considerable controversy over the relative performance of cladistic and phenetic methods in such tests of taxonomic congruence (Mickevich, 1978, 1980; Rohlf and Sokal, 1980; Schuh and Polhemus, 1980; Schuh and Farris, 1981; Sokal and Rohlf, 1981; Rohlf et al., 1983; Sokal et al., 1984). In the present study, I examine patterns of taxonomic congruence in a group of closely related ponerine ants which have undergone a modest radiation on the island of New Caledonia (Kanaky). In effect, these ants provide the opportunity to test the relative robustness of different taxonomic procedures when applied to a compact but speciose group.

The ant fauna of New Caledonia is notably disharmonic (i.e., taxonomically unbalanced) relative to the presumptive Indo-Australian source fauna (Emery, 1914; Ward, 1984). One of the genera that is disproportionately well represented on the island is *Rhytidoponera*, which accounts for 18 of the 152 ant species (12%), compared with about 100 species out of 3,000 (3%) in Australia (estimates derived from Brown, 1958; Ward, 1984; Ward, unpubl. data). The

genus is represented by a few additional species in Melanesia (Brown, 1958; Wilson, 1958). All of the New Caledonian species of *Rhytidoponera* are endemic to the island, and 17 of the 18 species can be diagnosed by a unique combination of characters (Ward, 1984), which suggests that they are more closely related to themselves than to any extant *Rhytidoponera* in Australia and New Guinea. The remaining species (*R. acanthoponeroides*) is taxonomically isolated and without clear affinities to any other taxa, due to a preponderance of unique (autapomorphous) features.

Using data sets based on morphology and allozymes, I compare the relative amounts of taxonomic congruence shown by rival cladograms and rival phenograms of the New Caledonian *Rhytidoponera*. To further examine the degree of uncertainty associated with estimates of the phylogeny of these ants, an attempt is made to assign confidence limits to the cladogram derived from the composite data set. These confidence limits are calculated using a bootstrap method advocated by Felsenstein (1985). Finally, a few biogeographic implications are presented, constrained by the limited resolution of phylogenetic relationships among the New Caledonian *Rhytidoponera*.

MATERIALS AND METHODS

Taxa and characters.—Of the 18 species of New Caledonian *Rhytidoponera*, one (*R. wilsoni*) has not been collected since its original description. This leaves 17 species, belonging to four, informal "species groups," for which complete morphological and allozyme data sets are available (Table 1). As an outgroup for cladistic analyses, I chose an Australian species, *Rhytidoponera confusa*, which is a member of the primitive *impressa* group (Ward, 1980). Relative to *R. confusa*, all of the New Caledonian *Rhytidoponera*, including *R. acanthoponeroides*, possess a number of apparently derived traits including: (i) a robust, ankylosed mesosoma; (ii) well-separated frontal carinae; and (iii) absence of winged queens. These traits are shared with most Australian species of *Rhytidoponera* (except the *impressa* group). While an Australian species or species group more closely similar to the New Caledonian *Rhytidoponera* might have served as a more appropriate outgroup, the isolated position of *R. acanthoponeroides* and uncertainty over the monophyly of the remaining New Caledonian species (which are diagnosed by a *combination* of characters rather than by a single unique feature) dictated a more conservative course in the choice of an outgroup.

TABLE 1. *Rhytidoponera* of New Caledonia. The "species groups" are informal taxonomic groupings which were recognized prior to detailed cladistic or phenetic studies (Ward, 1984).

Species group	Species
A (*acanthoponeroides* group)	*acanthoponeroides*
F (*fulgens* group)	*aquila*
	atropurpurea
	fulgens
	opaciventris
N (*numeensis* group)	*koumensis*
	numeensis
	wilsoni[a]
P (*pulchella* group)	*arborea*
	depilis
	insularis
	litoralis
	luteipes
	mimica
	nitidiventris
	pulchella
	terrestris
	versicolor

[a] *R. wilsoni* has been excluded from the present study due to lack of sufficient material.

Data set 1 (NC.ALLO) includes 46 binary characters, based on the presence (frequency > 0.05) or absence (frequency ≤ 0.05) of 46 electrophoretically detectable alleles from 11 loci (Appendix I). The justification for treating the allozyme data set in this manner (independent alleles model) is that in the *Rhytidoponera* species from New Caledonia most loci exhibit little or no intrapopulation polymorphism and most alleles are at or near fixation (Ward, 1984). Thus, there is not a great deal to be gained from a consideration of gene frequencies or allelic combinations.

Data set 2 (NC.MORPH) is comprised of 41 binary characters, derived from a num-

ber of binary and multistate morphological characters utilized as diagnostic features in Ward (1984). These include: (i) metric measurements and indices, which were gap-coded using a conservative a posteriori test of mean differences (Scheffé's test, $\alpha = 0.01$); (ii) qualitative morphological characters involving aspects of shape, sculpture, pilosity, and color; and (iii) three binary characters dealing with nest architecture and foraging. NC.MORPH is given in Appendix II, and details of character coding are provided in Appendix III.

Phenetic and cladistic analyses.—For both data sets, coefficients of average taxonomic distance (Sneath and Sokal, 1973) were calculated between all possible pairs of the 17 taxa, and UPGMA cluster analysis (Sneath and Sokal, 1973) was carried out manually to construct the two phenograms (there were no ties). For cladistic evaluations, the two data sets were also analyzed separately. The MIX program on Joseph Felsenstein's PHYLIP package was used to search for the most parsimonious (minimum-length) trees. Twenty-four different input orders of the 18 taxa were used (the same for both data sets). The trees were rooted at the point where *Rhytidoponera confusa* joined the network.

The trees produced by MIX are fully bifurcating. There were often several alternative, equally parsimonious schemes of character-state change for a minimum-length tree of given (fully bifurcating) topology, and in some cases these alternative schemes affected the number of branches lacking character transformations. When this occurred, I chose the arrangement which minimized the number of branches of zero length. In all cases internal branch lengths of zero were eliminated by substituting multifurcations, before any comparisons were made among trees.

I calculated both strict consensus trees (Sokal and Rohlf, 1981) and Adams-2 consensus trees (Adams, 1972) for all pairs of rival trees. The degree of agreement between the rival trees was assessed by measuring the degree of resolution of the consensus tree, using Colless' (1980) consensus fork index (CI_C), and Rohlf's (1982) consensus index, CI_1 (hereafter referred to as CI_R). A variety of other consensus methods and indices has been proposed (e.g., Mickevich, 1978; Margush and McMorris, 1981; Neumann, 1983; Day and McMorris, 1985; Stinebrickner, 1984), and some of the newer formulations are clearly more appropriate as general methods for assessing agreement among trees. However, the consensus trees and indices used here facilitate comparison of the present results with other recent literature on taxonomic congruence and stability (e.g., Rohlf et al., 1983; Sokal, 1983; Sokal et al., 1984). CI_C and CI_R suffer the disadvantage that, when rival trees are not fully bifurcating, these indices confound congruence among the trees with information content (Sokal et al., 1984). In the present study the rival phenograms were fully bifurcating and the rival cladograms were fully resolved or nearly so (0 to 3 multifurcations, mean 1.2; none more than a trifurcation) so this effect should not obscure the general patterns of congruence.

Assigning cladogram confidence limits.—NC.MORPH and NC.ALLO were combined into a single composite data set with 87 characters (NC.COMP), and a search was made for the minimum-length tree using the MIX program on PHYLIP. The confidence limits of this tree were estimated with a nonparametric method, the "bootstrap" (Efron, 1979), using an approach outlined by Felsenstein (1985): the characters were randomly sampled, *with replacement*, to obtain 87 characters and a minimum-length tree was sought on the basis of this character set. The "Weights" option on MIX was used to weight each character by the number of times it was sampled. The minimum-length tree was the shortest tree (or a random selection of one of several shortest trees) obtained with 24 different input orders of the 18 taxa. This character sampling and tree construction was repeated for 20 trials, and those tree partitions (subsets) which appeared in at least 19 out of 20 trees (95%) were considered significant at the 5% level.

The tree comprised solely of these significant subsets can be considered to represent the 95% confidence limits of the *estimate* of the phylogeny.

W. A. E. Day (pers. comm.) has suggested that one way to avoid random selection of a tree when several shortest trees appear in a trial, would be to score each subset according to the number of minimum-length trees in which it appears in the trial. Thus if a given subset appears in three of five shortest trees in a trial, it would be scored as appearing 0.6 times in that trial. Although this procedure was not used in the present study (because I could not be certain that all the shortest trees had been found with 24 different input orders), it would be a useful improvement in future applications of this method.

RESULTS

NC.MORPH and NC.ALLO generated phenograms which were similar in overall structure and which preserved the informal species-groups (Fig. 1). At the same time, clusterings *within* the two largest species groups were quite disparate, with the result that the strict consensus tree (Fig. 1C) is rather poorly resolved ($CI_C = 0.27$, $CI_R = 0.24$), although no less than consensus trees reported for other taxa and data sets (e.g., Rohlf et al., 1983:table 3). The Adams-2 consensus tree has substantially higher consensus indices ($CI_C = 0.67$, $CI_R = 0.51$), primarily as a result of increased resolution within the *pulchella* group (Fig. 1D).

Both data sets generated several equally parsimonious minimum-length trees. Two minimum-length trees (length 61) were obtained with NC.MORPH, and four minimum-length trees (length 89) with NC.ALLO (Fig. 2). (James Archie kindly ran the two data sets on David Swofford's PAUP program; several additional but no shorter minimum-length trees were found.) The differences between some of the alternative trees are not trivial (compare Fig. 2C and F). In most of the trees the informal species groups form discrete subsets. For all of the above resolutions, trees containing internal branch lengths

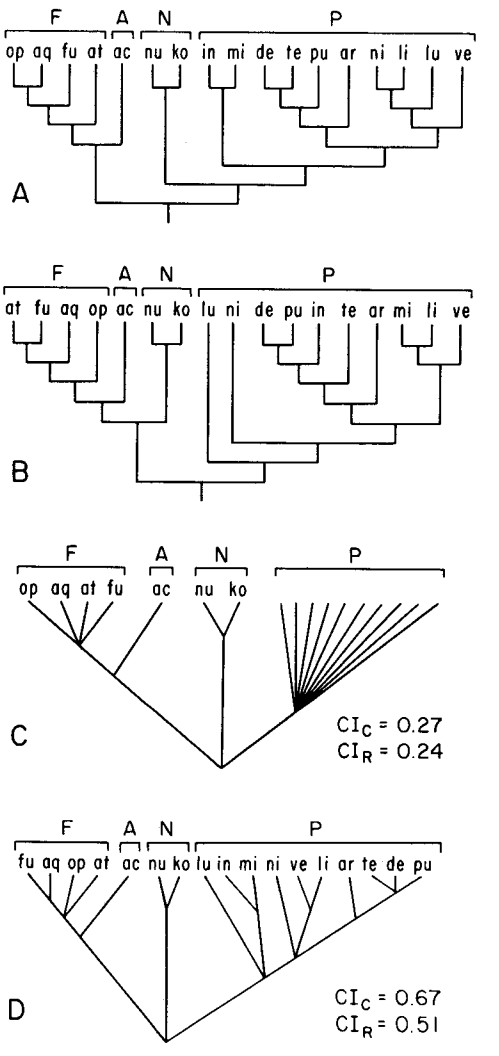

FIG. 1. UPGMA phenograms generated by (A) NC.MORPH and (B) NC.ALLO, as well as (C) strict consensus tree and (D) Adams-2 consensus tree of the two. Species are indicated by the first two letters of the specific epithet.

of zero were not included. If such trees are permitted the number of equally parsimonious trees is much larger; for example the two NC.MORPH trees can be decomposed into 36 fully bifurcating trees, all of length 61.

Strict consensus trees were calculated for all eight possible pairs of the rival cladograms; four different consensus trees were found (Fig. 3), each occurring twice. The

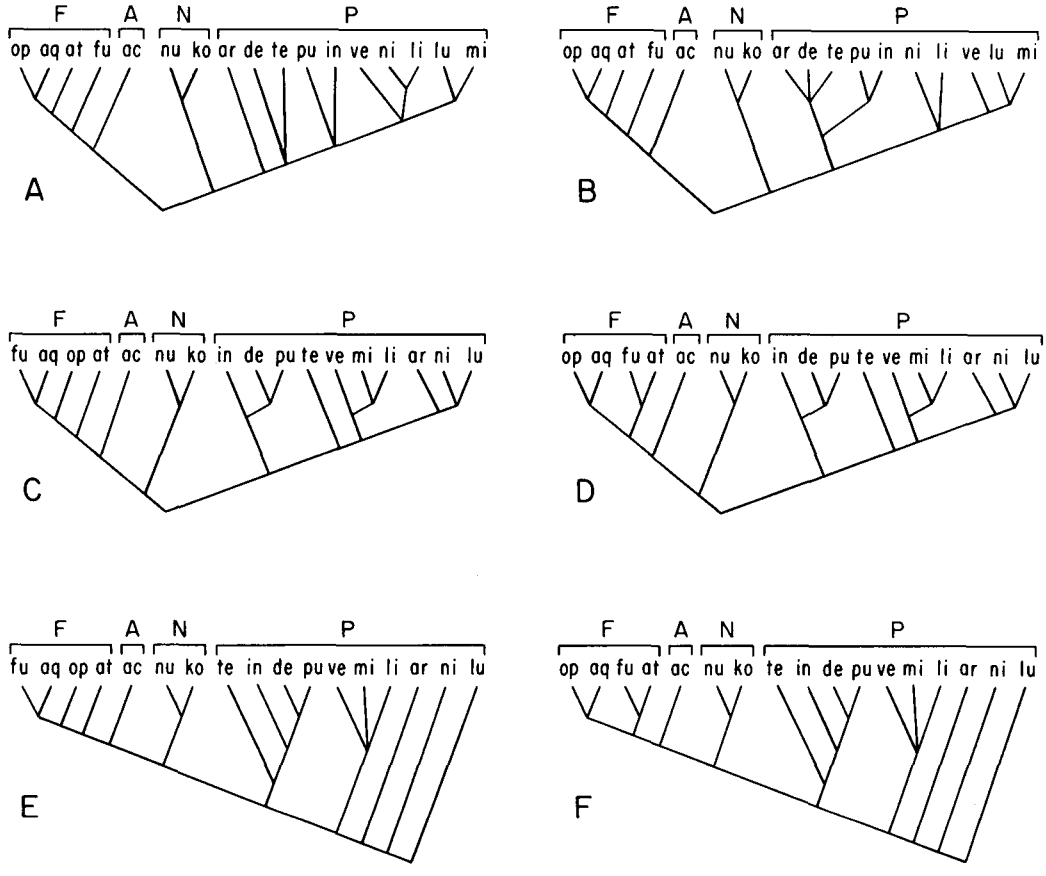

FIG. 2. (A and B) Equally parsimonious minimum-length trees obtained with the NC.MORPH data set and (C, D, E, and F) the NC.ALLO data set. All internal branches shown here are of nonzero length.

consensus trees are rather poorly resolved; as with the consensus phenogram, there is no resolution of species relationships within the *pulchella* group or (in half of the cases) the *fulgens* group. Half of the strict consensus trees do not even support monophyly of the *pulchella* group.

The consensus index values for these trees (CI_C = 0.20 to 0.33; CI_R = 0.07 to 0.26) encompass the single values obtained with the consensus phenogram, and they fall within the range of CI_C and CI_R values reported by Rohlf et al. (1983:154) for 12 pairs of data sets. The Adams-2 consensus trees between rival cladograms also show about the same level of resolution as the equivalent consensus tree between rival phenograms (CI_C = 0.60, CI_R = 0.47 to 0.62; Fig. 4). The present results provide no indication that cladistic classifications of the New Caledonian *Rhytidoponera* are more stable than phenetic classifications.

Since Adams-2 consensus trees depict both congruent subsets and *intersections* of subsets among rival trees (Adams, 1972), it is not surprising to find in the present instance that they are more fully resolved than the strict consensus trees (which contain only congruent subsets). The increased resolution may be partly illusory, at least from the point of view of recovering monophyletic groups. The additional information depicted in Adams-2 consensus trees is often in the form of sets not present in either of the rival trees (Rohlf, 1982). This is illustrated in Figure 4C and

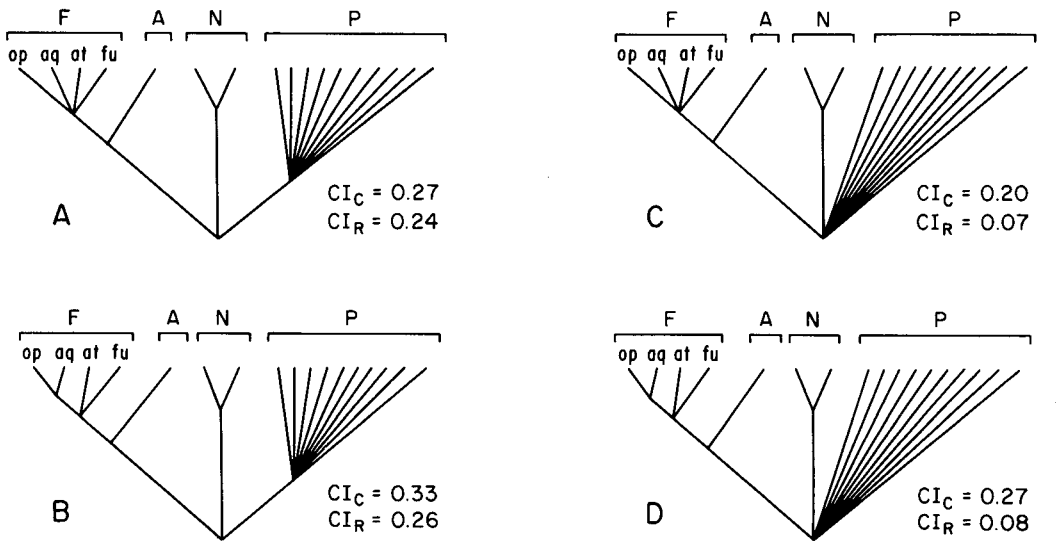

FIG. 3. Strict consensus trees obtained from the eight possible pairwise combinations of the most parsimonious NC.MORPH and NC.ALLO cladograms. Each of the consensus trees occurred twice. Tree C also represents the strict consensus tree of the entire set of six minimum-length trees.

D, where members of the *numeensis* species group (N) are placed within a subset of species from the *pulchella* group.

From the composite data set (NC.COMP), six different minimum-length trees were obtained (length 158). All of these trees were fully bifurcating (i.e., without branch lengths of zero). Two of the trees are illustrated in Figure 5; the other four were variations on these two, involving only minor rearrangements of two *fulgens* group taxa (*R. fulgens* and *R. atropurpurea*).

Twenty bootstrap trial estimations of the minimum-length tree for NC.COMP produced a variety of trees, and only a few

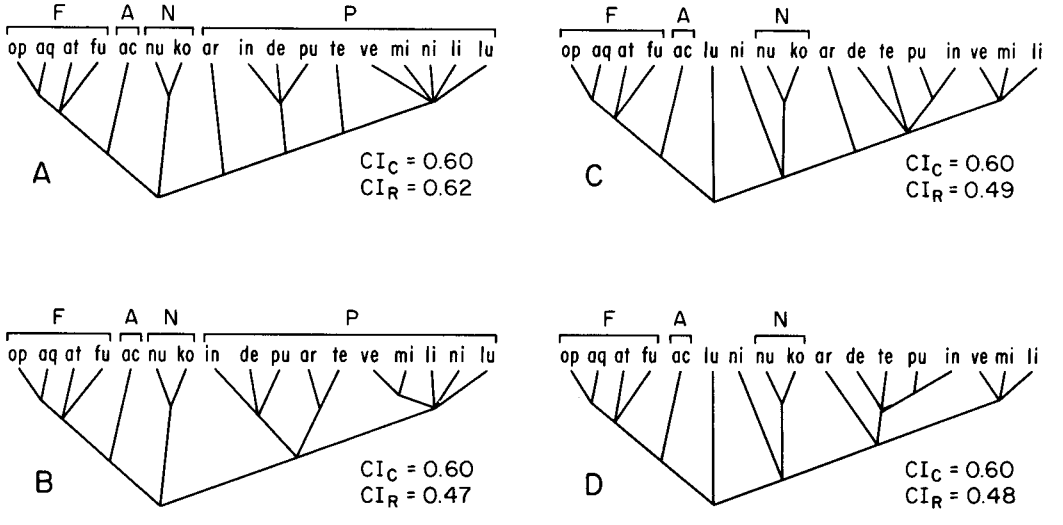

FIG. 4. Adams-2 consensus trees obtained from the eight possible pairwise combinations of the most parsimonious NC.MORPH and NC.ALLO cladograms. Each of the consensus trees occurred twice.

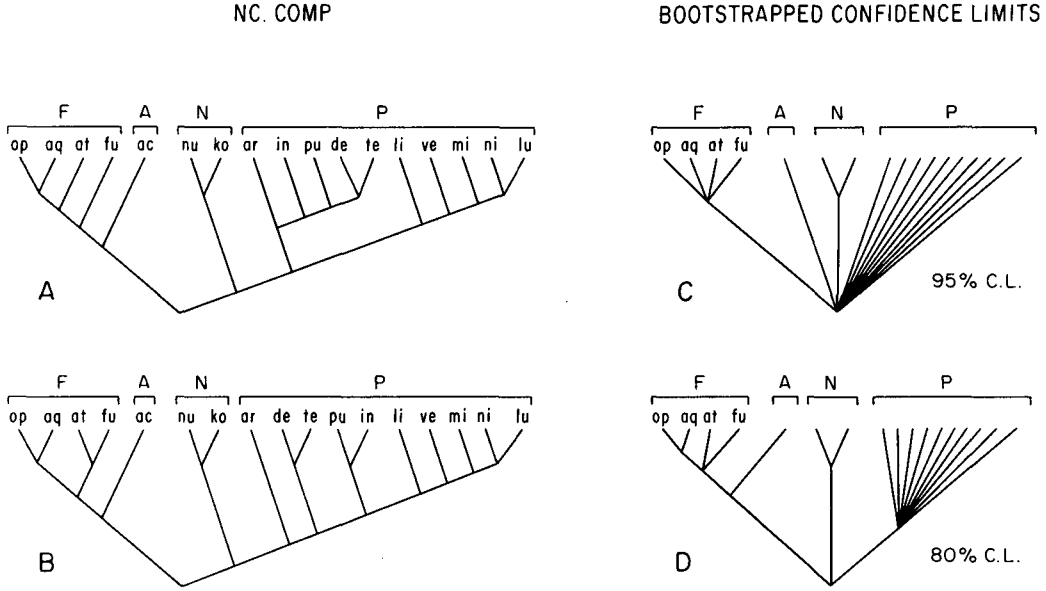

FIG. 5. (A and B) Two (of six) minimum-length trees obtained with NC.COMP; (C and D) bootstrapped confidence limits of the NC.COMP tree(s). See text for details.

subsets appeared consistently (Table 2). The five most common subsets (F, N, F + A, *op* + *aq*, and P) were separated by a large gap in frequency from the next most common subset (N + P, occurring in only half the replications). The majority of the remaining subsets occurred only once or twice. The frequency distribution of the subset frequencies was strongly bimodal—in fact, *J*-shaped—suggesting a few significant tree partitions, surrounded by a wealth of noise.

The tree partitions (subsets) appearing in 95% and 80% of the bootstrap replications are shown in Figure 5C and D, respectively. The estimated 95% confidence limits are disconcertingly broad, but also arguably conservative insofar as the bootstrap sampling treated all characters equally, even though some may be more "reliable" than others.

TABLE 2. Most frequent subsets in 20 bootstrap replications of the estimated minimum-length tree for NC.COMP.[a]

Subset	Frequency (out of 20)
F (*fulgens* group)	20
N (*numeensis* group)	20
F + A (F + *acanthoponeroides*)	18
op + *aq* (*opaciventris* + *aquila*)	17
P (*pulchella* group)	16
N + P	10
op + *aq* + *fu*	9
lu + *mi* + *ve* + *li*	8

[a] Species are referred to by the first two letters of the specific epithet.

The strict consensus trees obtained from the rival cladograms based on the separate data sets are only slightly more resolved than the 95% confidence limits of the NC.COMP tree. In fact, the most fully resolved strict consensus tree (Fig. 3B) is identical to the tree which represents the bootstrapped 80% confidence limits. Thus, to a rough approximation, the strict consensus trees obtained from rival cladograms based on disparate data sets correspond to the tree in which the combined data set allows us to have statistical confidence. Certainly, the latter is better represented by the strict consensus trees than by the Adams-2 consensus trees.

DISCUSSION

This study of taxonomic congruence, based on character sets extracted from an island-radiating ant fauna, provides fur-

ther evidence of the limited stability of both phenetic and cladistic classifications, at least when applied to speciose groups. The general stability of the higher-level "species groups" relative to clusters of more closely related congeners is striking and consistent. While neither taxonomic procedure proved superior to the other with respect to taxonomic stability, cladistic analysis provides heuristic insight not apparent with phenetic analysis (e.g., it points to the possibility that the *pulchella* group is paraphyletic) and it serves to focus attention on phylogenetic relationships and character-state change.

The limited resolution of phylogenetic relationships among these ants could be attributed to a high level of homoplasy in the data sets. However, the consistency levels (sensu Farris, 1969; the number of characters divided by the number of steps in the minimum-length tree) are not atypical for empirical real world data sets (0.672, 0.517, and 0.551 for NC.MORPH, NC.ALLO, and NC.COMP, respectively). The results from the assessment of taxonomic congruence and the bootstrapping of confidence limits simply demonstrate that there is greater uncertainty associated with the cladograms derived from such data sets than is generally acknowledged.

Alternative coding schemes for the morphological and allozyme data sets might improve the degree of congruence among rival trees or reduce the confidence limits, but the effects are not likely to be major. If the New Caledonian *Rhytidoponera* have been isolated on the island for a long period of time (see below), it could be argued that any electromorph similarity between the Australian outgroup species (*R. confusa*) and the New Caledonian species is due to convergence. This would render invalid the use of the outgroup to root the tree. However, rerooting the NC.ALLO cladograms so as to *maximize* the degree of agreement with the NC.MORPH trees (by placing the root along the branch between the *numeensis* group and *R. acanthoponeroides*) produces strict consensus trees which are still rather poorly resolved (CI_C = 0.33 to 0.40; CI_R = 0.42 to 0.43).

The present results allow some conclusions to be drawn about relationships among the New Caledonian *Rhytidoponera*. There is good support for a monophyletic origin of the *fulgens* group and of the *numeensis* group, and a strong indication that the enigmatic *R. acanthoponeroides* is closely related to the *fulgens* group. The status of the *pulchella* group is less clear—it appears as a subset in only 80% of the bootstrap replications and in only half the strict consensus trees between rival cladograms. On the other hand, the *pulchella* group is one of five subsets that occurred rather consistently during the bootstrap sampling and that were separated by a large gap in frequency from all remaining subsets. Moreover, the members of the *pulchella* group display a striking syndrome of foliage-foraging habits and (in most species) specialized nest architecture, unique to the genus (Ward, 1984). Thus, there is at least tentative evidence to support monophyly of the three major species groups.

If *R. acanthoponeroides* is indeed the sister-group of the *fulgens* group, this suggests that the *Rhytidoponera* radiation on New Caledonia may be traceable to a single founder. It seems unlikely that more than three founders were involved if the monophyly of the *pulchella* group is accepted. No *extant* species of *Rhytidoponera* from Australia or New Guinea possesses morphological features which would place it in any of the New Caledonian species groups, although the similarity of the relictual Australian species, *R. anceps*, to the *pulchella* group has been noted (Ward, 1984).

Like most members of the genus, the species of *Rhytidoponera* in New Caledonia lack winged queens and thus have limited dispersal capabilities. Hence, it seems reasonable to argue that the founder(s) would have to have been present on New Caledonia since at least the early Tertiary, at the time or not long after the island was separated from Australia (Holloway, 1979; Shields, 1979). Migration across an expanded Tasman Sea later in the mid-Tertiary seems less likely, even with the assistance of a lower sea level and greater

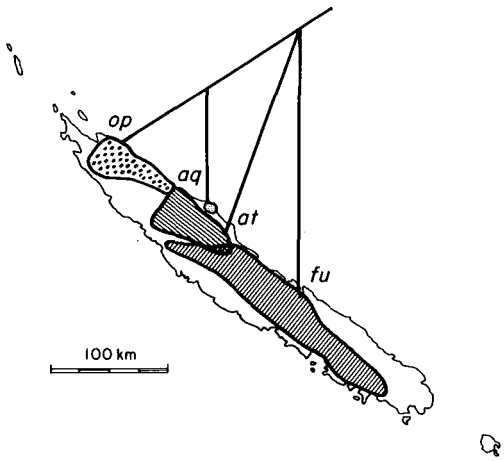

FIG. 6. Cladogram (inverted) of the *fulgens* group, imposed on the known geographical distribution of the species in New Caledonia.

exposure of the Chesterfield Reefs. Only 1 of the 18 species of *Rhytidoponera* in New Caledonia has reached the adjacent Loyalty Islands, another strong indication of limited vagility. Moreover, the New Caledonian *Rhytidoponera* are notably habitat-limited, being more or less confined to mesic forest environments (Ward, 1984).

The same arguments can be applied to other New Caledonian ants which belong to Indo-Australian genera (or species groups within genera) with wingless queens. These include the dolichoderine genus *Leptomyrmex*, and the ponerine genera *Leptogenys, Prionogenys, Cerapachys,* and *Sphinctomyrmex* (Emery, 1914; Wheeler, 1934; Wilson, 1957). These primitively apterous species impart an archaic, continental flavor to the ant fauna of New Caledonia. They can be constrasted with the more phylogenetically advanced myrmicine ants among which there is a conspicuous amount of *secondary* winglessness on New Caledonia (Wilson, 1971), presumably due to insular selection pressures against dispersal. Some of these myrmicines may represent more recent (mid-Tertiary) arrivals on the island. A parallel distinction has been made by botanists between ancient and more recent elements in the flora (e.g., Thorne, 1965).

The present study provides limited resolution of species-level relationships in the New Caledonian *Rhytidoponera*. If we accept a sister group relationship between *R. opaciventris* and *R. aquila*, then the partially resolved cladogram of the *fulgens* group can be mapped onto the known geographical distribution of the species. The result (Fig. 6) indicates that the history of this group is one of allopatric differentiation, limited dispersal, and marginal (if any) secondary sympatry. Ward (1984) suggested the same vicariance pattern for several *pulchella* group species, but the lack of confident resolution of species relationships within this group precludes confirmation of this pattern in the present study.

Finally, the radiation of the *pulchella* group into a foliage-gleaning niche unoccupied by congeners may have been relatively rapid, or at least involved multiple, contemporaneous differentiation of taxa. In this case, the evolutionary history of this group would be better represented by a multifurcating bush than by a "fully resolved" bifurcating tree.

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APPENDIX I

NC.ALLO Data Matrix[a]

Rhytidoponera species	Characters									
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46
acanthoponeroides	00000	00001	01000	00000	00101	00110	00100	00110	01010	0
atropurpurea	00000	00110	01000	00000	00101	00101	00010	01001	01000	1
fulgens	00000	10100	01100	00000	00101	00111	00010	01001	01000	1
aquila	00010	10100	11100	00000	00100	10110	00010	01001	01000	1
opaciventris	00111	10100	01000	00000	00101	00110	00011	01001	01000	1
numeensis	00001	00101	00000	10000	00100	10110	01000	10001	00100	1
koumensis	00000	00100	00000	01000	00100	11010	01000	10001	00100	1
depilis	01000	00000	01000	00000	10010	00110	10000	10000	10101	0
terrestris	01000	00000	00100	00100	00010	00110	10000	10001	10101	0
arborea	00010	00000	00100	00010	00010	00110	10000	10010	00101	0
nitidiventris	00011	00000	01000	00000	01010	01010	10000	10010	00101	0
luteipes	00111	11000	00100	00110	10010	01010	01000	10011	00101	0
pulchella	00010	00000	01000	00000	10010	00110	10000	10000	10101	0
insularis	10000	00000	01000	00010	00010	00110	10000	10000	10101	0
mimica	00110	00000	00010	00000	01010	00110	10000	10001	00101	0
litoralis	00100	00000	00001	00000	01010	00110	10000	10001	00101	0
versicolor	01110	00000	00100	00001	01010	00110	10000	10001	00101	0
confusa	00010	00000	00000	00100	10000	10010	01000	10000	10100	0

[a] Characters 1-46 represent alleles at the following loci: AMY (1-10), AO-2 (11-17), EST (18-23), SOD-1 (24-26), MDH (27-28), ME (29-30), PGM (31-35), LAP (36-38), GOT (39-41), IDH (42-43), LDH (44-46). Additional details on specific loci and designated alleles can be found in Ward (1984).

APPENDIX II

NC.MORPH Data Matrix

Rhytidoponera species	Characters								
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41
acanthoponeroides	11110	11001	00111	00011	00100	11101	00111	11000	1
atropurpurea	11111	10111	01100	11100	00000	00001	00100	11000	1
fulgens	11110	10111	00100	11100	00000	01101	00101	11000	1
aquila	11110	10111	01100	11100	00011	00101	00101	11000	1
opaciventris	11110	10111	01100	11100	00010	00101	00101	11000	1
numeensis	10000	00011	10010	00000	11010	00101	00100	11000	1
koumensis	10010	10011	10010	00000	01010	00101	00100	11000	1
depilis	10000	10011	00011	00000	00000	00100	11100	11011	1
terrestris	10000	10011	00011	00000	00000	00100	00100	11011	1
arborea	10010	10011	00011	00000	00000	00100	00100	11010	0
nitidiventris	10000	00011	00011	00000	00000	01101	01100	11011	1
luteipes	00000	00011	00011	00000	00000	01101	00100	11111	1
pulchella	00000	00011	00011	00000	00000	00100	00100	11011	1
insularis	00000	00011	00011	00000	00000	00100	01100	01010	1
mimica	00000	00011	00011	00000	00000	01101	01100	00110	1
litoralis	10000	00011	00011	00000	00000	01101	00100	11011	1
versicolor	00000	00011	00011	00000	00000	11111	00100	11011	1
confusa	10100	00100	00111	00000	00000	00101	00001	11000	1

APPENDIX III

Coding and Description of Morphological Characters

In the account given below, the following abbreviations are used for measurements, indices, and meristic counts: CI, cephalic index; ED, eye diameter; FCC, index of frontal carinal convergence; FCD, frontal carinal distance; FCI, frontal carinal index; FLI, funicular length index; FSC, fore femur setal count; HTI2, hindtibial index, using HW; HW, head width; LPI, lateral petiolar index; ML, mandible length; OLD, index of occipital lobe distance; PI, pronotal index; PNL, petiolar node length; SI, scape index; SLI (=SPL/PH), index of subpetiolar process length; SPI, index of subpetiolar process width; SSC, scape setal count. These terms are fully explained in Ward (1984).

NC.MORPH characters **1-15** are based on gap-coded mean differences of the following metric characters (number of gaps given in parentheses): HW (2), ML (1), FCD (2), PNL (1), CI (1), SI (1), FCI (1), PI (2), LPI (1), FLI (1), SLI (2). The gap-coding procedure was as follows: I used an a posteriori contrast test—Scheffé's test, as implemented on the SPSS package (Hull and Nie, 1981)—with an experimentwise alpha of 0.01. This test revealed homogeneous subsets of means based on comparisons among all possible linear combinations of the 18 species' means. I then assigned integral stepwise values (0, 1, 2, etc.) to completely *non-overlapping* subsets of means or sets of subsets. Finally, these values were recorded into additive binary code, as required by the MIX program. This conservative coding method resulted in the loss of some information; several measurements and indices were discarded because there were no discrete gaps between subsets of means. However, my intention was to code these morphometric characters in a manner which made them comparable to the remaining morphological characters. The latter encompass aspects of shape, sculpture, pilosity, and color, which were assessed qualitatively, and which tend to be non-overlapping and taxonomically diagnostic. These qualitative characters are described below (with quantitative bounds given where feasible). Multistate characters were converted into additive binary code using the linear transformation series indicated here.

16. Frontal carinae (1) anterolaterally expanded and strongly converging posteriorly (FCC 0.70–0.80), (0) parallel or weakly converging posteriorly (FCC 0.80–0.95). **17.** Inter-occipital lobe distance (1) about half the head width (OLD 0.52–0.58), (0) more than 0.6 times the head width (Old ≥ 0.60). **18.** Hind tibia (1) relatively long (HTI2 1.11–1.23), (0) relatively short (HTI2 0.85–1.10). **19.** In lateral view, occipital lobe (1) conspicuously produced, broader than ED, (0) at most moderately produced, less broad than ED. **20.** Petiolar node (1) with posterodorsal point, (0) without posterodorsal point. **21.** In lateral view, posterior margin of subpetiolar process (1) convex or angled outward, (0) concave or angled inward. **22.** Subpetiolar process consisting of (1) broad triangular or subrectangular keel, without spiniform point (SPI 0.44–1.23), (0) spiniform point (SPI 0.10–0.31) or very short and poorly developed. **23.** Dorsum of head (1) longitudinally carinate, (0) longitudinally rugostriate to rugose. **24.** Pronotal rugae (1) partially overlaid with fine, punctulate sculpture, (0) not overlaid with fine punctulae. **25.** Pronotum (1) densely and irregularly striate, rugae weak, (0) not densely and irregularly striate. **26-28.** Fourth abdominal tergite (111) shining, smooth, estriate, (011) shining, weakly striate to striolate, (001) opaque to subopaque, densely striate or striolate-imbricate, (000) opaque (matte), densely shagreened. **29, 30.** Appressed hairs on fourth abdominal tergite (11) lacking, (01) sparse to moderately common, separated by their lengths or more, (00) forming a dense pubescent mat. **31-33.** Erect setae (111) lacking on most of body dorsum, scapes, and femora (SSC 0, FSC 0), (011) present on body dorsum, but lacking on upper surfaces of scapes and femora (SSC 0–2, FSC 0), (001) present on body dorsum and on upper surfaces of scapes and femora (SSC 2–24, FSC 0–19), (000) abundant on body dorsum and appendages (SSC 20–34, FSC 17–26). **34.** Erect pilosity (1) consisting of long, thin flexuous setae, (0) consisting of short, thicker, nonflexuous setae. **35-37.** Body (111) unicolored, dark brown to black, with conspicuous greenish or violaceous iridescence, (011) unicolored, brown to black, without conspicuous greenish or violaceous iridescence, (001) bicolored, gaster constrastingly lighter than head and mesosoma, (000) bicolored, gaster and head contrastingly lighter than mesosoma. **38.** Body appendages (legs, mandibles, antennae) (1) ferrugineous brown to dark brown, usually not strongly contrasting with mesosoma, (0) pale luteous, strongly contrasting with dark mesosoma. **39.** Workers foraging predominantly (1) on low vegetation, (0) on the ground. **40, 41.** Nest located (11) in soil, with clay turret entrance, (01) in soil or logs, without turret, (00) arboreally.