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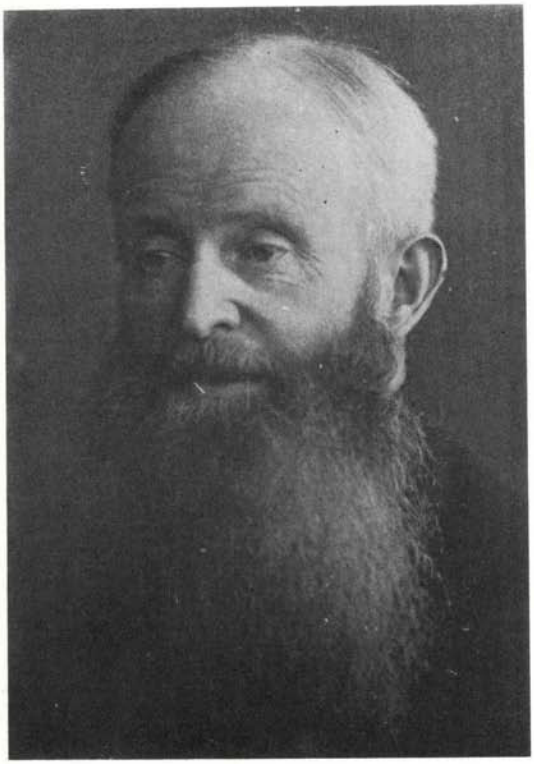

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REFLECTIONS ON THE EVOLUTION OF ARMY ANTS (Hymenoptera, Formicidae)

by

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Résumé: Réflexions sur l'évolution des fourmis voyageuses.

D'après Wilson (1958), il y aurait parmi les fourmis une évolution à degrés vers un syndrome adaptif des fourmis voyageuses. Ce plan évolutif peut être complété par d'autres aspects du comportement, et par le caractère apomorphe ou plésiomorphe de ces facteurs chez les différentes espèces. De cette manière, la position relative d'espèces dans un continuum évolutif hypothétique peut être analysée. La plupart des fourmis voyageuses peuvent être cetégorisées dans les groupes suivants, présentés dans un ordre progressif de leur évolution: (1) les espèces entierement hypogéiques; (2) les espèces quasi-hypogéiques; (3) les espèces quasi-épigéiques; et (4) les especes complètement épigéiques.

Mots-clés: *fourmis voyageuses, Ecitoninae, Dorylinae, écosystèmes tropicaux, comportement, évolution.*

Summary: Wilson (1958) hypothesized a series of steps through which ants evolve toward the army ant adaptive syndrome.

This scenario can be elaborated upon by including other behavioral characters and by determining whether the behavioral character states represented in the various species are plesiomorphic or apomorphic. This was done not to construct a series of genealogies but rather to analyze the relative position of species in any hypothesized evolutionary continuum. In this way species can be identified as relatively ancestral or derived. Most army ants can be categorized into the following groups. These groups are arranged from the least derived to the most highly derived: (1) truly hypogaeic species; (2) quasi-hypogaeic species; (3) quasi-epigaeic species; and (4) truly epigaeic species.

Key-words: *army ants, Ecitoninae, Dorylinae, tropical ecosystems, behavior, evolution.*

The true army ants, once regarded as monophyletic, are now placed in two subfamilies, the New World Ecitoninae, composed of the genera *Cheliomyrmex, Eciton, Labidus, Neivamyrmex,* and *Nomamyrmex,* and the Old World Dorylinae, with its two genera *Aenictus* and *Dorylus* (Snelling, 1981). The genus *Dorylus* is further divided into the six subgenera *Alaopone, Anomma, Dichthadia, Dorylus, Rhogmus,* and *Typhlopone.* These true army ants are therefore distinguished taxonomically from other ant-like species that do indeed exist but which clearly belong to other subfamilies (e.g., some ponerine species of the genus *Leptogenys).* Army ants are ubiquitous denizens of the world's tropics and

subtropics and are represented by at least 147 species in the New World (Watkins, 1976) and more than 100 species in the Old World (Gotwald, 1982).

Each army ant colony includes a single reproductive female or queen, numerous workers, and, on occasion, males. Army ant queens are dichthadiigynes, i.e., they possess a greatly enlarged gaster and waist, are blind or nearly so, are permanently wingless, and have well-developed legs (Wilson, 1971). The workers of all army ants, except *Aenictus* and some species of *Neivamyrmex*, are strongly polymorphic. Workers are blind or possess reduced compound eyes. Army ant males have an exceptional morphology. They have a large cylindrical gaster, modified mandibles, and uncommonly developed genitalia. They are winged and possess well-developed compound eyes and ocelli (Gotwald, 1982). Males appear occasionally in colonies as a part of sexual broods and function essentially as "flying sperm dispensers" (Wilson, 1971).

The impact of these ants on tropical ecosystems, vis-à-vis their effect on prey populations, can only be conjectured but must be considerable. Certainly prey biomass taken by individual colonies on a daily basis must be impressively large and the number of army ant colonies per given unit of area substantial. Leroux (1977) calculated that there were 3.16 colonies of the surface-active (epigaeic) army ant *Dorylus (Anomma) nigricans* per 10 hectares of forest and 0.79 colonies per 10 hectares of savanna in the Guinea Savanna of Ivory Coast,

and Franks (1982) estimated there to be 3.5 colonies of *Eciton burchelli* (also an epigaeic species) per square kilometer on Barro Colorado Island, Panama. These figures are, of course, deceptively low, since they do not include the more numerous colonies of the many cryptic, subterranean (hypogaeic) species.

The true army ants are also of special interest because they have coevolved with a menagerie of myrmecophilous colony guests and "camp followers" whose ecological and behavioral interactions are likely to be as complex as any yet investigated (Gotwald, 1982). Consider the fact that some New World species are followed by birds that feed on the arthropods flushed by the foraging ants (Willis, 1966, 1967) and by ithomiine butterflies that feed on the nitrogenous wastes and/or feces of these birds (Ray and Andrews, 1980).

Two features characterize army ants behaviorly: (1) they are group predators, meaning that they group raid and retrieve prey; and (2) they are nomadic, i.e., they periodically move from one nesting site to another, thus changing their trophophoric fields. It is the inextricable combination of these two behaviors that distinguish army ants, including such ponerines as *Leptogenys purpurea* and *Megaponera foetens*, from other ants (Gotwald, 1982).

Two foraging patterns (with graduations between the two) exist among the army ants: column raiding and swarm raiding (Schneirla, 1971). These patterns are species specific. A column raid consists of single base column of workers leading from the nest to the foraging area where the base column subdivides into numerous branches. Each of these branches terminates in small

groups of foraging workers. In a swarm raid, however, the base column divides into a series of anastomosing branches that fuse to form a single, advancing mass or swarm of workers. The trails formed by the raiding workers are both physical and chemical entities. Army ants can be either trophic specialists or generalists, but in each case, the workers carry the prey in their mandibles, slung beneath their bodies (Gotwald, 1982).

Theoretically, all army ants live in temporary nests and emigrate at least on occasion. Schneirla (1971) categorized army ants as belonging to either group A or group B depending on the regularity with which the various species moved. In group A he placed those species that exhibit a well defined cycle of alternating nomadic and statary phases (termed phasic here) that are conditioned by brood stimulative factors. In group B he placed species that conducted emigrations as single events separated by intervals of nonnomadic behavior of varying length (nonphasic).

The army ant adaptive syndrome is clearly successful in tropical ecosystems. Army ants are conspicuous elements of the ant fauna of most tropical forests and savannas; army ant behavior has arisen convergently as many as seven times (Wilson, 1958); and army ant behavior permits these ants to forage more efficiently and to expand their diet to include large arthropods and other social insects (i.e., dietary items normally not available to solitary foragers).

Because army ants are absent from the fossil record, their origins can only be inferred indirectly be examining their

geographic distribution patterns relative to past geologic events, especially continental drift. In such a study, Gotwald (1979) concluded that, if the true army ants arose in tropical habitats not earlier than the late Cretaceous or early Tertiary and if the apterous condition of the queens appeared early in the acquisition of army ant traits, the army ants as traditionally constituted (i.e., as a single subfamily) are triphyletic. He conjectured that the evidence suggests that these ants arose convergently on three separate occasions in three separate locations; *Aenictus* in Laurasia, *Dorylus* in Africa, and the Ecitoninae in South America.

Wilson (1958) hypothesized a series of steps through which ants evolve toward the army ant adaptive syndrome: (1) group predation initially permits specialized feeding on social insects; (2) the concurrent evolution of nomadism permits colonies to shift trophophoric fields; (3) diet may be expanded to include a variety of arthropods, giving rise to general predation; and (4) large colony size becomes a possibility. This scenario suggests that the essential behavioral characteristics that typify army ants can be polarized, i.e., the behavioral character states represented in the various species can be identified as ancestral (plesiomorphic) or derived (apomorphic). This was done for the present paper, not to construct a series of geneologies (based on shared apomorphies) but rather to assemble various combinations of character states that might be found in nature. Each constellation of character states can be placed on a continuum beginning with least derived and ending with most derived. Species in nature can

then be placed on this continuum by matching their behavioral characteristics to an appropriate hypothetical array of character states. To do so, however, does not imply evolutionary relationship, but rather demonstrates the degree to which any one species may be derived from an ancestral condition. In polarizing these characteristics, outgroup comparisons were made with the Cerapachyini, because it is possible that *Eciton* and *Aenictus* arose separately from cerapachyine ancestors (Brown, 1975).

Most army ants can be categorized into the following groups. These groups are arranged from the least derived to the most highly derived. It must be noted that some species fall outside the groups, because of slightly different arrays of character states.

1. Truly hypogaeic species: These nest, forage, and emigrate hypogaeically; they are column raiders, reproductively nonphasic, specialized predators of social insects, generally form small colonies, and have monomorphic workers. Examples: Some species of *Aenictus*.

2. Quasi-hypogaeic species: These are similar to the truly hypogaeic species except that they may occasionally forage and emigrate epigaeically. Example: *Aenictus asantei*.

3. Quasi-epigaeic species: These nest hypogaeically but forage and emigrate epigaeically; they are swarm raiders, reproductively nonphasic, general predators, form large colonies, and have polymorphic workers (with

a size-correlated division of labor). Example: *Dorylus (Anomma) nigricans*.

4. Truly epigaeic species: These nest, forage, and emigrate epigaeically; they are swarm raiders, reproductively phasic, oligophagic or are general predators, form large colonies, and have polymorphic workers. Example: *Eciton burchelli*.

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