

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

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ABSTRACT

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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

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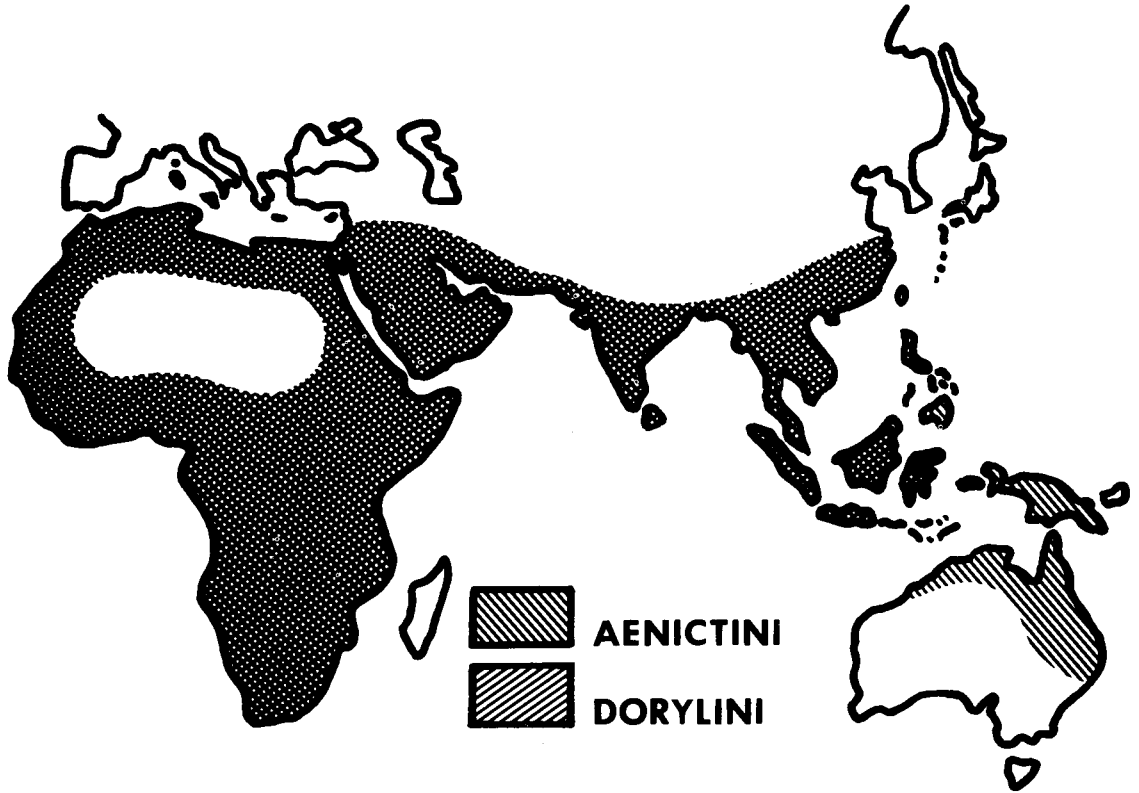


FIG. 1.—Distribution of Old World army ants of the tribes Aenictini and Dorylini.

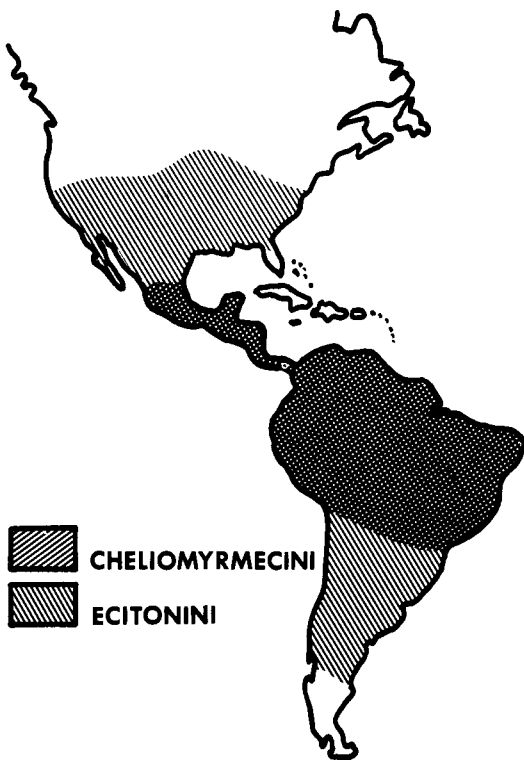


FIG. 2.—Distribution of New World army ants of the tribes Cheliomyrmecini and Ecitonini.

dropped from the analysis. The elimination of several such characters was the limit to which characters for this investigation were weighted (see Kim and Ludwig (1978) for a cogent discussion of the cladistic process). Even so, the compound eyes, which are reduced or absent in army ants, were arbitrarily retained in the analysis. Likewise, segmentation in the palpi and antennal funiculus and the promesonotal suture were included, even though they represent in their apomorphic character states simplification through reduction or fusion. Only the segmentation of the waist and the presence of pygidial spines can be considered additive or unique. The characters selected for analysis are presented in Table 1. The plesiomorphic state for each character, as found in the family Formicidae, is provided, and all apomorphic states for each character as found in the Ecitoninae and Dorylinae are included. Note that some characters, such as the number of antennal segments, form a morphocline series, i.e., they exist in more than one apomorphic state. The distribution of the character-states for the 7 selected characters among the New and Old World army ant genera and subgenera is given in Table 2. Based on this distribution a matrix of synapomorphy was assembled (Table 3), in which each numerical entry constitutes the number of shared derived character-states between any 2 taxa. Note that the 6 subgenera of *Dorylus* (*Alaopone*, *Anomma*, *Dichthadia*, *Dorylus*, *Rhogmus*, and *Typhlopone*) are treated individually.

All attempts to produce a cladogram that adequately explained, in phylogenetic terms, the apparent synapomorphies met with failure. Examination of the matrix of

Table 1.—Characters selected and their character-states for major workers of New and Old World army ants. Plesiomorphic states are for the family Formicidae.

Character	Plesiomorphic		Apomorphic	
No. of segments in maxillary palpus	6	2	1	
No. of segments in labial palpus	4	3	2	
No. of segments in antennal funiculus	11	10	9	8
Compound eyes	large, lateral	reduced	absent	
Promesonotal suture	complete	absent		
Segmentation of waist	uninodal	binodal		
Pygidial spines	absent	present		

Table 2.—Distribution of character-states of 6 characters. 0 = plesiomorphy, 1, 2, 3 = apomorphy and morphocline series. Characterstates: 1. maxillary palpus 6-(0), 2-(1), or 1-segmented (2); 2. Labial palpus 4-(0), 3-(1), or 2-segmented (2); 3. Antennal funiculus 11-(0), 10-(1), 9-(2), or 8-segmented (3); 4. Compound eyes large (0), reduced (1) or absent (2); 5. Promesonotal suture complete (0) or absent (1); 6. Waist uninodal (0) or binodal (1); 7. Pygidial spines absent (0) or present (1).

Tribe	Characters	1	2	3	4	5	6	7
Cheliomyrmecini	<i>Cheliomyrmex</i>	1	1	0	2	1	0	0
	<i>Eciton</i>	1	1	0	1	1	1	0
Ecitonini	<i>Labidus</i>	1	1	0	1	1	1	0
	<i>Neivamyrmex</i>	1	1	0	1	1	1	0
	<i>Nomamyrmex</i>	1	1	0	1	1	1	0
Aenictini	<i>Aenictus</i>	1	2	2	2	1	1	0
	<i>Alaopone</i>	2	2	3	2	0	0	1
	<i>Anomma</i>	1	2	1	2	0	0	1
Doryliini	<i>Dichthadia</i>	1	2	0	2	0	0	1
	<i>Dorylus</i>	1	2	1	2	0	0	1
	<i>Rhognus</i>	1	2	1	2	0	0	1
	<i>Typhlopone</i>	1	2	1	2	0	0	1

synapomorphy reveals that fewest derived character-states are shared by *Dorylus* and its subgenera with the New World genera *Eciton*, *Labidus*, *Neivamyrmex*, and *Nomamyrmex*. This is supportive of the taxonomic separation of New and Old World species into 2 subfamilies. But *Cheliomyrmex* shares as many derived character-states with the New World genera as it does with *Dorylus*. This is true of *Aenictus* as well, and any attempt to construct a cladogram is confounded by these 2 genera, at least for the selected characters. For instance, the binodal waist, an apomorphic character-state, is shared by *Aenictus* and all New World genera but *Cheliomyrmex*; however, the antennal funiculus of *Aenictus* and *Dorylus* is reduced (i.e., derived), while that of all New World genera is plesiomorphic. A cladogram cannot be constructed unless certain character-states are disposed of as convergently developed.

Resolution of this problem may be effected in possibly one of two ways. First, a much larger set of characters could be assembled and a weighting system applied

Table 3.—Matrix of synapomorphy based on 7 characters for the subfamilies Ecitoninae and Dorylinae. Numbers represent totals of shared derived character-states.

Tribe	Genus	<i>Cheliomyrmex</i>	<i>Eciton</i>	<i>Labidus</i>	<i>Neivamyrmex</i>	<i>Nomamyrmex</i>	<i>Aenictus</i>	<i>Alaopone</i>	<i>Anomma</i>	<i>Dichthadia</i>	<i>Dorylus</i>	<i>Rhognus</i>	<i>Typhlopone</i>
Cheliomyrmecini	<i>Cheliomyrmex</i>	X											
	<i>Eciton</i>	3	X										
Ecitonini	<i>Labidus</i>	3	5	X									
	<i>Neivamyrmex</i>	3	5	5	X								
	<i>Nomamyrmex</i>	3	5	5	5	X							
Aenictini	<i>Aenictus</i>	2	3	3	3	3	X						
	<i>Alaopone</i>	2	0	0	0	0	2	X					
	<i>Anomma</i>	3	1	1	1	1	3	4	X				
Doryliini	<i>Dichthadia</i>	3	1	1	1	1	3	4	5	X			
	<i>Dorylus</i>	3	1	1	1	1	3	4	6	5	X		
	<i>Rhognus</i>	3	1	1	1	1	3	4	6	5	6	X	
	<i>Typhlopone</i>	3	1	1	1	1	3	4	6	5	6	6	X

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 Magog 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 myrmecoid 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-

arating the continents. Brown (1973) noted in his zoogeographical analysis of Hylean and West Africa ant fauna that the Atlantic Ocean, for instance, has been a "formidable barrier" even to those genera that most likely could have rafted across the ocean in twig or log-housed nests. However, he also pointed out that there is a great deal of sharing of species groups between the Ethiopian and Oriental regions, a pattern to which the Old World dorylines conform. The existence of *Sphecomyrma* in the upper Cretaceous points to an earlier origin for the ants, and thus Gondwana, before it fragmented, was probably populated with an ant fauna distinguished by its lack of diversity. These earlier forms were able to cross the then surmountable barriers between the newly forming continents and served as the stock from which all extant ants arose.

However, ant distribution patterns are complicated by the appearance and disappearance of numerous land bridges linking the continents and by the evolution of species with improved dispersal capabilities. Late evolving genera such as *Pheidole*, *Crematogaster*, *Tetramorium*, and *Camponotus* have undergone a worldwide expansion since the mid-Tertiary, which speaks for their dispersal effectiveness (Brown 1973). If the "true army ants" were monophyletic as previously supposed, can land bridges explain their present-day distribution patterns? Wilson (1964) noted that, although army ants are not "adept" at crossing true barriers, "they are capable of living in a remarkable variety of marginal habitats that might serve as bridges in times of climatic amelioration."

Geological and faunal evidence suggests that evolution and diversification proceeded in Africa during long periods of isolation (Cooke 1972). Specifically, the Ethiopian Region remained in isolation from the late Cretaceous to the Miocene (Moreau 1952). Faunal exchanges, at least mammalian, were rare, the only ones of general significance probably occurring during the late Oligocene, late Miocene, and late Pliocene (Cooke 1972). South America was even more isolated in the Tertiary and remained so until the Panama bridge was established at the end of the Tertiary (Patterson and Pascual 1972). Therefore significant faunal exchange did not begin until then, at least in organisms that could not be wind-borne or raft easily. Ant distribution patterns tend to confirm both the Eurasian-African connection and the isolation of South America, and certainly the triphyletic hypothesis of army ant origins, in light of this evidence, better explains current distribution patterns than does a monophyletic or even diphyletic origin.

One other series of land bridges must be considered as a possible dispersal route for New and Old World faunal exchange. Eurasia and North America were periodically connected during much of the Tertiary by a North Pacific bridge that sometimes permitted intense faunal exchange. Kistner (1972) suggested, based on the relationship of Old and New World staphylinid myrmecophiles, that *Neivamyrmex*, a New World ecitonine, and *Aenictus* may share a common ancestry. This in turn suggests that the North Pacific bridge may have served as a dispersal route in this hypothesized relationship. However, Darlington (1957) pointed out that the groups exchanged across this bridge probably belonged to "rel-

atively cool, but not alpine, environments." For instance, some warmer climate mammals of Asia, such as civets, mongooses, and fruit bats, never crossed to North America (Darlington 1957). It is doubtful that such tropical forms as the army ants (including *Neivamyrmex*, which appears to have come from tropical South America) could have dispersed across the North Pacific bridge.

The geological data, when related to the present-day distribution patterns, indicate the following about army ant origins and dispersal: (1) the genus *Aenictus* arose in tropical Laurasia, possibly in the early Tertiary, and dispersed into Africa sometime between the late Oligocene and late Pliocene; because *Aenictus* was tropically adapted, dispersal to North America across the North Pacific bridge was not possible. (2) *Dorylus* evolved on the African continent during the early Tertiary, but did not disperse to Asia until late in the Tertiary, before the land connection narrowed and became arid. The lack of diversity in this genus in Asia alternatively suggests that dispersal may have occurred later, during Quaternary time (of course, competitive exclusion may account for the low number of *Dorylus* species in Asia, since *Aenictus* and perhaps other army ant-like species were already well established when *Dorylus* arrived). The climate of Africa during Quaternary time has undergone repeated change which at times no doubt created conditions favorable to dispersal. For example, during the early Holocene there was an expansion of evergreen forests in tropical Africa (Livingstone 1975), although probably not into the Saharan region (Moreau 1952). Indeed, Brown (1973) regarded *Dorylus* as being in an early stage of dispersal, and Emery (1920) held that *Dorylus* arose in Africa and diversified over a long period of time. The Old World army ants are thus diphyletic, although the Aenictini and Dorylini may have arisen from different groups within the Cerapachyini. (3) The Ecitonini and Cheliomyrmecini arose from a common ancestor, possibly a New World Cerapachyine, in tropical South America, the Ecitonini underwent tremendous diversification during a long period of geographic isolation, and neither tribe dispersed into North America until the end of the Tertiary. One genus, *Neivamyrmex*, has successfully dispersed into temperate environments.

While alternative explanations for army ant origins based on their geographic distribution no doubt could be conceived, the triphyletic interpretation is offered here as a working hypothesis to be refuted or supported as new morphological, behavioral, and hopefully fossil evidence accumulates.

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