

Phylogenetic Implications of Army Ant Zoogeography (Hymenoptera: Formicidae)¹

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ABSTRACT

Ann. Entomol. Soc. Am. 72: 462-467 (1979)

Army ants of the subfamilies Dorylinae and Ecitoninae are distributed throughout the Old and New World tropics, respectively. If these distribution patterns are examined relative to past geological events (i.e., continental drift) and assuming (1) that the dorylines arose in tropical habitats not earlier than the late Cretaceous or early Tertiary, and (2) that the apterous condition in the queens appears early in the acquisition of army ant traits, then it follows that the army ants as presently constituted, are not diphyletic but triphyletic. Evidence suggests that these ants arose convergently on 3 separate occasions in 3 separate locations; the Aenictini in Laurasia, the Dorylini in Africa, and the Ecitonini-Cheliomyrmecini in South America.

Army ants are found throughout most of the world's tropical and subtropical regions. Once viewed as a monophyletic group of species, the "true army ants" are now organized into 2 subfamilies. The Old World species comprise the subfamily Dorylinae; the New World species the Ecitoninae (Snelling 1979). This taxonomic arrangement reflects more accurately the suggestions and evidence for polyphyly in the army ants proposed by Brown (1954), Gotwald (1969), and Gotwald and Kupiec (1975). Army ant behavior includes 2 fundamental features: group predation and nomadism (Wilson 1958); but these patterns are not restricted to the dorylines and ecitonines and occur, to a limited extent, in some species of the subfamily Ponerinae (Wilson 1958, Gotwald and Brown 1966). These army ant behavior patterns thus appear to have been arrived at convergently in some tropical ponerine species.

The Dorylinae are divided into 2 tribes. The tribe Aenictini is composed of a single genus, *Aenictus*, represented by 34 species in Asia, New Guinea, and Queensland and by ca. 15 species in Africa (Fig. 1) (Wilson 1964). The Dorylini, also with a single genus, *Dorylus*, is well established in Africa with about 50 species, but poorly represented in Asia, with only 4 species (Fig. 1). Wilson (1964) pointed out that both Africa and the Indo-Australian areas contain distinctive endemic species of *Aenictus* and *Dorylus*. In the Ecitoninae there are ca. 147 species arrayed among 5 genera within 2 tribes, the Ecitonini and Cheliomyrmecini (Fig. 2) (Watkins 1976). Included in the Ecitonini is the widely dispersed genus *Neivamyrmex* that ranges to 40° latitude on either side of the equator. This genus contains the only army ant species that survive cold, temperate region winters.

The purpose of this paper is to examine these present-day distribution patterns in relationship to past geological events and to delineate the phylogenetic implications of this relationship. The observations recorded here are the product of a 10-yr period of research which included extensive field work at several African locations. An abridged and preliminary version of the conclusions drawn here was published previously (Gotwald 1977).

Discussion

Throughout the taxonomic literature, the cerapachyine ants are most frequently suggested as probable ancestors to the army ants. Emery (1895, 1901, 1904), e.g., concluded that the cerapachyines linked the dorylines to the subfamily Ponerinae. So convinced was Emery (1895) of this relationship that he even placed the cerapachyines in a tribe within the Dorylinae, although he later relented and described for them the section Prodorylinae in the Ponerinae. Because of their distinctiveness, the cerapachyines were eventually elevated to subfamily status, a position widely accepted by myrmecologists until when they were again relegated to tribal status within the Ponerinae (Brown 1975). Irresolvable as their taxonomic history appears, the cerapachyines remain viable ancestral candidates for the dorylines and/or ecitonines. Even though the true army ants are no longer regarded as monophyletic, Brown (1975) pointed out that "... Emery's notion that the Cerapachyini gave rise to the Dorylinae may have something to it still. . . ." Brown continued by suggesting that the Ecitoninae in the New World "and/or" *Aenictus* in the Old World evolved independently from cerapachyines. "At the moment," Brown (1975) noted, "we don't know enough to make more than wild guesses about these possibilities."

But if the dorylines are monophyletic, contrary to prevailing opinion, should it not be possible to demonstrate this relationship cladistically? Phylogenetic relationships investigated in this way, i.e., by means of cladistic analysis, are inferred on the basis of shared derived character-states (referred to as synapomorphy) (Hennig 1966). A preliminary attempt was made to produce such an analysis of the worker caste.

Seven morphological characters were selected for consideration from a precursory list of 15 characters. Theoretically, characters should be eliminated from consideration if found only in the primitive or plesiomorphic state and/or if they qualify as "loss character states." The latter are considered of little value cladistically because parallel losses are common. For example, ocelli are absent in all doryline workers, and it is not reasonable to assume that the absence of ocelli is a state derived from a common ancestor. For this reason, ocelli were

¹ Received for publication Jan. 30, 1978.