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Cladistic Phylogeny of the North American Species Complexes of *Pogonomyrmex* (Hymenoptera: Formicidae)

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ABSTRACT Four species complexes have been recognized for >20 yr; one is monotypic, and the compositions of the others have changed because of new descriptions and synonymy. An early prediction concerning the proper placement of one species is confirmed, and with this proviso, the three modified complexes are shown to be monophyletic. Two undescribed species are placed, resolutions of problematic relationships are offered, a new species complex is defined, range extensions are recorded, and a scanning electron micrographic study of North American *Pogonomyrmex* is concluded.

KEY WORDS Insecta, *Pogonomyrmex*, harvester ants, cladistics

THE NEW WORLD harvester ant genus *Pogonomyrmex* is represented by approximately 60 taxa; about half of these are North American (personal estimate). Most are large, reddish insects, famous in southern and southwestern United States for their conspicuous gravel mounds and disks as well as for their potent stings. Gustav Mayr described the genus in 1868, and W. M. Wheeler subsequently divided it into three subgenera: *Pogonomyrmex* and *Ephebomyrmex* (Wheeler 1902), and *Forelomyrmex* (Wheeler 1913). Herein, I follow recent precedents that accord each of these full generic status (Kempf 1972, Snelling 1981a, MacKay & MacKay 1984, Wheeler & Wheeler 1985). *Pogonomyrmex*, in this restricted sense, is the object of the current study. The subgeneric questions should be resolved by a study of the South American taxa, which I am currently undertaking.

Exactly 100 yr after *Pogonomyrmex* was described, the 20 North American species were revised by Cole (1968), but one of these has since been synonymized (Shattuck 1987), four new species have been described (MacKay 1980, Francke & Merickel 1981, Snelling 1981b), and two more will be added to the list (R. Snelling, personal communication). The four species complexes of Cole as currently recognized are (1) the *barbatus* complex, currently containing 11 species: *Pogonomyrmex rugosus* Emery, *P. barbatus* (F. Smith), *P. bigbendensis* Francke & Merickel (Fig. 1 and 2), *P. texanus* Francke & Merickel (Fig. 3 and 4), *P. desertorum* Wheeler, *P. wheeleri* Olsen (Fig. 5 and 6), *P. bicolor* Cole (Fig. 7 and 8), *P. tenuispina* Forel (Fig. 9 and 10), *P. apache* Wheeler, *P. anergismus* Cole, and *P. colei* Snelling; (2) the *occidentalis* complex, with seven species: *P. occidentalis* (Cresson), *P. brevispinosus* Cole, *P. salinus* Olsen (Fig. 11 and 12), *P. subdentatus* Mayr (Fig. 13 and 14), *P. subnitidus* Emery, *P. montanus* MacKay, and *P. anzensis* Cole (Fig. 15 and 16); (3) the *maricopa* complex, with four species: *P. comanche* Wheeler, *P. californicus* (Buckley), *P. maricopa* Wheeler, and *P. magnacanthus* Cole; and (4) the *badius* complex, with the single species *P. badius* (Latreille).

Creighton (1950) observed "good agreement" regarding the status of *Pogonomyrmex* and its subgenera, although he acknowledged taxonomic problems at the specific and infraspecific levels. Cole's (1968) revision solved many of these problems but made no serious attempt to establish relationships among the 20 species or among the four species complexes. My study offers a solution to these problems and answers questions raised by the revisionary work. Surprisingly, there has never been an attempt to reconstruct the evolutionary history of this familiar genus. I present herein such a phylogeny for the North American *Pogonomyrmex* harvester ants.

Materials and Methods

It is preferable to deal with monophyletic taxa when reconstructing a phylogeny, and the North American species are treated here as such for the following reasons: (1) no *Pogonomyrmex* sensu stricto occur in Central America, hence the North and South American taxa are greatly isolated; (2) the two continents have no species in common; (3) the North American taxa have undergone extensive character analysis, whereas comprehensive studies of the South American ants are lacking; and (4) my current study of the South American species indicates that many of these taxa are quite different from their North American congeners. Specifically, they tend to have more primitive character states. A future study will test this hypothesis.

The phylogeny was reconstructed using cladistic methods. The data were analyzed with two software packages (Swofford 1985, Farris 1988), and

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the results were compared. Both packages use parsimony criteria to identify trees of minimal length, although the programs often produce different results. Morphological characters were chosen from those in the revision (Cole 1968), but characters with excessive intraspecific variation or contradiction in either text or illustration, and those that were not readily scored by discrete character states, were excluded unless an examination of relevant specimens resolved the issue. The states within this reduced character set also were confirmed by direct examination. Specimens were obtained from the author's collection, the Natural History Museum of Los Angeles County, Calif., and the American Museum of Natural History, New York. With five exceptions, characters were obtained exclusively from the worker caste (in cases where such a caste exists). This was done for several reasons: reproductive castes are not well represented in museums, reproductives of several species are unknown, and genitalic characters were not found useful for species diagnosis in the generic revision (Cole 1968). An absence of reproductive forms must be expected in formicine systematics, as pointed out by Kempf (1951) in his revision of the tribe Cephalotini and by Shattuck (1987) in an analysis of character variation among *Pogonomyrmex*. Two North American taxa, *Pogonomyrmex anergismus* and *P. colei*, have no worker caste; these were placed within the appropriate species group after the construction of the initial tree. Characters taken from the reproductive castes were used to place these workerless social parasites.

Phylogenies were reconstructed using shared, derived characters, where character states found in the outgroup are primitive by definition. *Ephebomyrmex* is the closest relative of *Pogonomyrmex*, and *E. imberbiculus* Wheeler was chosen as the outgroup for character state polarization because it is a common and well-characterized species. The oldest known *Pogonomyrmex* is *P. fossilis* Carpenter from the Florissant shale (Oligocene) (Carpenter 1930), and the visible character states are those of the present outgroup.

Descriptions of the character states used in Table 1 are as follows: 1. Head width: narrow (0); broad (1). 2. Eye: anterior to center of head (0); at center of head or behind, rather convex (1); at center of head or behind, not convex (2). 3. Circumocular whorls: absent (0); occasional or weak (1); always present (2). 4. Cephalic rugae (density): low (0); not low (1). 5. Cephalic rugae (straightness): divergent (0); straight or only slightly divergent (1). 6. Cephalic areolation (ordered in decreasing density): (0); (1); (2); (3). 7. Frontal depression (walls): steep (0); not steep (1). 8. Clypeal projection: strong (0); moderate (1); weak (2). 9. Cephalic rugae (posterior corners): present (0); absent (1). 10. Mandibular teeth (no.): <7 (0); ≥ 7 (1). 11. Mandible (contour of basal margin): not (roughly) straight (0); roughly straight (1). 12. Mandible (length of teeth): no. 4 $<$ no. 3 (0); no. 4 $\geq$ no. 3 (1). 13. Antenna (basal trough): absent (0); weak to moderate (1); deep (2). 14. Antenna (lip): not bipartite (0); bipartite (1). 15. Propodeum (gradient of basal face): steep (0); not steep (1). 16. Petiolar node (rugae, ordered in decreasing density): (0); (1); (2). 17. Petiolar node (areolation, ordered in decreasing density): (0); (1); (2). 18. Petiolar peduncle (ventral hairs): absent (0); present (1). 19. Petiolar peduncle (ventral process): present, well developed (0); variable (1); absent or very weak (2). 20. Petiolar node (nipple): absent (0); often present (1). 21. Postpetiole (rugae, ordered in decreasing density): (0); (1); (2). 22. Postpetiole (areolation, ordered in decreasing density): (0); (1). 23. Postpetiole (ventral process): strong (0); not strong (1). 24. Postpetiole: robust (0); not robust (1). 25. Sculpture: head and thorax typically coarse (0); head and thorax not typically coarse (1). 26. Antenna (scape base; development): weak (0); moderate (1); strong (2). 27. Antenna (lip of scape base): weak (0); not weak (1). 28. Mandible (contour of basal margin in male): not concave (0); concave (1). 29. Mandible (no. teeth in male): <4–5 (0); 4–5 (1); >4–5 (2). 30. Male coloration: blackish (0); not blackish (1). 31. Propodeal spines: usually present (0); usually absent (1). 32. Nest material (superstructure): not gravel (0); gravel (1). 33. Habitat: no preference for piney habitats (0); preference for piney habitats (1).

Primitive states are 0 except in characters 17, 21, 22, and 29, where the outgroup states (primitive by definition) are either intermediate in development (17, 21, 29) or are coded for consistency with similar characters (22). In characters 17, 21, and 29, the primitive state within the transformation series is coded as 1 for proper recognition in an ordered analysis. As expected, characters often exhibit intraspecific variability; in these instances, I have scored the prevailing character state. Three characters (6, 24, 31) vary widely within a few species, and these states were represented by a "?". Question marks in columns 28–30 of the character matrix indicate missing data because males are undescribed (unknown). Similarly, nest data (character 32) are unavailable for three species. Many of these characters are illustrated in a two-part scanning electron micrographic study. Fourteen of the described species with worker castes have been illustrated (Taber et al. 1987), and the remaining eight are illustrated here (Fig. 1–16). A worker of the unusual monotypic South American subgenus *Forelomyrmex* also is shown (Fig. 17 and 18). The male and ergatoid queen of *P. (Forelomyrmex) mayri* Forel are illustrated elsewhere (Kugler 1978). Four North American *Pogonomyrmex* were not photographed because material (the two social parasites and the two undescribed species) was limited.

All 33 characters were ordered and analyzed by HENNIG86 (Farris 1988) using the "mhennig*" and "bb" options. Options that guarantee the identification of minimal-length trees were unable to recover these within a reasonable time period (less than 1 wk on an IBM XT). The results were checked

TABLE 1. Pogonomyrmex character matrix

character taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
E. imberbiculus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0
P. apache	1	2	0	1	1	3	0	0	1	1	1	1	2	1	0	1	1	1	0	0	2	1	1	0	1	2	1	0	0	0	1	0	0
P. barbatus	1	2	0	1	1	?	0	1	0	1	0	1	1	0	1	0	1	1	0	0	1	1	0	0	1	2	1	0	2	1	0	1	0
P. bicolor	1	2	0	1	1	2	0	1	0	1	0	1	0	0	1	1	1	1	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0
P. desertorum	1	2	0	1	1	1	0	2	1	1	0	1	0	0	1	2	1	1	0	0	2	1	1	0	1	0	0	0	2	0	0	0	0
P. rugosus	1	2	0	0	1	1	0	1	0	1	1	1	1	0	1	0	1	1	0	0	1	1	0	0	0	2	1	0	2	1	0	1	0
P. tenuispina	1	2	0	1	1	2	0	0	1	1	0	1	2	1	1	2	1	1	1	0	2	1	1	0	1	2	0	?	?	?	0	0	0
P. wheeleri	1	2	0	1	1	1	0	1	0	1	0	1	2	1	1	1	1	1	0	0	1	1	0	0	1	2	1	0	2	0	0	1	0
P. bigbendensis	1	2	0	0	1	3	1	1	1	0	0	1	0	0	1	2	2	1	0	0	2	1	1	0	1	0	0	?	?	?	1	0	0
P. texanus	1	2	0	1	1	2	0	0	1	1	1	1	2	1	1	2	1	1	0	0	2	1	1	0	1	2	1	0	0	0	1	0	0
P. anzensis	0	1	2	0	0	2	1	2	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	0	?	?	?	1	?	0
P. brevispinosus	0	1	0	0	0	0	1	2	0	1	1	0	0	1	1	0	0	0	2	1	1	0	0	0	0	2	1	1	2	1	0	0	0
P. occidentalis	0	1	0	0	0	0	1	2	0	1	1	0	0	0	1	1	0	0	2	1	2	0	0	0	0	2	1	1	2	1	0	1	0
P. salinus	0	1	1	0	0	0	1	2	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	2	1	0	1	0	0	1	1
P. subdentatus	0	1	0	0	0	0	1	2	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	1	1	0	0	0	0
P. subnitidus	0	1	0	0	0	?	1	2	0	1	1	0	0	0	1	1	0	0	1	1	1	0	0	0	0	2	1	0	1	0	0	0	0
P. montanus	0	1	1	0	0	0	1	2	0	1	1	0	0	0	0	0	0	0	2	1	0	0	0	0	0	2	0	0	2	1	0	0	1
P. californicus	0	1	2	0	0	?	1	2	0	1	1	0	0	0	0	1	1	0	1	1	2	1	1	1	0	0	0	0	0	0	1	0	0
P. comanche	0	1	2	0	0	0	1	2	0	1	1	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0
P. magnacanthus	0	1	2	0	0	0	1	2	0	1	1	0	0	0	0	2	1	0	2	1	2	1	1	0	1	0	0	0	0	1	1	0	0
P. maricopa	0	1	2	0	0	0	1	2	0	1	1	0	0	0	0	2	1	0	1	1	2	1	1	?	1	0	0	0	0	0	?	0	0
P. badius	0	0	0	0	0	0	0	2	0	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	0	1	1	0	2	0	1	0	0
Species A	1	1	2	1	0	1	1	2	0	1	1	0	0	0	1	1	1	0	1	1	1	1	1	0	0	0	0	?	?	?	1	?	0
Species B	0	1	1	0	0	1	1	2	0	1	0	0	0	0	1	2	1	0	2	0	2	1	1	1	1	0	0	0	0	1	1	?	0

using PAUP version 2.4 with global branch swapping and maximal tree retention.

Placing the social parasites required a separate analysis because they have no worker caste. These species are members of the *barbatus* complex, as is their common host *P. rugosus*, and both are thought to be closely related to one another (Snelling 1981b). A close relationship of each with the host also is expected, in accordance with Emery's rule (Wilson 1971). A phylogeny of the parasites and the host species *P. barbatus* and *P. rugosus* was reconstructed using characters from the reproductive castes, with *P. wheeleri* as the outgroup. This tree was then joined to that of the remaining species, resulting in the complete phylogeny of the North American taxa.

Descriptions of the character states used in Table 2 are as follows. 1. Mandible (no. of distinct teeth in male): 5 (0); >5 (1). 2. Hair (male): long, flexuous (0); short, stiff (1). 3. Coloration (male): blackish (0); blackish–reddish (1); yellowish–reddish (2). 4. Size: large (0); small (1). 5. Life history: worker caste present (0); worker caste absent, parasite (1). 6. Node of petiole (female): without impression (0); with impression (1). 7. Petiolar node (female): rugosity weak or absent (0); rugosity not weak (1). 8. Antenna (scape of female): lip prominent (0); lip weak (1). 9. Petiolar node (female): not conical (0); conical (1). 10. Coloration (female): light red (0); dark red (1); blackish (2).

Primitive states are "0" except for character 10, where the primitive state is of intermediate development and is therefore coded as 1. The ordered data were analyzed by HENNIG86 using the "ie" option, which guarantees the identification of all trees of minimal length.

Results

For those species with a worker caste, each software package identified only one tree of minimal length; this was the same tree in each case. PAUP version 2.4 reported five additional trees. A single tree was found in each case of one, two, and three additional steps. Two trees were four steps longer than the shortest tree. Two equally parsimonious

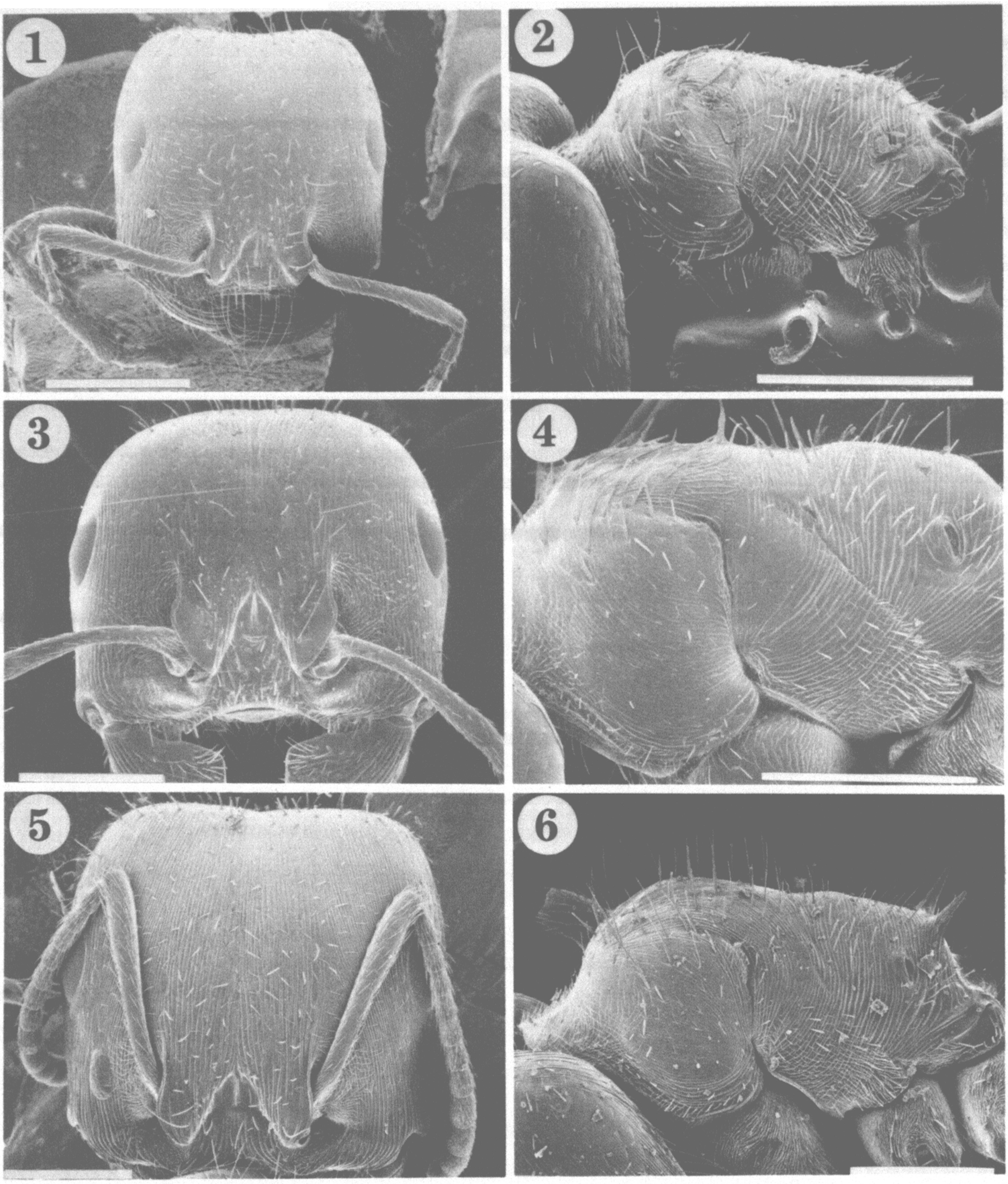

Fig. 1–6. Morphology of *Pogonomyrmex* spp. (1–2) *P. bigbendensis* (paratype; The Basin, Big Bend National Park, Brewster Co., Tex., 9-VIII-79). (1) Head, frontal view. (2) Alitrunk, lateral view. (3–4) *P. texanus* (paratype; 23 mi NW Rankin, Upton Co., Tex., 5-VI-79). (3) Head, frontal view. (4) Alitrunk, lateral view. (5–6) *P. wheeleri* (15 mi S Villa Union, Sinaloa, Mex., 31-I-64). (5) Head, frontal view. (6) Alitrunk, lateral view. Scale line, 1.0 mm.

phylogenies were found for the social parasites and their hosts, but only one of these was found when the characters were unordered. This was combined with the original tree to produce the complete phylogeny of the North American species (Fig. 19). The merging process presented no problems because the larger tree contained a monophyletic group in which a common ancestor gave rise to *P. wheeleri* and the ancestor of *P. barbatus* and *P. rugosus*. These retained their sister status in the final version, where they share a common ancestor with the social parasites.

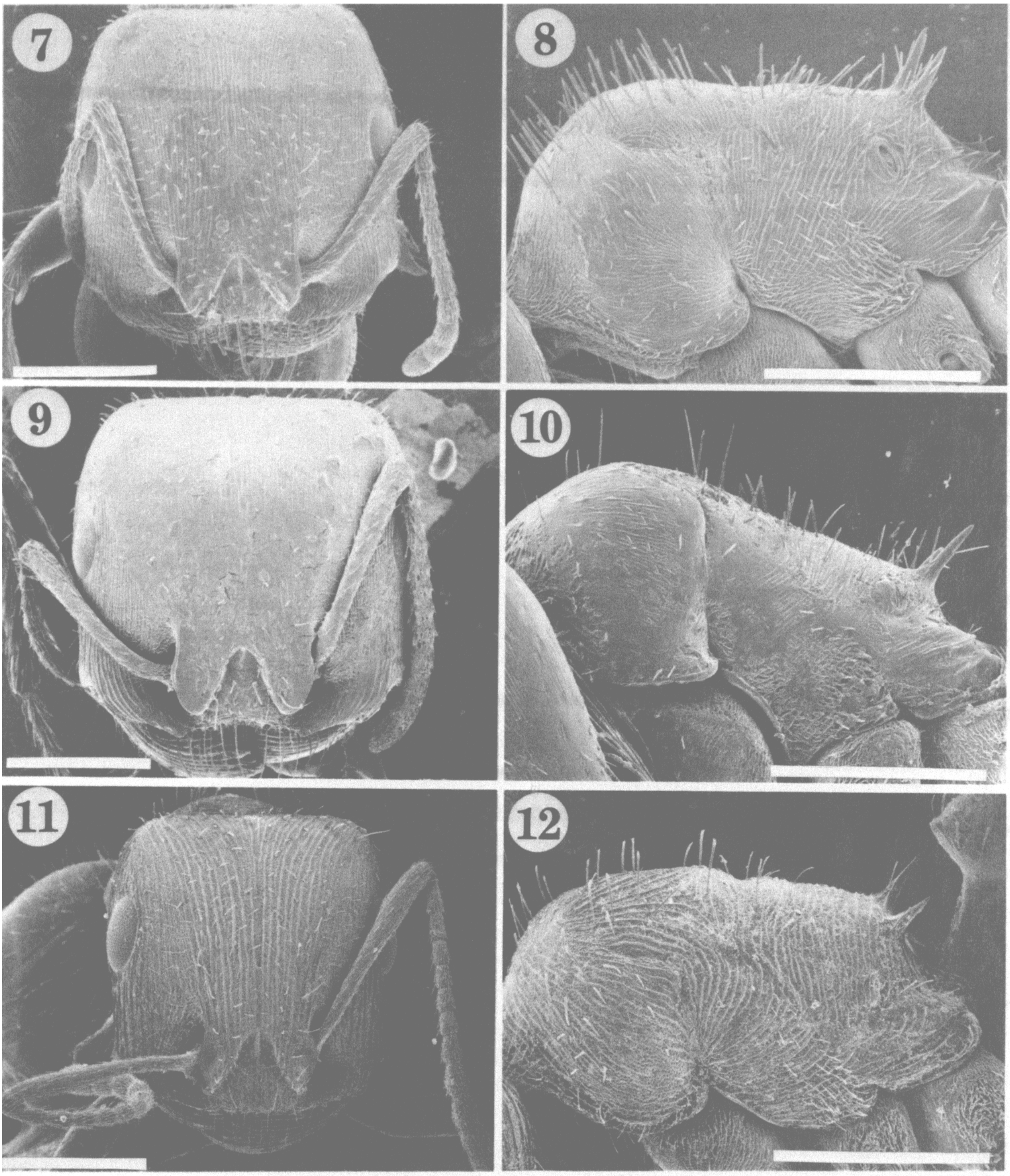

Fig. 7–12. Morphology of *Pogonomyrmex* spp. (7–8) *P. bicolor* (7 km N Obregon, Sonora, Mex., 3-VIII-83). (7) Head, frontal view. (8) Alitrunk, lateral view. (9–10) *P. tenuispina* (12 km S Jct. Highway 19 & Highway 1, Baja Cal. del Sur, Mex., 11-XI-82). (9) Head, frontal view. (10) Alitrunk, lateral view. (11–12) *P. salinus* (Lovelock, Pershing Co., Nev., 9-VII-54). (11) Head, frontal view. (12) Alitrunk, lateral view. Scale line, 1.0 mm.

The sensitivity of the original tree to character ordering was then determined. When unordered, transitions among all character states are equally probable, and this specification is appropriate if hypotheses concerning character transformations are lacking. Under these conditions and without the parasites, the original HENNIG86 program options produced 20 trees of identical length (six steps shorter than the tree generated from ordered characters). The consensus tree contained an identical *occidentalis* complex, but relationships within the other groups shifted somewhat, and the *barbatus*

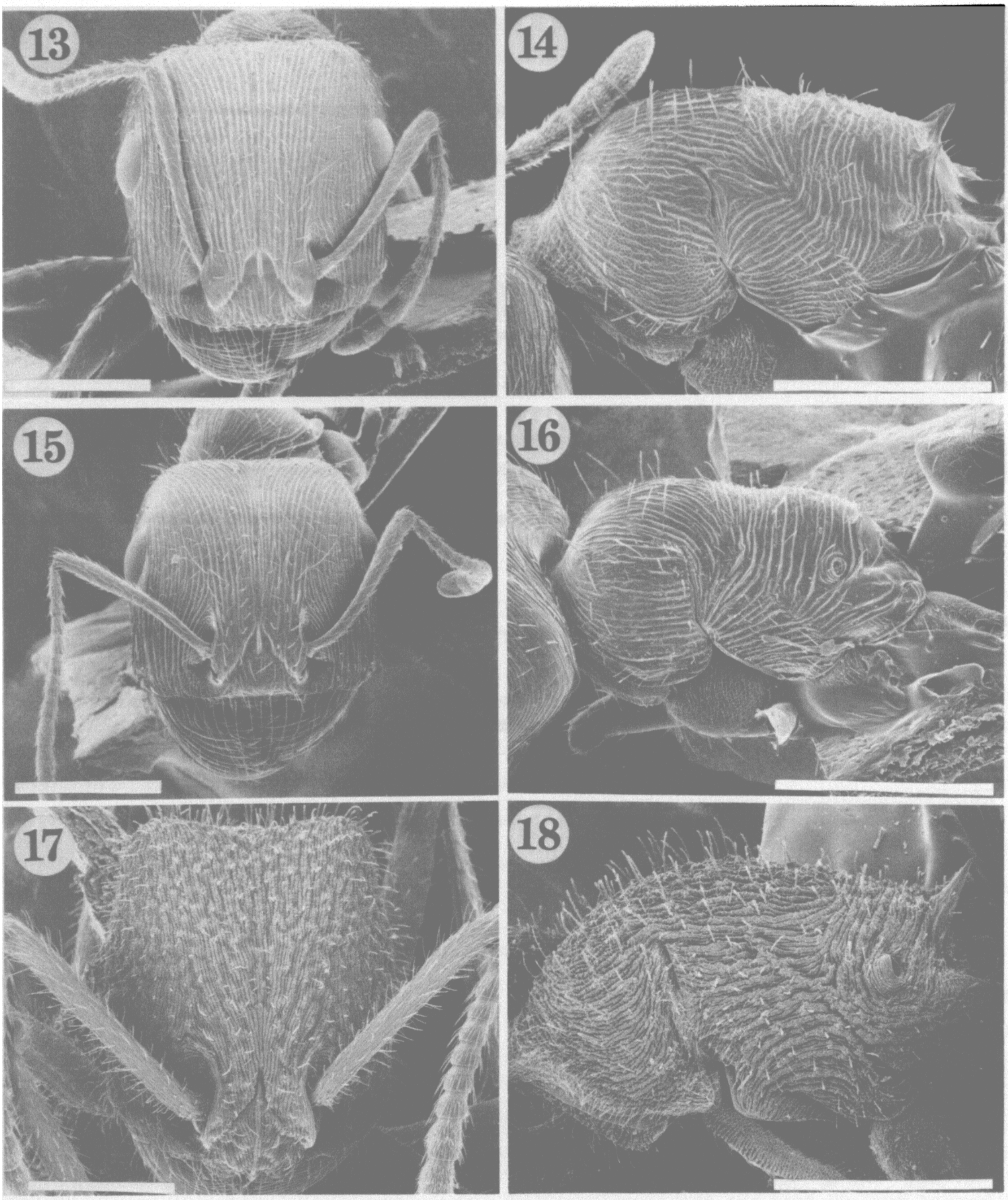

Fig. 13–18. Morphology of *Pogonomyrmex* spp. (13–14) *P. subdentatus* (25 mi N Fallon, Churchill Co., Nev., 3-VI-65). (13) Head, frontal view. (14) Alitrunk, lateral view. (15–16) *P. anzensis* (type; Split Mt., Anza Desert State Park, San Diego Co., Cal., 22-IV-52). (15) Head, frontal view. (16) Alitrunk, lateral view. (17–18) *P.* (*Forelomyrmex*) *mayri* (Rio Frio, Magdalena, Colombia, 13-VIII-74). (17) Head, frontal view. (18) Alitrunk, lateral view. Scale line, 1.0 mm.

complex arose from the immediate ancestor of Species B. PAUP version 2.4 found the same number of trees at 116 steps, but it also reported 97 trees just two steps longer. The results here are similar in many ways to those produced with ordered characters, but they were rejected because the nature of the characters is such that they are readily divided into reasonable transformation series; transitions between extremes in the case of three or more states appear to be less likely than other transitions.

Certain characters are variable or difficult to represent adequately by discrete states. Chief among these are petiolar and postpetiolar sculpture. When these four characters are deleted (16, 17, 21, 22), an ordered analysis by HENNIG86 ceases at the overflow value of 100 trees. The correct ordering of states in character 2 (eye type) is not obvious. When this alone is unordered, two trees are recovered; the original tree and one in which *P. badius* is the sister of the *occidentalis* + *maricopa* clade. It is not certain that no shorter trees exist than that shown in Fig. 19, but a recent review of software (Platnick 1989) identified the "mhennig*" + "bb" and "tr" + "bb" options of HENNIG86 as the approximation methods of choice, often finding the shortest tree(s) as demonstrated by exact methods. When the monophyletic *barbatus* and *occidentalis* + *maricopa* groups were treated separately by the exhaustive method, the topology of the first was upheld, and two trees were found in the second case: the original and a trichotomy at the root involving the outgroup, *P. badius*, and the set of remaining species.

There has occasionally been doubt as to the monophyly of Cole's original species complexes and, as a matter of historical interest, I deleted the new taxa and processed the ordered character set. Twelve trees were found, and the consensus tree corroborates the erection of the four original species groups, with the proviso that *P. anzensis* is moved to the *maricopa* group, as Cole (1968) anticipated.

Character choice and ordering will obviously affect tree number and topology, but the selection of an appropriate outgroup also is important. The sister genus (or subgenus) of *Pogonomyrmex* is *Ephebomyrmex* and, up to this point in the analysis, *E. imberbiculus* served as the outgroup taxon. This species was now replaced by *Ephebomyrmex huachucanus* Wheeler, and the original program specifications and options were invoked. The choice of *E. huachucanus* as outgroup held particular interest because it has been placed in each genus (subgenus). Wheeler, in the original description (1914), placed this species in subgenus *Pogonomyrmex*, where Creighton (1950) retained it. Cole later moved the species to *Ephebomyrmex* in his generic revision (1968).

The choice of *E. huachucanus* as outgroup resulted in 13 equally parsimonious trees (HENNIG86), and these were one step shorter than that found using *E. imberbiculus*. However, one of the trees has a topology identical to that shown in Fig. 19 and this tree, diagnosed by PAUP version 2.4, had the lowest *F* value, a measure of homoplasy. Among the remaining twelve trees, the *barbatus* and *maricopa* groups remain relatively unchanged, but relationships within the *occidentalis* complex are unstable.

Table 2. *Pogonomyrmex wheeleri* subcomplex character matrix

taxon \ character	1	2	3	4	5	6	7	8	9	10
P. wheeleri	0	0	0	0	0	0	0	0	0	1
P. barbatus	1	0	2	0	0	0	1	0	0	1
P. rugosus	1	0	1	0	0	0	1	0	0	2
P. anergismus	0	1	2	1	1	1	0	1	1	0
P. colei	0	1	2	1	1	1	1	1	1	1

Discussion

The species groups as defined up to this study are monophyletic, once *P. anzensis* is moved from the *occidentalis* complex to the *maricopa* complex, as noted above. No conjectures regarding the placement of undescribed Species A were made previously, although the correct group affinity of Species B was noted by Snelling (personal communication). Current species groups are defined in Fig. 19. These follow the terminology of Cole (1968) as far as possible to avoid confusion. I suggest only two changes: the clade containing *P. badius* and the modified *maricopa* complex be known henceforth as the *californicus* complex; and the monotypic *badius* complex be dropped, unless the results for the entire genus, including the South American taxa, warrant its preservation.

The immediate ancestor of the North American *Pogonomyrmex* species differed in four characters from the immediate ancestor of *Pogonomyrmex* and *Ephebomyrmex*. The rather convex eye (Table 1, character 2) moved back along the side of the head, resembling that found in most of the ants of the *occidentalis* and *californicus* groups. The strong clypeal projection (8) was reduced to a moderate development; an additional mandibular tooth appeared (10), probably arising at the basal margin; and the scape base increased in development (26) from weak to moderate.

In the following discussion, all shared characters are synapomorphies unless otherwise indicated. Unique synapomorphies of the *barbatus* complex include a roughly centered, flattened eye (2); straight cephalic rugae (5); subequal third and fourth mandibular teeth (12); and a petiolar peduncle with hairs near the position of the ventral process (18). Additional support for the monophyly of the group is provided by the broad head (1) of each species, although this apomorphy is not unique. Synapomorphies of the *wheeleri* subcomplex (excluding the social parasites) include a well-developed scape base (26) with a strong lip (27), a male mandible with numerous teeth (29), and a tendency to construct gravel nests (32). The petiolar nodes of *P. barbatus* and *P. rugosus* often are covered with rugae (16), and the males of both species are light in color (30). Members of the *bicolor* subcomplex have a weak postpetiolar ventral process (23). Taxa above *P. bicolor* have weakly rugose postpetiolar rugae (21), and (a unique synapomorphy) a lack of occipital rugae (9). *P. desertorum* and *P. bigbendensis* each have a weak scape base (26). Members of the *tenuispina* group have a strong clypeal projection (8), a deep trough at the base of the antenna (13), a bipartite lip (14), and a strongly developed scape base (26). *P. apache* and *P. tex-*

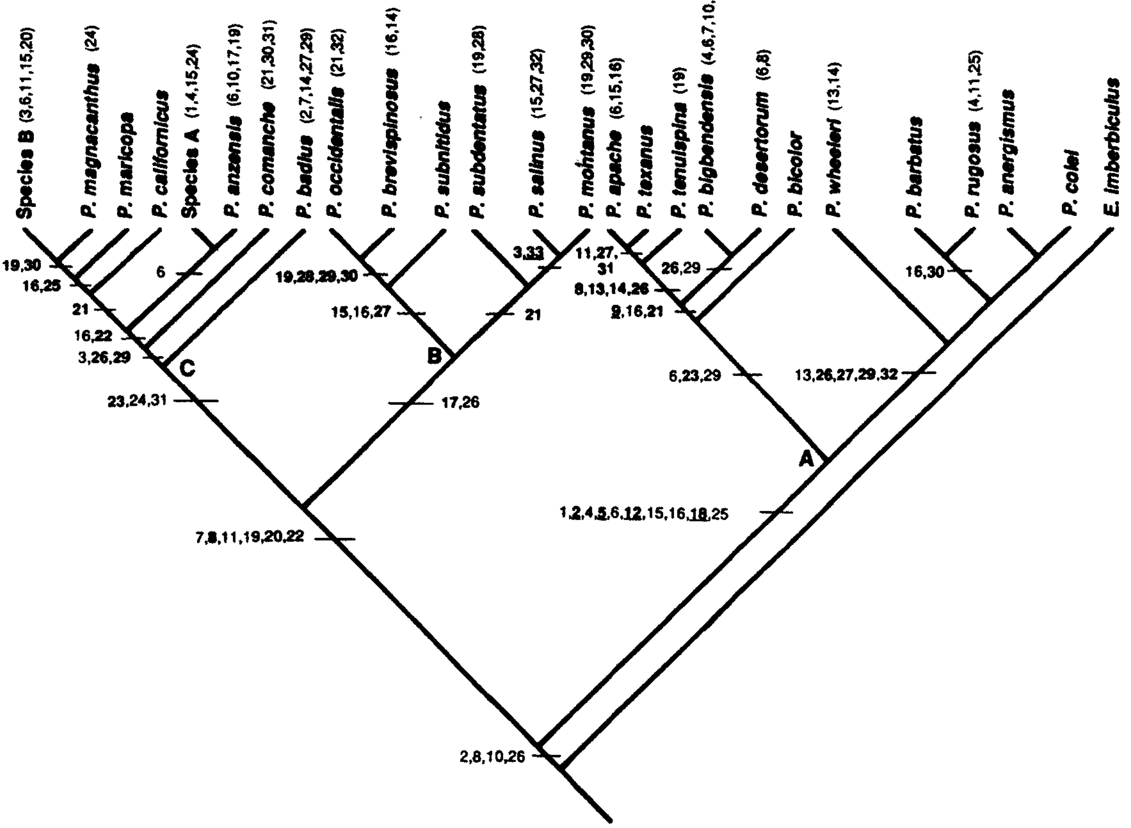

Fig. 19. The phylogeny of the North American *Pogonomyrmex* harvester ants. Tree length, 122; consistency index, 0.369. (A) *barbatus* complex. (B) *occidentalis* complex. (C) *californicus* complex. Branches and species are labeled with character apomorphies; synapomorphies are in bold type, and unique synapomorphies are underlined. Apomorphies do not apply to social parasites.

anus have a roughly straight basal mandibular margin (11), a strongly developed lip (27), and no propodeal spines (31).

Recent collections extend the range of two species of the *barbatus* complex. Scott A. Stockwell collected *P. barbatus* from several localities in Oaxaca, Mexico, including a sample from "21 km E Mitla 17-VIII-1988 5600'." This extends the range of the species by approximately 320 km to the southeast. I collected a sample of *P. apache* from Coy City, Karnes Co., Tex. 20-V-85, extending the southern limit of this species in Texas by approximately 120 km.

The *occidentalis* and *californicus* complexes have a single synapomorphy: a very weak or absent clypeal projection (8). The single synapomorphy of the *occidentalis* group is the densely areolate petiolar node (17). The *subdentatus* group is characterized by a densely rugose postpetiolar node (21) and, within that group, *P. salinus* and *P. montanus* have occasional or weak cirumocular whorls (3), as well as a preference for piney habitats (a unique synapomorphy) (33). In each member of the *subnitidus* group, the basal face of the propodeum is straight (15), and the scape lip is strongly developed (27). *P. occidentalis* and *P. brevispinosus* have four synapomorphies: a weak or absent ventral peduncular process (19), a male mandible with a concave basal margin (28) and numerous teeth (29), and light-colored males (30).

The single synapomorphy of the *californicus* complex is a weak ventral postpetiolar process (23). Taxa above *P. badius* each have a weak scape base (26), and the known males have few mandibular teeth (29). Species above *P. comanche* have sparsely areolate postpetioles (22), and those taxa above the ancestor of Species A and *P. anzensis* (excluding these two species) have weakly rugose postpetioles (21). *P. maricopa*, *P. magnacanthus*, and Species B have weakly rugose petiolar nodes (16) and rather fine sculpture (25). The latter two species have absent or very weak ventral processes of the petiolar peduncle (19) as well as light-colored males (30). Geographic distributions are discussed in Cole (1968) and in the original descriptions of the newer species; these distributions are quite consistent with the cladogram.

Most of the synapomorphies within the separate phylogeny of the *wheeleri* subcomplex containing the social parasites and their hosts support the monophyly of the first two species. These include short, stiff hairs (male) (Table 2, character 2), small size (4), lack of a worker caste (5), impressed petiolar node (female) (6), weak scape lip (female) (8), and a conical petiolar node (female) (9). The males of *P. barbatus* and *P. rugosus* have six or more distinct mandibular teeth (1), a shared, derived character.

The cladistic phylogeny supports many of the previous hypotheses concerning relationships within the genus. For example, *P. rugosus* was a subspecies of *P. barbatus* until Cole (1968) separated these with minor reservations; these are indeed sister taxa according to the tree. Cole also identified *P. desertorum* as the closest relative of *P. bicolor* and the closest relative of *P. wheeleri* as *P. barbatus.* When the new species *P. bigbendensis* is deleted from the analysis, the first hypothesis is supported, and the tree is always consistent with the second. Francke & Merickel (1981) added *P. bigbendensis* and *P. texanus* to the complex and identified *P. apache* as the closest relative of both. The tree indicates a rather distant relationship between *P. bigbendensis* and *P. apache* but supports the second hypothesis. The relationship between *P. apache* and *P. texanus* is further supported by the excised clypeus, which is apparently never observed in other taxa.

The proper placement of the social parasites has been problematic. Cole (1968) placed *P. anergismus* in the *barbatus* complex but described its affinities to other members of the group as "unfathomable." He cited behavioral similarities to *P. rugosus* and *P. barbatus*. Rissing (1983) suggested *P. colei* as intermediate between *P. rugosus* and *P. anergismus,* whereas Snelling (1981b) postulated an ancestor that gave rise to *P. rugosus* in one line and both parasites in another. The cladistic tree supports the latter hypothesis.

Cole cautioned that *P. anzensis* (known to this day from a single nest), might have to be moved from the *occidentalis* complex to the *maricopa* group. His prediction is confirmed here. Cole also felt that *P. subdentatus* might be the closest relative of the new species, *P. brevispinosus*, but proposed this affinity with little enthusiasm. Indeed, the tree indicates a rather distant relationship between the two ants. The close relationship of *P. subdentatus* to *P. salinus* is, however, clear. *P. owyheei* was synonymized with *P. salinus* by Shattuck (1987). His suggestion that *P. salinus, P. occidentalis, P. subdentatus,* and *P. montanus* might form a monophyletic group is not supported here. MacKay (1980) described *P. montanus*, assigned it to this complex, and identified *P. salinus* as its closest relative. The tree supports that affinity.

In his revision of the genus, Cole (1968) reported that no species was "more grossly misunderstood" than *P. comanche*. This ant was originally a subspecies of *P. occidentalis* and, indeed, displays some characteristics of that complex (e.g., dense cephalic areolation and well-developed spines). Cole placed it instead in his *maricopa* complex, and that assignment is supported by the present study. The monotypic complex *P. badius* is often confused with *P. comanche*, which is its closest relative. It is worth noting that *P. badius* is the only harvester ant found east of the Mississippi River and its range is roughly contiguous with that of *P. comanche*. Within the *californicus* group, Cole identified *P. californicus* as the closest relative of his new species, *P. magnacanthus*. It appears that *P. maricopa* is a closer relative and that the new Species B is actually the sister of *P. magnacanthus*. The unusual Species A is the sister of *P. anzensis*. Geographic data support this result; Species A is known from a single collection in Baja California and *P. anzensis* is known from a single collection in the Anza Borrego Desert State Park in southern California, close to the Baja border.

Rates of evolution tend to be greater in the *barbatus* complex than in the other groups (see branch apomorphies in Fig. 19). The greatest mean patristic (path length) distance from the outgroup is that of *P. apache* (0.939). Species B is second with a distance of 0.906, but the next three positions are held by *barbatus* group members *P. bigbendensis, P. texanus,* and *P. tenuispina* (0.867, 0.848, and 0.833, respectively). Species B is currently represented by only one worker, and more material is needed before its character variabilities can be properly assessed. The shortest distances from the outgroup are those of *P. subdentatus* and *P. subnitidus* (0.455 and 0.469, respectively). Indeed, rates of evolution within the *occidentalis* complex are the lowest of any group. *P. occidentalis* and *P. brevispinosus* each have a patristic distance of 0.636, the highest in the complex, but only twelfth overall.

The evolution of two characters merits a short discussion. The presence or absence of propodeal spines traditionally has been important in the identification of *Pogonomyrmex* species. Well-developed spines apparently have been lost twice in the *barbatus* complex (in the ancestor of *P. apache* and *P. texanus*, and in *P. bigbendensis*), and in the ancestor of the *californicus* group, only to reappear in *P. comanche* and occasionally in *P. maricopa*. Behavioral characters were avoided in this study, but one of these is familiar to many inhabitants of the southwestern United States and Mexico; *Pogonomyrmex* delivers an excruciating sting. This is a derived trait (not shared by the outgroup), and such a defense is used readily by only a few species (Creighton 1950; Cole 1968; MacKay, personal communication); these include *P. maricopa, P. californicus, P. subnitidus, P. occidentalis, P. rugosus, P. barbatus, P. wheeleri,* and some populations of *P. salinus*. *P. montanus* can be aggressive as well. The evolution of the sting in general is a subject of current controversy. Starr (1989) and Kukuk et al. (1989) agreed that as eusociality evolved and colony size increased, the nest became a bigger target for vertebrate predators, and a potent sting had great adaptive value. This hypothesis can be tested with *Pogonomyrmex*. MacKay (1981) compiled a list of harvester ant species and colony sizes, and from that report and from personal observation, it is clear that a positive correlation exists between maximal colony size and ready use of the sting in defense. Based on the phylogenetic tree, this behavior probably arose in the ancestor of *P. wheeleri* in the *barbatus* complex, but its history elsewhere is not so readily determined.

Homoplasies are common in the genus, as indicated by the rather low consistency index (0.369). Parallel evolution occurred in 25 characters, reversals occurred in 18 characters, and both occurred in 14 characters. For example, there were five character-state changes in the development of the lip at the base of the scape (Table 1, Character 27), five changes in male coloration (30), and three changes in nest covering material (32). In each case, all changes were parallelisms to the derived state. Five of the six changes in the inclination of the basal face of the propodeum also were parallel changes to the derived state. Further detailed analyses of the data are available upon request.

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