

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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