Generic-level relationships within the ant subfamily Dolichoderinae (Hymenoptera: Formicidae)

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Abstract. A cladistic analysis was undertaken to determine relationships among extant genera of the ant subfamily Dolichoderinae. Twenty-one of the twenty-two currently recognized genera within the subfamily were examined using 104 morphological characters. A single fully resolved, most-parsimonious tree was found when a combination of ordered and unordered characters was used. When all characters were coded as unordered, seventy most-parsimonious trees were found. The following results were found with both character coding methods. *Leptomyrmex* was placed basal to the remainder of the subfamily and the monophyletic sets *Dolichoderus + Liometopum + Axinidris + Tapinoma + Technomyrmex, Froggattella + Iridomyrmex + Ochetellus + Papyrius + Philidris + Turneria, and Bothriomyrmex + Dorymyrmex + Forelius + Loweriella* were suggested. The genera *Linepithema* and *Doleromyrma* showed a small amount of instability in moving between neighbouring sister groups when the character coding method changed. The genera *Anillidris* and *Anonychomyrma* were difficult to place as they showed major differences in their positions between the two character coding methods.

Introduction

The ant subfamily Dolichoderinae forms one of the larger groups within the family Formicidae. The approximately 1000 described extant species have been placed in up to forty-two genera and subgenera. The most recent generic-level revision considered twenty-two genera to be valid (Shattuck, 1992b). Members of the subfamily occur world-wide in all geographic regions although they are most species-rich in the tropics and Australia (Table 1). Most genera contain relatively few species (approximately one-third contain fewer than ten) but several genera are large (*Azteca, 130 species; Dolichoderus, 154 species; Tapinoma, 95 species; Technomyrmex, 88 species*). Biogeographically, genera range from limited areas to worldwide. In some cases this apparent endemism may be caused by limited collection records, for example the genera *Anillidris* (Argentina, Brazil), *Echthorella* (Angola) and *Loweriella* (Sarawak, Brunei) are known from three or fewer collections each. In other cases the taxa concerned are regularly collected and appear to have genuinely restricted ranges. These include *Doleromyrma* (Southern Australia) and *Papyrius* (Australia, New Guinea). At the other end of the spectrum are genera with essentially worldwide distributions, for example *Dolichoderus* and *Tapinoma*. Most taxa show patterns between these extremes. These include *Bothriomyrmex* (Europe to Australia), *Dorymyrmex* (North and South America) and *Ochetellus* (southeast Asia to Australia). For detailed discussion of distribution patterns by genus, see Shattuck (1992b).

Table 1. Approximate number of extant, described dolichoderine species and subspecies by geographic region. Geographically widespread species are recorded for more than one region. Numbers in parentheses indicate introduced species occurring outside their normal, native range. Regions follow Brown (1973) and are abbreviated as follows: Ne, Neartic; No, Neotropic; Pa, Paleartic; Et, Ethiopian; Ma, Malagasy; Or, Oriental; Au, Australian.

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From an ecological perspective, dolichoderines vary from minor components to dominant members of local faunas. One of the most important groups ecologically is *Iridomyrmex* in Australia. Species of the *Iridomyrmex parvus* species group have been shown to be dominant members of communities and to have a strong impact on the foraging activities of other ant species with which they interact (Andersen & Patel, 1993, 1994; Greenslade, 1976). Several species are also notable pests. *Linepithema humile* (the Argentine ant), *Tapinoma melanocephalum* and *Technomyrmex albipes* are widely dispersed by human activity and can have a negative impact on local insect faunas (Bond & Slingsby, 1984; Ward, 1987). These species also commonly invade houses and buildings.

Taxonomically, the generic-level classification of these ants has recently been reviewed. The entire subfamily was examined by Shattuck (1992b) including workers, queens, males and larvae, and all previously proposed genus-group names were evaluated. Substantial changes were proposed in the classification based on an analysis of approximately 180 morphological characters. In the system proposed by that study, all recognized genera were defined as sets of species possessing derived characters or unique sets of characters and thus were arguably monophyletic. That study did not, however, examine the relationships among the genera of the Dolichoderinae.

In the present paper, all extant genera in the subfamily are examined to determine the cladistic relationships among them. The closely related subfamilies Formicinae and Anecurineae (Baroni Urbani et al., 1992; Bolton, 1990; Shattuck, 1992a; Ward, 1990) are used in the analysis to assist in the interpretation of the results. Characters which support the proposed relationships are discussed, and an attempt is made to quantify the relative strength of data supporting individual sets of taxa through the use of the bootstrap and an examination of trees slightly longer than the most parsimonious. Relationships among the majority of genera are considered, although a single genus, *Ectophocaena*, could not be placed with confidence because of the lack of character information from the single known worker and unknown queen and male castes and therefore it is excluded from the analysis.

**Previous studies on dolichoderine relationships**

There has been little discussion of the relationships among the genera of the Dolichoderinae. Earlier studies were limited primarily to ‘classifications’ (lists of taxa grouped into sets (most often tribes)). These classifications were generally intended to reflect evolutionary patterns within the group, but were based on the overall similarities of the taxa considered and seldom on detailed character studies combined with explicit phylogenetic (or other) methodologies. Although these methods limit the usefulness of these studies, they can be used as a first approximation of the relationships among the taxa.

In the following discussion, the genus *Anecurine*, previously placed in the Dolichoderinae, has been excluded. This is based on several recent studies (Baroni Urbani et al., 1992; Bolton, 1990, 1994; Hübeldohr & Wilson, 1990; Shattuck, 1992a; Snelling, 1981), suggesting that *Anecurine* be placed in a separate subfamily, the Anecurineae.

One of the first studies of dolichoderine relationships was that of Emery (1888). He produced a tree for ten dolichoderine genera, and included an ancestor and the most closely related nondolichoderines. Although his proposed relationships are limited to a subset of the currently recognized dolichoderine genera, some of the proposals are still accepted today. These include the close relationships of *Tapinoma* and *Technomyrmex*, and *Bothriomyrmex*, *Dorymyrmex* and *Forelius*. Also, the basal placement of *Leptomyrmex* within the subfamily is still accepted. In most other aspects, however, Emery’s relationships have not been supported. The most notable are the close relationships between *Bothriomyrmex* and *Iridomyrmex*, and the fact that Emery was uncertain of the monophyly of the Dolichoderinae.

One of the only other statements on the generic-level relationships for the entire subfamily was that of Brown (1973), who compiled a list of the world ant genera in which the ordering of the genera was intended to indicate the relative primitiveness of a group. Thus he placed ‘primitive’ taxa near the top of his list and more ‘advanced’ taxa near the bottom. However, because evolution of taxa is better viewed as occurring in multi-dimensional space, rather than linearly, this method of presentation has limited value. Given this limitation, the following patterns are noteworthy. First, *Leptomyrmex* is placed at the remaining taxa of the subfamily. Second, *Dolichoderus* is considered fair identity within the subfamily. And finally, the following subsets of taxa are considered closely related: *Dolichoderus* + *Monocevatorinex* (treated as congeneric by Shattuck, 1992b), *Axinidris* + *Liogetopos* + *Semonius* (*Semonius* is treated as congeneric with *Tapinoma* by Shattuck, 1992b), *Progotettrella* + *Iridomyrmex* + *Turnerie*, *Bothriomyrmex* + *Dorymyrmex* + *Forelius* + *Neoforelius* (*Forelius* and *Neoforelius* are considered congeneric by Shattuck, 1992b), *Engyromma* + *Tapinoma* + *Technomyrmex* + *Zatopina* (*Engyromma* and *Technomyrmex*, and *Tapinoma* and *Zatopina* are considered congeneric by Shattuck, 1992b). However, several placements have not been supported during more recent studies. First, Brown (1973) placed *Linepithema* near *Dolichoderus*. Second, *Axinidris* + *Liogetopos* + *Semonius* were placed close to *Linepithema* or *Turnerie*. Shattuck (1990) placed *Turnerie* near *Progotettrella* and *Iridomyrmex*, and Shattuck (1992b) synonymized *Semonius* with *Tapinoma*.

The only other broad-based classification systems proposed within the Dolichoderinae are at tribal level. Emery (1912) proposed a classification of the subfamily consisting of three tribes: *Dolichoderini* (*Dolichoderus*, *Linepithema*) *Leptomyrmecini* (*Leptomyrmex*) and *Tapinomini* (the remaining genera of the subfamily). Forel (1917) modified this system by placing the *Dolichoderini* and *Leptomyrmecini* together (as ‘Prodolichoderinae’), separate from the *Tapinomini* (in ‘Eudolichoderinae’). These modifications were not followed by subsequent authors who continued to use the system proposed by Emery. Two additional tribes, *Axinidridi* (*Axinidris*) (Weber, 1941) and *Anonymomyrmex* (*Anonymomyrmex*) (Donisthorpe, 1947), were added later, but no discussion was given as to the relationships among these tribes and the previously recognized ones. An additional tribe, *Liogetopopos* (*Liogetopos* and the fossil-based *Asymphylomyrmex*), was added to the Dolichoderinae by Dussky & Fedoseeva (1988), along with two additional tribes based on fossil taxa and therefore not considered.
in the present study. This brings to six the number of tribes containing extant taxa within the subfamily. Several factors limit the usefulness of these tribes in determining relationships within the Dolichoderinae. First, four of the six proposed tribes are monotropic and thus contain minimal information on subsets of relaxed taxa. Second, there has been no attempt to determine the relationships among these tribes by the authors who have proposed them. And finally, a recent revision of the Dolichoderinae at the generic-level (Shattuck, 1992b) determined that one of the earlier tribes (Dolichoderini) was polyphyletic. In general, the tribal classification has been of little value and therefore Shattuck (1992b) did not recognize any tribes within the subfamily.

Materials and Methods

Taxis and characters examined

All twenty-two extant, valid genera of the Dolichoderinae were coded based on the characters examined during the generic-level revision of the subfamily by Shattuck (1992b). These generic characterization were developed by examining material representing as many species as possible and distributed throughout the known geographic range of each genus. This material varied from the single known specimen of Ecphorella to over 10,000 individuals representing more than fifty species of Iridomyrmex. (For sources and geographic distributions of material examined, see Shattuck (1992b).) Eighty-eight of the approximately 180 characters utilized by Shattuck (1992b) were found to be suitable for the present cladistic analysis (i.e. non-continuous and thus divisible into discrete states and non-polymorphic across the majority of taxa). These characters are morphological and were drawn from the worker, queen, and male castes. In addition, sixteen characters were included which were found to be useful for defining the relationships among the subfamilies Aneuretinae, Dolichoderinae and Formicinae (Shattuck, 1992a). These characters were included because representatives of these subfamilies were used as outgroups (see below). Brief descriptions of the characters used are listed below; for more detailed discussions, see Shattuck (1992a, b). Character states are given in parentheses and are not intended to indicate plesiomorphic or apomorphic status (see Cladistic analysis below).

Worker characters

1. Compound eyes (1) absent, (2) with 10–50 omnitidia, (3) with more than 50 omnitidia.
2. Compound eyes (1) relatively posterior on head, (2) relatively anterior on head (coded as unknown ("?")) when eyes absent (character 1, state 1).
3. Ocelli (1) present, (2) absent.
4. Anterolateral clypeal margin (1) posterior to the mediolateral region, (2) even with the mediolateral region, (3) with the corners expanded slightly anterior to the mediolateral region.
5. Anteromedial clypeal margin (1) entire, without a central notch or concavity of any type; (2) with a broad, shallow concavity; (3) with a distinct central notch; (4) with a central projection, either pointed or rounded (sometimes only feebly projecting).
6. Anterior clypeal setae (1) short, less than twice the maximum scape diameter; (2) about the same length as the closed mandibles; (3) long and surpassing the distal edge of the closed mandibles.
7. Anterior clypeal setae (1) straight, (2) moderately curved ventrally, (3) strongly curved ventrally.
8. Posterior clypeal margin (1) even with or anterior to the anterior surface of the antennal condyle, (2) between the anterior and posterior surfaces of the antennal condyle, (3) even with or posterior to the anterior surface of the antennal condyle.
9. Medial hypostoma (1) entire, (2) notched, (3) absent.
11. Number of mandibular teeth (1) < 4, (2) 5–10, (3) > 10.
12. Number of mandibular denticles (1) < 3, (2) 4–5, (3) > 5, uniformly distributed along margin; (4) > 5, grouped in subsets along margin.
13. Apical tooth of mandible (1) subequal in length to the subapical tooth, (2) slightly longer than the subapical tooth, (3) elongate and much longer than the subapical tooth.
14. Basal angle of mandible (1) distinct, with a well-developed tooth or angle separating the masticatory and basal margins; (2) weakly defined by a denticle; (3) indistinct, with a relatively uninterrupted curve between the two margins.
15. Basal margin of mandible (1) smooth and without teeth or denticles; (2) denticulate distally, smooth proximally; (3) denticulate along entire surface.
16. Dorsal face of propodeum (1) longer than the declivitous face, (2) subequal in length to the declivitous face, (3) shorter than the declivitous face.
17. Propodeal spiracle (1) lateral and ventral of the propodeal dorsum, (2) dorsal and medial along the basal propodeal face, (3) dorsal and posterior, near the propodeal angle.
18. Petiolar scale (1) present, (2) reduced, (3) absent.
19. Petiolar scale (1) vertical and not inclined anteriorly, (2) moderately inclined anteriorly but with the anterior and posterior faces approximately the same length, (3) strongly inclined anteriorly and with the anterior face much shorter than the posterior face (coded as 3 when scale absent (character 18, state 3)).
20. Venter of petiole (1) with a well-developed lobe, (2) with a slight or weakly developed lobe, (3) without a lobe.
21. First gastric tergite (1) elongated posteriorly; (2) vertical and not concealing the petiole in dorsal view; (3) projecting anteriorly, but not concealing the petiole in dorsal view; (4) projecting anteriorly and concealing the petiole in dorsal view.
22. First gastric tergite (1) smooth and without a groove or indentation, (2) with a groove or indentation for the reception of the basal portion of the petiole, (3) with a groove or indentation for the reception of the entire height of the petiole.
23. Anterior tergosternal suture of the first gastric segment (1) extending laterally from the helcium, without or with at most a very weak dorsal arch; (2) extending laterally from the helcium in a distinct dorsal arch which is approximately the same height as the helcium dorsum; (3) extending laterally from the helcium in a distinct arch which extends dorsally of the dorsal helcium surface; (4) very weakly developed immediately lateral of the helcium and forming a distinct arch which extends dorsally of the dorsal helcium surface; (5) absent immediately lateral of the
helcium and with the lateral section of the suture terminating immediately above the helcium; (6) absent immediately lateral of the helcium and with the lateral section of the suture extending anterodorsally and terminating near the dorsal surface of the gaster.

24. Gastral compression (1) lateral, (2) dorsoventral, (3) absent (gaster circular in cross section).

25. Fourth gastric sternite (1) keel-shaped posteriorly, (2) flat across entire posterior border.

26. Proventricular cupola (1) narrow relative to bulb, (2) slightly broader than bulb, (3) much broader than bulb.

27. Proventricular cupula (1) with long pile, (2) with short pile, (3) without pile.

28. Proventricular cupula (1) with very broad phragma, (2) with narrow phragma, (3) with short, lateral phragma, (4) without phragma.

29. Proventricular bulb (1) exposed in lateral view, (2) partially hidden by cupola in lateral view, (3) completely hidden by cupola in lateral view.

30. Proventricular longitudinal muscle No. 1 (1) present, (2) absent.

31. Proventricular occlusory tract (1) present, (2) absent.

*Queen characters*

32. Anterolateral clypeal margin (1) posterior to the mediolateral region, (2) even with the mediolateral region, (3) with the corners expanded slightly anterior of the mediolateral region.

33. Anteromedial clypeal margin (1) entire, without a central notch or concavity of any type; (2) with a broad, shallow concavity; (3) with a distinct central notch; (4) with a central projection, either pointed or rounded (sometimes only feebly projecting).

34. Anterior clypeal setae (1) short, less than twice the maximum scape diameter; (2) about the same length as the closed mandibles, (3) long and surpassing the distal edge of the closed mandibles.

35. Anterior clypeal setae (1) straight, (2) moderately curved ventrally, (3) strongly curved ventrally.

36. Posterior clypeal margin (1) even with or anterior to the anterior surface of the antennal condyle, (2) between the anterior and posterior surfaces of the antennal condyle, (3) even with or posterior to the posterior surface of the antennal condyle.


38. Number of mandibular teeth (1) <4, (2) 5–10, (3) >10.

39. Number of mandibular denticles (1) <4, (2) >4, uniformly distributed along margin, (3) >4, grouped in subsets along margin.

40. Apical tooth of mandible (1) subequal in length to the subapical tooth, (2) slightly longer than the subapical tooth, (3) elongate and much longer than the subapical tooth.

41. Basal angle of mandible (1) distinct, with a well-developed tooth or angle separating the masticatory and basal margins; (2) weakly defined by a denticle; (3) indistinct, with a relatively uninterrupted curve between the two margins and without a distinct tooth or angle.

42. Basal margin of mandible (1) smooth and without teeth or denticles; (2) denticulate distally, smooth proximally; (3) denticulate along entire surface.

43. Episternal suture (1) complete, (2) complete but weakly developed anteriorly, (3) weak, nearly absent.

44. Axilla (1) parallel, (2) constricted medially, (3) absent dorsally.

45. Axilla (1) entire, (2) with a suture medially.

46. Anterior axillar suture (1) straight, (2) angular medially.

47. Dorsal face of propodeum (1) longer than the declivitous face, (2) subequal in length to the declivitous face, (3) shorter than the declivitous face.

48. Radial cell (1) closed, (2) open.

49. Number of forewing cubital cells (1, 2).

50. Number of forewing discoidal cells (0, 1, 2).

51. Number of hindwing cells (0, 1, 2, 3).

52. Petiolar scale (1) present, (2) reduced.

53. Petiolar scale (1) vertical and not inclined anteriorly, (2) moderately inclined anteriorly but with the anterior and posterior faces approximately the same length, (3) strongly inclined anteriorly and with the anterior face much shorter than the posterior face.

54. Venter of petiole (1) with a well-developed, rounded lobe, (2) with a slight or weakly developed lobe, (3) without a lobe, (4) with a well-developed, angular lobe.

55. First gastric tergite (1) elongated posteriorly, (2) vertical and not concealing the petiole in dorsal view, (3) projecting anteriorly, but not concealing the petiole in dorsal view, (4) projecting anteriorly and concealing the petiole in dorsal view.

56. First gastric tergite (1) smooth and without a groove or indentation, (2) with a groove or indentation for the reception of the basal portion of the petiole, (3) with a groove or indentation for the reception of the entire height of the petiole.

*Male characters*

57. Scape length (1) shorter than the length of funicular segments 2 + 3, (2) at most only slightly longer than the length of funicular segments 1 + 2 + 3, (3) much longer than the length of funicular segments 1 + 2 + 3 but not exceeding the occipital border, (4) much longer than the length of funicular segments 1 + 2 + 3 and exceeding the occipital border.

58. First funicular segment (1) cylindrical or cone-shaped, (2) barrel-shaped.

59. Second funicular segment (1) straight, (2) with a lateral bend.

60. Anteromedial clypeal margin (1) entire, without a central notch or concavity of any type; (2) with a broad, shallow concavity; (3) with a distinct central notch; (4) with a central projection, either pointed or rounded (sometimes only feebly projecting).

61. Anterior clypeal setae (1) short, about as long as the maximum diameter of the scape; (2) about the same length as the closed mandibles; (3) long and surpassing the distal edge of the closed mandibles.

62. Posterior clypeal margin (1) even with or anterior to the anterior surface of the antennal condyle, (2) between the ante-
rior and posterior surfaces of the antennal condyle, (3) even with or posterior to the posterior surface of the antennal condyle.
63. Pulp formula (1) 6:4, (2) < 6:4.
64. Number of mandibular teeth (1) < = 4, (2) 5 - 10, (3) > 10.
65. Number of mandibular denticles (1) < = 5, (2) > 5.
66. Apical tooth of mandible (1) absent (tip of mandible rounded and without a differentiated tooth), (2) distinct and shorter than subapical tooth, (3) subequal in length to subapical tooth, (4) slightly longer than subapical tooth, (5) elongate and much longer than subapical tooth.
67. Basal angle of mandible (1) distinct, with a well-developed tooth or angle separating the masticatory and basal margins, (2) weakly defined by a denticle, (3) indistinct, with a relatively unirrupted curve between the two margins and without a distinct tooth or angle.
68. Basal margin of mandible (1) smooth and without teeth or denticles, (2) denticulate distally, smooth proximally, (3) denticulate along entire surface.
69. Axilla (1) parallel or subparallel, (2) constricted mediately, (3) absent dorsally.
70. Axilla (1) entire, (2) with a suture medially.
71. Anterior axillary suture (1) straight, (2) angular medially.
72. Dorsal face of propodeum (1) longer than the declivitous face, (2) subequal in length to the declivitous face, (3) shorter than the declivitous face.
73. Radial cell (1) closed, (2) open.
74. Number of forewing cubital cells (0, 1, 2).
75. Number of forewing discoidal cells (0, 1, 2).
76. Number of hindwing cells (0, 1, 2).
77. Petiolar scale (1) vertical and not inclined anteriorly, (2) strongly inclined anteriorly and with the anterior face much shorter than the posterior face.
78. Venter of petiole (1) with a well developed lobe, (2) with a slight or weakly developed lobe, (3) without a lobe.
79. Attachment of petiole to gaster (1) narrow, (2) intermediate, (3) broad.
80. First gastral tergite (1) elongated posteriorly, (2) vertical and not concealing the petiole in dorsal view, (3) projecting anteriorly, but not concealing the petiole in dorsal view, (4) projecting anteriorly and concealing the petiole in dorsal view.
81. First gastral tergite (1) smooth and without a groove or indentation, (2) with a groove or indentation for the reception of the basal portion of the petiole, (3) with a groove or indentation for the reception of the entire height of the petiole.
82. Pygostyles (1) present; (2) present, reduced; (3) vestigial or absent.
83. Posterior margin of subgenital plate (1) convex, (2) even across entire width, (3) concave, (4) with a 'V'-shaped notch.
84. Paramere (1) divided by a membranous region, (2) entire.
85. Digitus (1) linear, without a down-turned tip; tip sometimes slightly swollen; (2) linear, with a slight ventral arch; (3) with a down-turned tip.
86. Cuspis (1) parallel with digitus, (2) ventral of digitus, (3) absent.
87. Ventral lobe of volsella (1) present as a swelling, (2) present as concave lobe, (3) absent.
88. Aedeagus (1) with teeth ventrally, (2) without teeth ventrally.

Subfamily-level characters

89. Hind coxal cavities (1) open, (2) closed.
90. Anterodorsal margin of hemiscutum (1) excised, (2) entire.
91. Lateral regions of hemiscutum sternite (1) retracted posteriorly relative to lateroventral hemiscutum tergite and with sternite and tergite fusion occurring for a length less than one half tergite length, (2) approximately the same length as lateroventral hemiscutum tergite and with sternite and tergite fusion occurring for a length greater than one half tergite length.
92. Pygidial (= anal) gland (1) present, (2) absent.
93. Cyclopentanoid monoterpenes production by the pygidial glands (1) present, (2) absent.
94. Acidopore (1) present, (2) absent.
95. Formic acid production (1) present, (2) absent.
96. Sting (1) fully developed, (2) reduced and non-functional.
97. Furcula (1) free from sting base, (2) fused with sting base.
98. Larval neck (1) well-defined, (2) reduced.
99. Larval hairs (1) abundant, (2) sparse.
100. Larval mandibles (1) heavily sclerotized, (2) lightly sclerotized.
101. Larval mandibles with (1) three teeth, (2) less than three teeth.
102. Larval maxillary palp and galea (1) paxilliform, (2) reduced to sensilla.
103. Larval sericteries (1) wide, (2) small.
104. Papal cocoons (1) present, (2) absent.

Cladistic analysis

The computer programs Hennig86 (Ver. 1.5), written by S. Farris, and PAUP (Ver. 3.0s), written by D. Swoford, were used to determine the most parsimonious tree(s) (as unrooted networks) for the dataset (Table 2). The Hennig86 options 'mh*' followed by 'bb*' and 'rt*' followed by 'bb*', and PAUP heuristic methods (using the default settings), were used to find these trees. Two analyses were performed on the dataset. First, all characters were treated as ordered (= additive) except 5, 12, 17, 24, 27, 28, 33, 39, 44, 54, 60, 69, 83, 86, and 87, which were considered unordered (= non-additive) because of the lack of obvious relationship among their states. In the second analysis all characters were treated as unordered. Character states were not explicitly polarized and the resulting trees were rooted using an outgroup. The subfamilies Anceuinae and Formicinae have been shown to be closely related to the Dolichoderinae (Baroni Urbani et al., 1992; Bolton, 1990; Shattuck, 1992a), and therefore genera within these subfamilies were selected as outgroups. The Anceuinae contains only a single extant species and this was included in the analysis. The subfamily Formicinae contains forty-nine extant genera placed in thirteen tribes (Bolton, 1994). For this study, four genera in four tribes (Camponotus: Camponotini, Formica: Formicini, Melophorus: Melophorini and Pareatrechina: Lasini) were selected. While the results presented below show relationships among the outgroup taxa, the characters used in this study were derived with primary concern for resolving relationships among taxa of the Dolichoderinae. Thus the relationships among the outgroup taxa of the Formicinae should not be
treated with confidence as the characters used to derive them may not be the most appropriate or informative for these taxa.

The robustness of the conclusions from the first analysis was evaluated by a bootstrap analysis. Hennig86 was utilized for this, in conjunction with custom-written software to construct input data files and to analyse the resulting trees. Five hundred replicates were completed which resulted in a total of 5343 most-parsimonious trees being found. The number of most-parsimonious trees occurring during any given replicate varied from one to seventy-eight. Two methods were used to calculate the representation of monophyletic sets within the replicates. In the first method, all trees were considered equal (i.e., individual replicates were not taken into account) and the representation of any given monophyletic set was calculated as the percent occurrence of that set within all trees found. In the second method, monophyletic sets were inversely weighted by the number of trees found during the replicate, then summed across replicates, and finally presented as the percent occurrence within all replicates. The rationale for this second approach was that some replicates would, by chance, be composed of a larger proportion of highly homoplastic characters than other replicates. These replicates would result in a larger number of most-parsimonious trees being found and would, therefore, contribute more monophyletic sets to the overall analysis when compared to replicates producing few trees. By taking into consideration the number of trees found, the contribution of each replicate can be equalized across all replicates. In practice, the method of calculating the representation of monophyletic sets within the bootstrap replicates had only a minor effect on the placement of sets relative to each other. The only effect was to slightly decrease the percent representation of all sets found using the second method (weighted) when compared to the first (total occurrence). Because of this, the second method was used to calculate the values presented in this study.

Finally, to assess the impact of relaxing the parsimony assumption used during the cladistic analysis, trees slightly longer than the most-parsimonious were examined. These suboptimal trees were used to determine how many steps must be added to upset relationships occurring in the most-parsimonious tree found during the first analysis. The results indicate that some topologies do not occur in trees one step longer than the shortest, while others are retained in trees four steps longer. These less parsimonious trees were found using PAUP and retaining all trees one to four steps longer than the most parsimonious (trees greater than four steps longer than the most parsimonious were too numerous to be retained using the available computer hardware).

Initial character selection and coding

During the original selection and coding of characters, the number of mandibular denticles in workers (char. 12) and queens (char. 39) were coded with one less state each (the last two states as listed above were combined as a single state). Analysis of this dataset using ordered characters resulted in eight equally most parsimonious trees being found. In this set of trees, the placement of two taxa, Leptomyrmex and Linepithema, was especially notable. These taxa occurred as sister genera and were placed basal to the Axinidris + Dolichoderus + Liometopus + Tapinoma + Technomyrmex clade in five of the trees, whereas in the remaining three trees Leptomyrmex was placed basal to all other dolichoderine genera and Linepithema was placed near the base of the Bothriomyrmex + Dolomyrmex + Dorymyrmex + Forelius + Loweriella clade (see Fig. 1 for the approximate
placement of these groups relative to each other in the eight equally most parsimonious trees). These two placements were surprising because they occurred in widely separate regions of the trees.

To determine the cause of these disparate placements, the character states suggesting a sister-group relationship between *Leptomyrmex* and *Linepithema* were examined. These states were: (12) number of mandibular denticles in workers greater than five, (39) number of mandibular denticles in queens greater than four, (40) apical tooth of mandible in queens elongate and much longer than the subapical tooth, (65) number of mandibular denticles in males greater than five, and (72) dorsal face of propodeum in males longer than the declivitous face. Four of the five characters unifying these taxa were mandibular and three involved an increase in the number of teeth and denticles compared to other taxa within the subfamily. A closer examination of mandibular morphology revealed that although these two taxa share the characters as originally coded, they differed significantly in detail suggesting that this apparent similarity was due to convergence rather than homology. In *Leptomyrmex* the mandibular teeth and denticles occur in a graded size series along the masticatory margin, with larger teeth anteriorly and smaller teeth/denticles posteriorly. In *Linepithema*, teeth and denticles are distributed in sets along the entire length of the masticatory margin, with both occurring anteriorly as well as posteriorly (see Shattuck, 1992b, for additional details). It seems likely that the increase in number of teeth and denticles has occurred by different methods in these two taxa and that these characters do not support a close relationship between *Leptomyrmex* and *Linepithema*. Reanalysis after recoding characters 12 and 39 (and those taxa affected) to more accurately reflect these traits supports this conclusion, as only three equally most-parsimonious trees were found and the placements of *Leptomyrmex* and *Linepithema* were stable across all trees.

Analysis with this modified dataset resulted in three equally most parsimonious trees being found (length 495, consistency index 0.36, retention index 0.51). Among these three trees, only a single genus varied in placement. *Ephorella* was placed as the sister group of (i) *Bothriomyrmex* + *Doleromyrmex* + *Doromyrmex* + *Forestius* + *Loweriella*, (ii) *Froggattella* + *Iridomyrmex* + *Ochetellus* + *Papyrius* + *Philidris* + *Turneria*, or (iii) *Aniliarius*. The most likely cause for this lack of resolution is the absence of known queens and males in *Ephorella*. Additionally, the worker caste is known from only a single individual and its slightly damaged condition prevents examination and coding of worker characters 14 and 15 (basal angle and margin of mandible), 25 (shape of fourth gastric sternite), and 26–31 (proventricular morphology). These characters were coded as unknown in the analysis. As a result, an exact placement of *Ephorella* within the subfamily was difficult to determine. It seems clear that additional material, including queens and males, will be required before this taxon can be placed with confidence. Because of this, *Ephorella* was excluded from further analysis in this study.

**Results**

Using the full dataset without *Ephorella*, the first analysis method (coding characters ordered and unordered) resulted in a single, fully resolved, most parsimonious tree (Fig. 1) being found by both Hennig86 and PAUP (length 491, consistency index 0.36, retention index 0.52). The results of the 500-replicate bootstrap are presented in Fig. 1, where each node is labelled with the percent representation of the set subtended by that node. The occurrence of sets within the single most parsimonious tree varied from 3% to 91%. Also shown in Fig. 1 is the number of steps which must be added to this most parsimonious tree to cause disruption of relationships (numbers preceded by ' + ' or ' > '). These values are presented at the node which is basal to the taxa affected by the addition of the number of steps indicated.

When this same dataset was analysed with all characters treated as unordered (the second analysis method) Hennig86 found fifty-six equally most parsimonious trees (length 431) when using both 'mh*:bh*' and 'tr:rb*' search methods. PAUP found seventy most parsimonious trees (length 431) when using the heuristic search method and random addition sequence with five replicates. These seventy trees included the fifty-six found by Hennig86. A majority-rule consensus tree was calculated for these seventy trees and is shown in Fig. 2, together with the per cent representation of each subset.

**Discussion**

Data supporting groups found during the cladistic analyses are discussed using (i) character data (character state assignments on trees), (ii) tests of dataset structure or robustness (bootstrapping, effects of allowing the addition of steps to trees), (iii) group representation among the set of most parsimonious trees, and (iv) biogeographic considerations. Characters are discussed in the format 'character number (state number)' to save space. The numbers follow those listed above under *Taxa and characters examined*. Geographic distribution data are derived from Shattuck (1992b). Those groups found during both analyses (with ordered and unordered characters, and with all characters unordered) will be discussed first followed by those groups which differ between the two analyses.

**Groups found during both analyses**

The placement of *Leptomyrmex* as basal to the remaining Dolichoderinae is supported by characters 2(2), 8(2), 22(2), 27(2), 31(2) and 56(2) (these characters unite all the taxa of the Dolichoderinae less *Leptomyrmex*). The bootstrap analysis suggests fairly good support for such a large, basal group, with 12.2% representation in the replicates. Although only one step needs to be added to the tree to disrupt the group, the result is to place *Leptomyrmex* as the sister group to *Dolichoderus + Liometopum + Axinidris + Tapinothrix + Technotermes*, which is still near the base of the Dolichoderine clade. This basal placement also occurred in 80% of the most parsimonious trees when all characters were coded unordered. These results for *Leptomyrmex* are consistent with most previous treatments of the genus, which have considered the taxon to be morphologically divergent (thus its placement in a monotypic tribe) and relatively primitive within the subfamily. Biogeographically, this basal placement is supported by the occurrence of fossil *Leptomyrmex* in the Dominican amber (Baroni Urbani, 1980; Baroni Urbani & Wilson, 1987).
combined with its current, extant distribution in Australia and New Guinea. This pattern suggests a Gondwanan origin.

The group Dolichoderus + Liometopum + Axinidris + Tapinoma + Technomyrmex is supported by characters 13(1), 15(3), 64(3) and 69(2). The bootstrap analysis provides moderate support, with the group present in 33.5% of the replicates. It is fairly resistant to adding steps to the tree, requiring three additions before relationships are disrupted. The group also occurred in 86% of the trees found when all characters were coded unordered. The monophyly of Dolichoderus + Liometopum + Axinidris + Tapinoma + Technomyrmex has not been suggested before. Dolichoderus has generally been considered a primitive member of the Dolichoderinae and has been placed in its own tribe (Dolichoderini). The other taxa have been treated as members of the Tapinomini, a group consisting of most of the remaining dolichoderines except Dolichoderus and Leptomyrmex. Liometopum is fairly distinct within the subfamily, enough so that Dlussky & Fedoseeva (1988) placed it in a separate tribe,
Fig. 2. Majority-rule consensus tree for seventy equally parsimonious trees (length 431, ci: 0.41, ri 0.50) found when all characters were treated as unordered. Numbers at nodes are the percent representation of the group within the set of most-parsimonious trees.

the Liometopini. Its placement within the subfamily has not been speculated on before, although it is superficially similar to Azteca in its overall habitus, polymorphic worker caste, arboreal habits, and occurrence in the New World.

Within this clade, Axinidris + Tapinoma + Technomyrmex is well supported by characters 21(3), 23(5), 24(2), 25(2), 49(1), 51(0), 53(3), 55(3), 77(2) and 80(3) (it should be noted that 21(4), 23(6), 55(4) and 80(4) occur in Tapinoma + Technomyrmex, but as these states are considered derived from the states which occur in Axinidris when characters are coded as ordered, this is consistent with support for the entire group). This set is one of the most strongly supported within the subfamily, being present in 86.5% of the bootstraps, requiring the addition of more than four steps before it is disrupted, and being present in all seventy of the trees found in the second analysis. The pair Tapinoma + Technomyrmex are very similar morphologically and their sister relationship is supported by the characters 16(3), 18(3), 21(4), 22(3), 23(6), 47(3), 52(2), 55(4), 72(3) and 80(4). This pair had
the highest occurrence in the bootstrap replicates, being present in 91.0%; requires more than four steps to be added to the tree before disruption; and occurred in all trees found during the second analysis. *Tapinoma* and *Technomyrmex* have been considered closely related by most previous workers, and *Aznaridris* was placed near them in a recent review of that genus (Shattuck, 1991).

Most of the genera in these groups are broadly sympatric over much of their ranges, especially with their closest relatives. *Dolichoderus* is essentially world-wide although it is absent from Africa and the Middle East to India. *Lionetopum* is Holarctic and completely sympatric with *Dolichoderus* and *Tapinoma*. *Aznaridris* is limited to sub-Saharan Africa, where it is sympatric with both *Tapinoma* and *Technomyrmex*. *Tapinoma* and *Technomyrmex* have similar ranges in southern Africa, southeast Asia and Australia, although *Tapinoma* is more widely distributed in the New World, Europe and northern Africa. These distribution patterns are consistent with these taxa being closely related.

*Aztecra* was placed basal to the remaining taxa of the Dolichoderinae (those not discussed above) by both character coding methods. The only instability in this placement is that two taxa, *Aniliadris* and *Anonychomyrma*, varied significantly in their placement and were placed basal to *Aztecra* when characters were coded as ordered and contained within the sister group of *Aztecra* when characters were coded unordered. Both coding methods, however, placed *Aztecra* in approximately the same central location within the subfamily as a whole.

The group *Froggattella + Iridomyrmex + Ochetellus + Pappius + Philidris + Turmeria* forms a distinct, Indo-Australian-based set of taxa supported by characters 4(1), 14(2), 23(3), 25(2), 28(2), 32(1), 43(2) and 80(1). The group was well supported in the bootstrap analysis, being present in 54.6% of the replicates, requires the addition of three steps to the tree before it is no longer monophyletic, and occurred in all of the trees when characters were coded unordered. Four of the genera (*Ochetellus, Pappius, Iridomyrmex* and *Philidris*) have until recently been treated as congeneric (Shattuck, 1992b), and the remaining two (*Froggattella* and *Turmeria*) were treated as sister taxa and were thought to be close to *Iridomyrmex* during a study of *Turmeria* (Shattuck, 1990). The available evidence strongly supports this as a natural grouping.

The set comprised of *Bothriomyrmex + Dryopterismyrmex + Forelius + Loweriella* is supported by the characters 6(2), 15(1), 35(2), 57(2), 58(1), 83(1) and 84(2) (state 57(3) occurs in *Bothriomyrmex*, and the state is unknown in *Loweriella*; character 83 is unknown in *Loweriella*; character 84 is unknown in *Forelius* and *Loweriella*). The group occurred in 27.0% of the bootstrap replicates, requires four additional steps to be added to the tree to disrupt it, and was found in 97% of the trees when characters were coded unordered. Within this set, *Dryopterismyrmex* was found to be the sister taxon of *Forelius* and *Bothriomyrmex* the sister taxon of *Loweriella*. These relationships are supported by their distribution patterns, with *Dryopterismyrmex* and *Forelius* occurring in North and South America and being broadly sympatric. *Bothriomyrmex* and *Loweriella* are similarly sympatric, with *Bothriomyrmex* occurring from Australia north and west into Europe, and *Loweriella* limited to northern Borneo.

Morphologically, *Bothriomyrmex* and *Loweriella* are very similar and share several characters not found in other dolichoderine taxa. *Doromyrmex* and *Forelius* are less similar, but this is likely caused by the specializations found within *Doromyrmex*. Six genus-groups names have been proposed within *Doromyrmex*, based largely on the configuration of the palps, pscammophore and propodeal angle.

**Taxa whose placements differ between analyses**

Although the majority of taxa could be placed with confidence, several genera presented difficulties when using the current dataset. *Doromyrmex* and *Lineipithema* showed relatively minor instability in being placed basal to *Doromyrmex* and relatives when characters were coded as ordered, and as basal to *Iridomyrmex* and relatives when characters were coded unordered. Since the groups containing *Doromyrmex* and *Iridomyrmex* were found to be closely related in both analyses, this variation in the placement of *Doromyrmex* and *Lineipithema* is not completely unexpected.

In contrast to this, *Aniliadris* and *Anonychomyrma* differed significantly in their placement when the character coding method was varied. They were placed basal to *Doromyrmex* and relatives when characters were coded as ordered, but were placed basal to *Dolichoderus* and relatives when coded as unordered. These two placements suggest significantly different relationships to other members of the subfamily. The instability in *Aniliadris* may be explained by its morphology and habits. As mentioned by Shattuck (1992b), this genus has been collected only a few times and is one of the most unusual in the subfamily, possessing many autapomorphic character states. This specialization might be expected to make phylogenetic placement difficult. *Anonychomyrma* on the other hand, is common within its distributional range and has typical dolichoderine morphology. The most unusual feature of the genus is that no autapomorphies could be found to define it, and Shattuck (1992b) diagnosed it by a unique set of character states which individually occurred in other taxa. This lack of autapomorphies would suggest that *Anonychomyrma* might not be monophyletic and therefore would be expected to be difficult to place within a cladistic analysis.

However, the monophyly of *Anonychomyrma* is indicated by (i) the overall morphological similarity of the taxa placed in the genus, (ii) the degree of variation among the included taxa which is similar to or less than that found in other genera of the subfamily, (iii) the relatively limited and overlapping geographic distribution of known taxa, and (iv) the ecological similarity among the included taxa. Additionally, Shattuck (1992b) could not find any indication, based on a detailed morphological analysis of workers, queens, males and larvae, that *Anonychomyrma* was a composite of unrelated taxa. This led to the recognition of *Anonychomyrma* as a valid genus within the subfamily.

Another potential cause for the unstable placement of *Anonychomyrma* would be the presence of a large number of unknown and/or polymorphic characters (those coded as "?" during the analysis). However, the number of unknown/polymorphic characters for *Anonychomyrma* is not unusually high when compared to other taxa in this analysis. Specifically, nineteen characters were coded as "?" for *Anonychomyrma*, which is less
than the number found in Bothriomyrmex (25), Loweriella (64), Tapinoma (24) and Technomyrmex (23), and is the same as that for Iridomyrmex. These latter taxa were placed relatively stably within this analysis, suggesting that this is not the cause for the instability found in Anonychomyrma.

**Higher classification within the Dolichoderinae**

The tribal classification previously used in the Dolichoderinae was abandoned by Shattuck (1992b). The results of this study support that action in that only one of the earlier tribes, Leptomyrmicini, was found to be monophyletic and the four monotypic tribes Anonychomyrminini, Axinidrini, Dolichoderini and Lioinetopini made the tribe Tapinomatini paraphyletic. At the same time, this study does suggest several well defined monophyletic sets of genera which may benefit from informal naming. These sets include: Dolichoderus genus-group (Axinidris, Dolichoderus, Lioinetopum, Tapinoma, Technomyrmex), Iridomyrmex genus-group (Froggattella, Iridomyrmex, Ochettellus, Papyrius, Philidris, Turneria), Leptomyrmex genus-group (Leptomyrmex) and Dorymyrmex genus-group (Bothriomyrmex, Dorymyrmex, Forellus, Loweriella). The placement of the remaining taxa (Anonychomyrma, Antilidris, Azteca, Linepithema, Dolieromyrma) were not well supported with the current dataset and their placement varied when the analytical method was changed. Because of this, the above genus groups should be considered provisional until these remaining taxa can be placed with confidence among the other members of the Dolichoderinae.

**Conclusions**

A cladistic analysis of the relationships among twenty-one genera of the subfamily Dolichoderinae, using 104 characters, resulted in a single fully resolved, most parsimonious tree being found when a combination of ordered and unordered characters were used. When all characters were coded as unordered, seventy most parsimonious trees were found. A majority rule consensus tree was calculated from these seventy trees and this tree compared to the single tree found using the previous character coding method. The following results were found to be in common to both methods. Leptomyrmex was placed basal to the remainder of the subfamily and the monophyletic sets Dolichoderus + Lioinetopum + Axinidris + Tapinoma + Technomyrmex, Froggattella + Iridomyrmex + Ochettellus + Papyrius + Philidris + Turneria, and Bothriomyrmex + Dorymyrmex + Forellus + Loweriella were suggested. These sets were consistent with available biogeographic information and were well supported during a bootstrap analysis. The genera Linepithema and Dolieromyrma showed a small amount of instability in moving between neighbouring sister groups when the character coding method changed. The genera Antilidris and Anonychomyrma were the only taxa which were difficult to place with confidence as they showed major differences in their placements between the two character coding methods.

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**References**


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