to eliminate characters with little information content. Second, if we accept the assumption that the true army ants are diphyletic, as reflected in their higher classification, the analysis should be extended to include the subfamily Ponerinae, especially the Cerapachyini. A cladistic analysis of this magnitude is not within the province of this paper. It is my assumption in this paper that the army ants are at least diphyletic.

Army ants are completely absent from the fossil record and little can be inferred about their origins from the general fossil ant fauna. Prior to the discovery of the Cretaceous ant, *Sphecomyrma freyi,* an ant for which the subfamily Sphecomyrminae was described, the earliest known ant fossils were of Eocene age (Carpenter 1929). Other Cretaceous ants have been subsequently discovered and all have been assigned to the Sphecomyrminae (Burnham 1978). Although Carpenter (1930) noted that since some genera in the Florissant shales showed Neotropical affinities and was "suggestive that during the mid-Tertiary the nearctic ant fauna was rich in genera which are now restricted to the neotropical region," army ants of the Neotropical genera are not present. Even though Wheeler (1914) found the Baltic Amber to contain a diverse ant fauna, in which 56% of the genera represented are extant, the Dorylinae are not represented. Wheeler (1914) speculated that the dorylines were either restricted to the tropics during the Oligocene or were so subterranean in their habits as to preclude their entrapment in amber.

The antiquity of social behavior in insects remains enigmatic, although a member of the termite family Hodotermitidae from the mid-Cretaceous of Labrador indicates that sociality among insects was developed at least by the early Cretaceous (Carpenter 1976). That the development of sociality in the ants also extends back to a time prior to the mid-Cretaceous was established with the discovery of *S. freyi,* the earliest known fossil that can be clearly assigned to the aculeate Hymenoptera (Wilson et al. 1967a,b). Found in amber from the Magothy Formation, *S. freyi* can be dated with reasonable certainty to the lower part of the Upper Cretaceous. Since this ant exhibits a mosaic of wasplike and antlike characters, Wilson et al. (1967a,b) concluded that while the discovery of *S. freyi* pushed back the origin of social life in the Hymenoptera to ca. 100 million yr ago, social life in this order might not be much older than that. The possibility does exist that the poneroid complex of ants (to which the Dorylinae and Ecitoninae are assigned) and the myrmecioid complex (which is linked to the solitary wasps by *S. freyi*) diverged from one another before these groups fully acquired sociality (Wilson et al. 1967a,b). Thus the family Formicidae may be diphyletic. Nevertheless, the primitive nature of *Sphecomyrma,* the apparent widespread distribution of sphecomyrmine ants, and the diversity of the Oligocene ant fauna, together suggest a late Cretaceous, possibly early Tertiary (or even later), origin for the doryline and ecitonine ants. Schneirla (1971) hypothesized a similar time of origin for these ants. In the Old World, the distinctive endemic elements of both Aenictini and Dorylini prompted Wilson (1964) to speculate that this faunal differentiation occurred "largely or entirely since Miocene times."

In order to assess the impact of past geological events on the distribution of doryline and ecitonine ants, it is necessary to evaluate the effectiveness with which these army ants disperse. Colonies of doryline and ecitonine ants each possess a single, apterous queen technically referred to as a dichthadiigyne (Schneirla 1971, Wilson 1971). This type of female reproductive is found only in the dorylines and ecitonines and in some species of the Ponerinae that are evolving toward the army ant adaptive syndrome (Gotwald and Brown 1966). Because winglessness has already evolved in such incipient, non-doryline, non-ecitonine army ants as *Simopelta oculata* (Gotwald and Brown 1966), it is probable that the apterous trait appears early in the acquisition of army ant characteristics. Queen winglessness coupled with the fact that new army ant colonies result from the fission of existing colonies (and not from single, mobile foundress queens) (Schneirla 1971, Raignier 1972) make the army ants poor dispersers, particularly across water barriers where rafting or air-borne mechanisms are the only feasible means of dispersal.

The biogeography of some animals, such as nematodes (Ferris et al. 1976) and mammals (Keast 1972), can be explained, in part, as a consequence of continental drift. Brothers (1975) provided an elaborate scheme for the dispersal of mutillid wasps that takes into consideration the relative positions of the continents during the course of time since the Permian. Indeed, plate tectonics can be used to explain the distribution of "tropical disjuncts" [i.e., related organisms that are found throughout the world's tropical regions but are now separated by oceanic barriers (Keast 1972)]. But to do so, the ancestors of such organisms must have been well established on the postulated pre-Jurassic supercontinents.

The theory of continental drift holds that today's continents once formed a single land mass (Pangaea) which, by the late Triassic to mid-Jurassic, began to split into a northern cluster of continents (Laurasia) and a southern cluster (Gondwana) (Dietz and Holden 1970). Subsequently, Laurasia and Gondwana fragmented into the northern and southern continents, respectively. By the end of the Cretaceous, South America and Africa were well separated and the South Atlantic had widened to 3000 km (Dietz and Holden 1970). Early in the Cenozoic, the North Atlantic rift completed the breakup of Laurasia, separating North America from Eurasia (Dietz and Holden 1970). Thus by the end of the Cretaceous, the 3 tropical areas in which the "true army ants" are currently found were separated by substantial oceanic barriers. Even Arabo-Africa and Eurasia were separated from one another during much of the Mesozoic and Tertiary by the pre-Mediterranean Tethys Sea (Cooke 1972).

Doryline and ecitonine ants superficially resemble tropical disjuncts, although an exchange of *Dorylus* and *Aenictus* between tropical Asia and Africa occurred in relatively recent times. Since the Dorylini and Aenictini and the ecitonines arose after the breakup of Gondwana and Laurasia, a factor that prevented effective dispersal, they do not share a common ancestry. Instead they arose convergently on 3 separate occasions at 3 separate tropical loci. The probability is low that the army ants, as poor dispersers, proceeded to move out from a single place of origin across the significant ocean barriers sep-